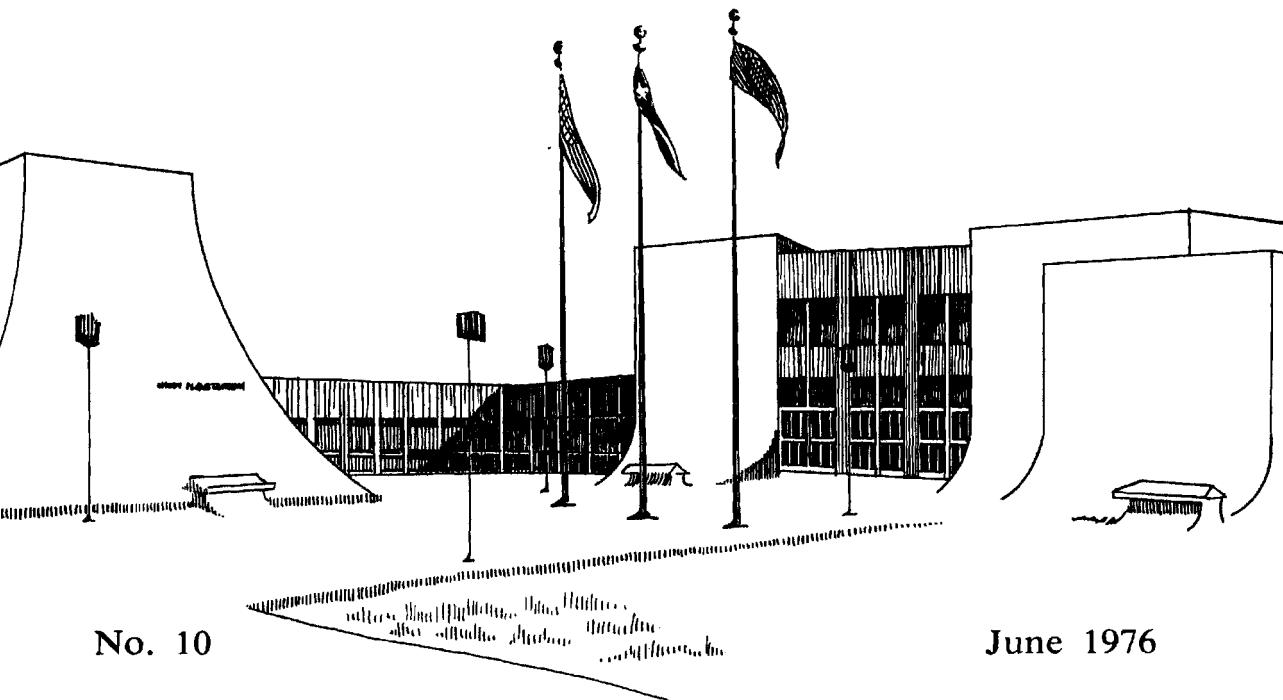
SPECIAL PUBLICATIONS
THE MUSEUM
TEXAS TECH UNIVERSITY

Biology of Bats of the New World Family Phyllostomatidae. Part I

Edited by
Robert J. Baker, J. Knox Jones, Jr., and Dilford C. Carter



No. 10

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INTRODUCTION

Because of their adaptive diversity and, in many instances, unique morphological attributes, bats of the family Phyllostomatidae have long fascinated biologists. Known only from the New World, most genera of phyllostomatids are strictly limited to tropical environs, 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 in the Bahamas and on the islands of the Greater and Lesser Antilles. With the advent in relatively recent years of improved methods of collecting bats (see Tuttle, this volume), a tremendous wealth of information on phyllostomatids has been gathered and it is the purpose of this publication, which ultimately will contain more than 20 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 further 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 parts. Each part will be a separately numbered 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, the annotated checklist by Jones and Carter 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 the next without the handicap of conflicting names for the same organism.

Manuscripts for most contributions first were solicited in 1973. Most manuscripts had been received by the end of 1974. As editorial work progressed, some authors provided up-dated information and all authors of chapters in Part 1 had the opportunity to insert limited materials at the time they received galley proofs (in most cases October 1975). Therefore, content is as current as reasonably could be anticipated for a project of this kind. Organization and editorial style follows 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 will 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 this collected series are carried in text as "this volume," which does not necessarily indicate that the chapter appears in the same part of the series as the one in which it is cited.

November 1975

Robert J. Baker
J. Knox Jones, Jr.
Dilford C. Carter

ANNOTATED CHECKLIST, WITH KEYS TO SUBFAMILIES AND GENERA

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

Leaf-nosed bats of the New World family Phyllostomatidae are primarily limited in distribution to tropical and subtropical regions. A few species reach subtemperate areas. The family has a known fossil record dating back to Miocene times. Most phyllostomatids are fruit eaters or nectar feeders, but some, primarily species in the subfamily Phyllostomatinae, are carnivorous or insectivorous, and the unique desmodontines are sanguivorous.

The family is unusually diverse from an evolutionary point of view, comprising six subfamilies, 49 currently recognized Recent genera, and 137 Recent nominal species. Twenty-four genera are monotypic. The subfamilies contain the following numbers of genera and species as here recognized: Phyllostomatinae, 11 and 32; Glossophaginae, 13 and 32; Carolliinae, two and seven; Stenoderminae, 17 and 54; Phyllonycterinae, three and seven; and Desmodontinae, three and three.

Systematic inquiry in the past decade has tended to reduce the number of recognized genera and species, but the discovery of new taxa continues. Some species are rare in museum collections and their relationships poorly understood. Various new techniques applied in recent years to the study of phyllogenetic relationships have resulted in recognition of new taxonomic alignments—for example, inclusion of the vampire bats as a subfamily of the Phyllostomatidae (Forman *et al.*, 1968) and exclusion of the Mormoopidae (Smith, 1972), formerly regarded as a subfamily of this group.

As standard references for a point of departure in compilation of this annotated list, we used Hall and Kelson (1959) for North America and Cabrera (1958) for South America. A variety of publications has appeared subsequent to these two basic documents in which the distribution and systematics of phyllostomatids are treated. Of these, revisions and reviews are cited at the appropriate places in the accounts. Faunal reports of special interest are noted below. Recourse to the literature we have cited will lead the interested researcher to most of the published sources used in compiling this synopsis.

Villa-R. (1967) summarized material on Chiroptera of México. Publications since that time on Chihuahua (Anderson, 1972), Jalisco (Watkins *et al.*, 1972), Oaxaca (Goodwin, 1969), Sinaloa (Jones *et al.*, 1972), the Yucatán Peninsula (Jones *et al.*, 1973), and Zacatecas (Genoways and Jones, 1968; Matson and Patten, 1975) treat major faunal units as a whole. For Central America, the papers of Jones (1966) on Guatemala, Burt and Stirton (1961) on El Salvador, Jones *et al.* (1971*b*) and Baker and Jones (1975) on Nicaragua, Starrett and Casebeer (1968) and Gardner *et al.* (1970) on Costa Rica, and Handley (1966) on Panamá are useful, as well as those by Davis *et al.* (1964) and Carter *et al.* (1966)

on the region as a whole. Choate and Birney (1968), Koopman (1968) and Jones and Phillips (1970) are useful recent references to bats in the Antillean region.

Relatively few major contributions have been published on South America since Cabrera's (*op. cit.*) compendium, those on Trinidad and Tobago (Goodwin and Greenhall, 1961), Surinam (Husson, 1962), Perú (Tuttle, 1970), Colombia (Aellen, 1970; Marinkelle and Cadena, 1972), and Uruguay (Ximenez *et al.*, 1972) being especially noteworthy. Studies of a more limited scope, such as Hill's (1964) report of a small collection from Guyana, Brosset's (1965) and Baker's (1974) papers on Ecuador, and the publication by Villa-R. and Cornejo (1969) on northern Argentina also have proved useful (see also the appendix of the contribution on zoogeography by K. F. Koopman in this volume). It is of interest that few reports on the Brazilian fauna have appeared since Cabrera's work, papers by Handley (1967) on the Belem area and by Pine *et al.* (1970) on a collection from Mato Grosso, and Peracchi and de Albuquerque (1971) on the states of Rio de Janeiro and Guanabara being notable exceptions. [See also Gardner's (1976) recent paper on Perú.]

In a recent paper on the mammalian fauna of the Antilles, Varona (1974) incorporated a number of systematic changes with respect to bats found in that region. For example, he regarded all species of *Ardops*, *Ariteus*, and *Phyllops* as assignable to the subgenus *Ariteus* of the genus *Stenoderma*, and placed *Monophyllus* as a subgenus of *Glossophaga*. Because Varona presented no evidence supportive of these and other changes, we have not followed his arrangement here.

We are indebted to a number of colleagues, principally Robert J. Baker, Alfred L. Gardner, Hugh H. Genoways, Clyde Jones, Karl F. Koopman, and Don E. Wilson, for scrutinizing an early draft of this manuscript.

Subfamily Phyllostomatinae

Genus Micronycteris Gray

Micronycteris megalotis (Gray, 1842)

Distribution.—Western (Jalisco) and eastern (Tamaulipas) México southeastward through Middle America and much of northern and central South America to Amazonian Perú and São Paulo, Brazil; also recorded from Grenada in the Lesser Antilles.

Systematics.—Four subspecies currently are recognized: *megalotis* (most of South American segment of species distribution); *homezi* (northwestern Venezuela); *mexicana* (México south to western Nicaragua and adjacent Costa Rica); *microtis* (eastern Nicaragua southeastward to Panamá and adjacent parts of northwestern South America).

Micronycteris schmidtorum Sanborn, 1935

Distribution.—Yucatán Peninsula of México southeastward to northwestern South America.

Systematics.—*M. schmidtorum* is a monotypic species.

Micronycteris minuta (Gervais, 1855)

Distribution.—Nicaragua southeastward to South America (including Trinidad) at least to Brazil and eastern Perú.

Systematics.—*M. minuta* is currently regarded as a monotypic species. Together with *megalotis* and *schmidtorum* this species represents the subgenus *Micronycteris.*

Micronycteris hirsuta (Peters, 1869)

Distribution.—Honduras southeastward to northern South America (Colombia, Venezuela, Guyana, Trinidad, and Perú).

Systematics.—*M. hirsuta* is a monotypic species and the sole representative of the subgenus *Xenoctenes.*

Micronycteris brachyotis (Dobson, 1878)

Distribution.—Oaxaca southeastward through Central America to Amazonian Brazil.

Systematics.—*M. brachyotis* is a monotypic species and represents the subgenus *Lampronycteris.* The specific name *platyceps,* widely used for this bat for several decades, is a synonym of *brachyotis.*

Micronycteris pusilla Sanborn, 1949

Distribution.—Northern Brazil, eastern Colombia, probably adjacent regions of South America.

Systematics.—*M. pusilla* is a monotypic species and represents the subgenus *Neonycteris.*

Micronycteris nicefori Sanborn, 1949

Distribution.—Nicaragua to northern South America (including Trinidad and south at least to northern Brazil and northern Amazonian Perú).

Systematics.—*M. nicefori* is a monotypic species and the only representative of the subgenus *Trinycteris.*

Micronycteris sylvestris (Thomas, 1869)

Distribution.—Western (Nayarit) and eastern (Veracruz) México southeastward through Central America to Panamá and into northern South America at least as far east as Trinidad, northeastern Brazil, and eastern Perú.

Systematics.—*M. sylvestris* is thought to be a monotypic species.

Micronycteris behni (Peters, 1865)

Distribution.—Known only from central Brazil and Perú.

Systematics.—This nominal species is poorly known. Along with *M. sylvestris,* with which it evidently is closely related, *behni* constitutes the subgenus *Glyphonycteris.*

Micronycteris daviesi (Hill, 1964)

Distribution.—Reported only from Guyana and Amazonian Perú.

Systematics.—*M. daviesi* is a monotypic species and represents the subgenus *Barticonycteris*, which some authors have regarded as a valid genus.

Genus MACROTUS Gray

Macrotus waterhousii Gray, 1843

Distribution.—Western (north to Sonora) and central México southward to the Yucatán Peninsula and Guatemala; also on islands of Greater Antilles and Bahamas.

Systematics.—According to Anderson and Nelson (1965) and Davis and Baker (1974), six subspecies are recognizable: *waterhousii* (Hispaniola and southern Bahamas); *bulleri* (western and central México); *compressus* (islands of Grand Bahaman Bank and Watling Island); *jamaicensis* (Jamaica); *mexicanus* (southern México and adjacent Guatemala); *minor* (Cuba and Grand Cayman).

Macrotus californicus Baird, 1858

Distribution.—Southern California, southern Nevada, and Arizona southward to northwestern México (Baja California, Sonora, and northern Sinaloa).

Systematics.—*M. californicus* is a monotypic species. It was regarded by Anderson and Nelson (1965) as a subspecies of *M. waterhousii*, but Davis and Baker (1974) recently have presented morphometric and karyotypic evidence demonstrating the specific distinctness of this bat.

Genus LONCHORHINA Tomes

Lonchorhina aurita Tomes, 1863

Distribution.—Southern México (Oaxaca, Tabasco, and Quintana Roo) southeastward through Middle America to South America, where species occurs southward to Brazil, Bolivia, and Perú; also known from Trinidad and questionably reported (G. M. Allen, 1911) from New Providence in the Bahamas.

Systematics.—Considerable geographic variation is evident (Tuttle, 1970) among specimens referred to *L. aurita* from western South America, but this variation presently is poorly understood. *L. occidentalis* Anthony, described from western Ecuador, has been treated by most recent authors as a subspecies of *aurita*, in which no other geographic races currently are recognized. *Lonchorhina* is deserving of systematic review.

Lonchorhina orinocensis Linares and Ojasti, 1971

Distribution.—Presently known only from the type locality on the Río Orinoco in Estado Bolívar, Venezuela.

Systematics.—*L. orinocensis* is a monotypic species.

Genus MACROPHYLLUM Gray

Macrophyllum macrophyllum (Schinz, 1821)

Distribution.—Tabasco, México, southeastward to northern and central South America (to Minas Gerais, Brazil, and northern Argentina).

Systematics.—*M. macrophyllum* is a monotypic species.

Genus TONATIA Gray

Tonatia bidens (Spix, 1823)

Distribution.—Guatemala southeastward through Central America and into northern South America (Colombia, Venezuela, Trinidad, eastern Brazil, Amazonian Perú); also known as a fossil from Jamaica.

Systematics.—Two subspecies are recognized, *bidens* in Central and South America and *saurophila*, known only as a fossil from Jamaica.

Tonatia brasiliense (Peters, 1866)

Distribution.—Known from central and eastern Brazil and adjacent Perú.

Systematics.—The relationships of this monotypic species are poorly understood.

Tonatia carrikeri (J. A. Allen, 1910)

Distribution.—Known only from Venezuela, Surinam, Bolivia, and Perú.

Systematics.—*T. carrikeri* is a monotypic species.

Tonatia nicaraguae Goodwin, 1942

Distribution.—Southern México (Veracruz) southeastward through Central America and South America, south to Amazonian Perú and east to Trinidad.

Systematics.—*T. nicaraguae* is a monotypic species, *minuta* being a synonym.

Tonatia sylvicola (D'Orbigny, 1835)

Distribution.—Southern México (Veracruz) southeastward through Central America to South America, east to the Guianas and lower Amazon Basin and south to Bolivia and northern Argentina.

Systematics.—Two subspecies are recognized, *sylvicola* (México to western South America) and *laephotis* (Guianas and northeastern Brazil).

Tonatia venezuelae (Robinson and Lyon, 1901)

Distribution.—Known only from Venezuela.

Systematics.—The relationships of this monotypic species are not well understood.

Genus MIMON Gray

Mimon bennettii (Gray, 1838)

Distribution.—Known only from eastern South America (Guyana and Surinam south to the Brazilian state of São Paulo).

Systematics.—As presently understood, this species is monotypic. Several authors, however, have noted the resemblance between *M. bennettii* and *M. cozumelae* and some have treated *cozumelae* as a subspecies of the former.

Mimon cozumelae Goldman, 1914

Distribution.—Southern México (Oaxaca, Veracruz, Yucatán Peninsula) southeastward to northern Colombia.

Systematics.—The close relationship between *M. cozumelae* and *M. bennettii* has been noted above. These two species comprise the subgenus *Mimon.*

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

Distribution.—Middle America north at least to southern Yucatán Peninsula; widely distributed in tropical South America south at least to Amazonian Perú, Bolivia, and Brazil.

Systematics.—Four subspecies currently are recognized (Handley, 1960): *crenulatum* (Trinidad, eastern Venezuela, the Guianas, and northeastern Brazil); *keenani* (eastern Ecuador northwestward to southern México); *longifolium* (Amazonian Ecuador and Perú, Bolivia, Mato Grosso in Brazil, Colombia, and Venezuela); *picatum* (known only from Lamarão, Bahia, Brazil).

Mimon koepckeae Gardner and Patton, 1972

Distribution.—Known only from the vicinity of the type locality at Huanhuachayo, Ayacucho, Perú.

Systematics.—*M. koepckeae* is a monotypic species. Together with *M. crenulatum* it represents the subgenus *Anthorhina* (Gardner and Patton, 1972), although Handley (1960) regarded *Anthorhina* as indistinguishable at the subgeneric level from *Mimon*, and Husson (1962) retained full generic rank for it.

Genus PHYLLOSTOMUS Lacépède

Phyllostomus discolor (Wagner, 1843)

Distribution.—Southern México (Oaxaca and Veracruz) south to northern Argentina.

Systematics.—Two subspecies generally have been recognized, *discolor* (Margarita, Trinidad, and mainland South America, east of the Andes, from Venezuela south to extreme northern Argentina, but not recorded from Paraguay and Uruguay) and *verrucosus* (southern México southeast to Colombia and Ecuador west of the Andes). Recently, however, Power and Tamsitt (1973) suggested this species probably is monotypic.

Phyllostomus hastatus (Pallas, 1767)

Distribution.—Honduras south to Bolivia and southeastern Brazil.

Systematics.—Two subspecies are recognized, *hastatus* (Trinidad, Tobago, and South America east of Lake Maracaibo and south of Cordillera de Mérida to Bolivia and southeastern Brazil, *curaca* a synonym) and *panamensis* (Honduras south to Colombia west of Lake Maracaibo and the Andes).

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

Distribution.—East of Andes from Colombia, Venezuela, Guyana, and Surinam south to eastern Perú, Bolivia, and southeastern Brazil.

Systematics.—*P. elongatus* is a monotypic species.

Phyllostomus latifolius Thomas, 1901

Distribution.—Reported only from southeastern Colombia and the type locality, Kanuka Mountains, Guyana.

Systematics.—*P. latifolius* is a monotypic species closely related to *P. elongatus*, with which some think it may prove conspecific when more specimens are available. At present, however, Guyanan specimens of the two species are readily separable.

Genus PHYLLODERMA Peters

Phylloderma stenops Peters, 1865

Distribution.—Known from Chiapas, Honduras, and Panamá in North America, and in northern South America south to northeastern Brazil and Perú.

Systematics.—Following Handley (1966), two subspecies are recognized—*stenops* (Panamá to Brazil) and *septentrionalis* (Chiapas and Honduras).

Genus TRACHOPS Gray

Trachops cirrhosus (Spix, 1823)

Distribution.—Southern México (Oaxaca, Veracruz, Yucatán Peninsula), through Central America, to South America, where species is widely distributed as far south as southern Brazil and Bolivia.

Systematics.—Three nominal subspecies are: *cirrhosus* (Costa Rica southward through most of South American range of species); *coffini* (México to Nicaragua); *ehrhardti* (southern Brazil and Bolivia).

Genus CHROTOPTERUS Peters

Chrotopterus auritus (Peters, 1856)

Distribution.—Southern México (Oaxaca, Veracruz, Yucatán Peninsula) southeastward to southern Brazil, Paraguay, and northern Argentina.

Systematics.—Three nominal subspecies are: *auritus* (México southeastward to Panamá and adjacent parts of northern South America); *australis* (southern

part of range of species in southern Brazil, Paraguay, and northern Argentina); *guianae* (Venezuela, the Guianas, and northern Brazil). Handley (1966) doubted that geographic races should be recognized in this species.

Genus VAMPYRUM Rafinesque

Vampyrum spectrum (Linnaeus, 1758)

Distribution.—Southern México (southern Veracruz) southeastward through Central America to South America, where species is widespread in Colombia, Venezuela, Trinidad, the Guianas, Ecuador, Perú, and northern and central Brazil; also reported from Jamaica.

Systematics.—According to Husson (1962) and Handley (1966), *V. spectrum* is a monotypic species. Some recent authors, however, have continued to recognize the subspecies *nelsoni* as occurring from Colombia northwestward to México.

SUBFAMILY GLOSSOPHAGINAE

Genus GLOSSOPHAGA É. Geoffroy St.-Hilaire

Glossophaga soricina (Pallas, 1766)

Distribution.—One of the most widely distributed phyllostomatids, occurring from northern México (Sonora in the west and Tamaulipas in the east) southeastward into South America to Paraguay and northern Argentina; also reported from Jamaica and the Bahamas.

Systematics.—Four subspecies probably are valid: *soricina* (most of South American range including Trinidad); *antillarum* (Jamaica and questionably the Bahamas); *leachii* (México and Middle America, *mutica* a synonym); *valens* (western Ecuador and Perú).

Glossophaga alticola Davis, 1944

Distribution.—Central México (Guerrero, Morelos, Tlaxcala) southward to Costa Rica.

Systematics.—As presently known, *G. alticola* is a monotypic species.

Glossophaga commissarisi Gardner, 1962

Distribution.—Western México (Sinaloa) southeastward to Panamá and undoubtedly adjacent South America.

Systematics.—*G. commissarisi* is a monotypic species as presently understood.

Glossophaga longirostris Miller, 1898

Distribution.—Northern South America and adjacent Caribbean islands.

Systematics.—Four nominal subspecies are recognized: *longirostris* (Colombia and Venezuela); *elongata* (islands of Aruba, Bonaire, and Curaçao); *major* (Trinidad and Tobago); *rostrata* (Lesser Antillean islands from Grenada north to Dominica).

Genus MONOPHYLLUS Leach

Monophyllus redmani Leach, 1821

Distribution.—Greater Antilles and southern Bahamas.

Systematics.—Three subspecies (Schwartz and Jones, 1967) are as follows: *redmani* (Jamaica); *clinedaphus* (Cuba, Hispaniola, and southern Bahamas); *portoricensis* (Puerto Rico).

Monophyllus plethodon Miller, 1900

Distribution.—Lesser Antilles from Anguilla to Barbados; subfossils known from Puerto Rico.

Systematics.—Three subspecies (Schwartz and Jones, 1967) are recognized: *plethodon* (Barbados); *frater* (subfossil, Puerto Rico); *luciae* (Lesser Antilles from Anguilla south to St. Vincent).

Genus LEPTONYCTERIS Lydekker

Leptonycteris nivalis (Saussure, 1860)

Distribution.—Southern Texas southward through much of México to Guatemala.

Systematics.—*L. nivalis* generally is regarded as a monotypic species.

Leptonycteris sanborni Hoffmeister, 1957

Distribution.—Southern Arizona and New Mexico southward through México at least to El Salvador. Prior to a review of *Leptonycteris* by Davis and Carter (1962), and in some subsequent publications, specimens of *sanborni* were reported as *nivalis*, making the precise distribution of the two species difficult to delimit. Nevertheless, the two seem to be broadly sympatric through much of México.

Systematics.—*L. sanborni* is a monotypic species. Some recent authors have used the specific name *yerbabuenae* for this bat (see Watkins *et al.*, 1972:16).

Leptonycteris curasoae Miller, 1900

Distribution.—Dutch Caribbean islands of Aruba, Bonaire, and Curaçao, and adjacent South American mainland in Colombia and Venezuela.

Systematics.—We follow Davis and Carter (1962) in regarding *curasoae* as a species distinct from *nivalis*. It may be monotypic, although the subspecific name *tarlosti* (based on specimens from Margarita Island, Venezuela) may apply to mainland populations and those on adjacent offshore islands.

Genus LONCHOPHYLLA Thomas

Lonchophylla hesperia G. M. Allen, 1908

Distribution.—Known only from Perú.

Systematics.—*L. hesperia* is a monotypic species.

Lonchophylla mordax Thomas, 1903

Distribution.—Reported from Ecuador, Bolivia, and Brazil.

Systematics.—*L. mordax* is considered here to be a monotypic species but may include *concava* as a northern subspecies.

Lonchophylla concava Goldman, 1914

Distribution.—Reported from Costa Rica, Panamá, Colombia, and Perú.

Systematics.—*L. concava* is recognized provisionally as a monotypic species distinct from *mordax*, with which it may be conspecific. Handley (1966) considered *concava* to be a northern subspecies of *mordax*, but recent authors have not followed that arrangement.

Lonchophylla robusta Miller, 1912

Distribution.—Reported from Nicaragua, Costa Rica, Panamá, Colombia, Venezuela, and Perú.

Systematics.—*L. robusta* is a monotypic species.

Lonchophylla thomasi J. A. Allen, 1904

Distribution.—Known from Panamá, Venezuela, Guyana, Surinam, Brazil, Perú, and Bolivia.

Systematics.—*L. thomasi* is a monotypic species.

Genus LIONYCTERIS Thomas

Lionycteris spurrelli Thomas, 1913

Distribution.—Eastern Panamá and northern South America (recorded from Guyana, northern Brazil, Venezuela, Colombia, and Amazonian Perú).

Systematics.—*L. spurrelli* is a monotypic species.

Genus ANOURA Gray

Anoura geoffroyi Gray, 1838

Distribution.—Western (Sinaloa) and eastern (San Luis Potosí) México south to southeastern Brazil and northwestern Argentina.

Systematics.—Three nominal subspecies are: *geoffroyi* (Venezuela, Surinam, Trinidad, Brazil, Argentina, and Bolivia); *lasiopyga* (México south to northern Colombia); and *peruana* (Colombian Andes south to Perú).

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

Distribution.—Northern South America south to Perú and Brazil.

Systematics.—Two subspecies currently are recognized: *caudifer* (Colombia east through Venezuela and the Guianas and south in eastern Brazil to São Paulo); *aequatoris* (Ecuador and Perú).

Anoura cultrata Handley, 1960

Distribution.—Known from Costa Rica, Panamá, and Venezuela.
Systematics.—*A. cultrata* is a monotypic species.

Anoura werckleae Starrett, 1969

Distribution.—Known only from Costa Rica.
Systematics.—*A. werckleae* is a monotypic species closely related to *A. cultrata.*

Anoura brevirostrum Carter, 1968

Distribution.—Recorded from Colombia (Santander) and eastern Perú.
Systematics.—As presently known, *A. brevirostrum* is a monotypic species.

Genus SCLERONYCTERIS Thomas

Scleronycteris ega Thomas, 1895

Distribution.—This rare species is known only from Brazil and Venezuela.
Systematics.—*S. ega* is a monotypic species.

Genus LICHONYCTERIS Thomas

Lichonycteris degener Miller, 1931

Distribution.—Known only from lower Amazon region of Brazil.
Systematics.—*L. degener* is a monotypic species.

Lichonycteris obscura Thomas, 1895

Distribution.—Guatemala southeastward to South America at least as far as Surinam and east-central Perú.
Systematics.—*L. obscura* is a monotypic species.

Genus HYLONYCTERIS Thomas

Hylonycteris underwoodi Thomas, 1903

Distribution.—Western México (north to Jalisco) southeastward to western Panamá.
Systematics.—Two subspecies (Phillips and Jones, 1971), *underwoodi* (Veracruz and northern Oaxaca southeastward to Panamá) and *minor* (western México), are recognized.

Genus PLATALINA Thomas

Platalina genovensium Thomas, 1928

Distribution.—This rare bat is known only from Perú, principally west of the Andes.
Systematics.—*P. genovensium* is a monotypic species.

Genus CHOERONISCUS Thomas

Choeroniscus godmani (Thomas, 1903)

Distribution.—Western México (Sinaloa) southeastward to Colombia and Venezuela.

Systematics.—*C. godmani* is a monotypic species.

Choeroniscus minor (Peters, 1868)

Distribution.—Recorded from Brazil, Colombia, Ecuador, Perú, and Surinam.

Systematics.—*C. minor* is a monotypic species closely related to *C. inca* and *C. intermedius.*

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

Distribution.—Thought to be restricted to Trinidad, but reported also from Perú by Tuttle (1970).

Systematics.—*C. intermedius* is a monotypic species closely related to *C. minor* and *C. inca.*

Choeroniscus inca (Thomas, 1912)

Distribution.—Recorded from Guyana, Ecuador, Perú, and Venezuela.

Systematics.—*C. inca* is a monotypic species closely related to the two preceding taxa. Specimens of the genus *Choeroniscus* are rare in museum collections. Only about two dozen individuals of the *minor-intermedius-inca* complex have been reported in the literature, and the characteristics of the three species never have been defined in a comparative sense. Clearly, this group is in need of systematic review. It may well be that *minor, intermedius,* and *inca* represent a single species.

Choeroniscus periosus Handley, 1966

Distribution.—Known only from Pacific Coast of Colombia.

Systematics.—*C. periosus* is a distinctive, monotypic species.

Genus CHOERONYCTERIS Tschudi

Choeronycteris mexicana Tschudi, 1844

Distribution.—Extreme southern parts of California, Arizona, and New Mexico southward to Honduras.

Systematics.—*C. mexicana* is here regarded as a monotypic species. However, Pirlot (1967) described a subspecies (*ponsi*) from northwestern Venezuela; we are unconvinced by Pirlot's brief description that his two specimens are referable to the genus *Choeronycteris.*

Genus MUSONYCTERIS Schaldach and McLaughlin

Musonycteris harrisoni Schaldach and McLaughlin, 1960

Distribution.—Presently known only from the states of Colima and Guerrero in western México.

Systematics.—*M. harrisoni* is a monotypic species. Although some recent authors have regarded *Musonycteris* as a synonym of *Choeronycteris*, we follow Phillips (1971) in regarding it as a distinct genus.

SUBFAMILY CAROLLIINAE

Genus CAROLLIA Gray

Carollia castanea H. Allen, 1890

Distribution.—Honduras southeastward through Colombia, Ecuador, and Perú to Bolivia.

Systematics.—According to Pine (1972), *C. castanea* is a monotypic species.

Carollia subrufa (Hahn, 1905)

Distribution.—Western México (Jalisco) southeastward, mostly in the Pacific versant of Middle America, to Nicaragua.

Systematics.—*C. subrufa* was regarded by Pine (1972) as a monotypic species.

Carollia brevicauda (Schinz, 1821)

Distribution.—Eastern México (southern San Luis Potosí and adjacent Veracruz) southeastward to northern and western South America (northeastern Brazil, Colombia, Venezuela, Ecuador, Amazonian Perú, and Bolivia).

Systematics.—As in the case of the previous two species of *Carollia*, Pine (1972) considered *C. brevicauda* to be monotypic.

Carollia perspicillata (Linnaeus, 1758)

Distribution.—Veracruz and Oaxaca southeastward to South America, where the species is widely distributed south to Bolivia, Paraguay, and southern Brazil; also reported from Trinidad, Tobago, and the Antillean island of Grenada (recorded occurrences on Jamaica and Redondo Island, in the northern Lesser Antilles, are questionable).

Systematics.—Two subspecies currently are tentatively recognized (Pine, 1972), *perspicillata* in much of the South American range of the species and *azteca* in Middle America and adjacent northwestern South America. Pine (*op. cit.*) also noted that the name *C. p. tricolor* might apply to specimens from the southern part of the range of the species.

Genus RHINOPHYLLA Peters

Rhinophylla pumilio Peters, 1865

Distribution.—Northern South America in Guyana, Surinam, Venezuela, Colombia, Brazil, and eastern Ecuador and Perú.

Systematics.—*R. pumilio* is a monotypic species.

Rhinophylla alethina Handley, 1966

Distribution.—Known only from western Colombia.

Systematics.—*R. alethina* is a monotypic species.

Rhinophylla fischerae Carter, 1966

Distribution.—Known only from Amazonian parts of Perú and Brazil, and adjacent Colombia and Ecuador.

Systematics.—*R. fischerae* is a monotypic species.

SUBFAMILY STENODERMINAE

Genus STURNIRA Gray

The systematics of bats of the genus *Sturnira* are, for the most part, poorly understood. Several new species have been named in the past decade or so. The list presented here is provisional, pending publication of Luis de la Torre's long awaited revision of the genus.

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

Distribution.—Widely distributed from western (Sonora) and eastern (Tamaulipas) México southward through Middle America and throughout most of tropical and subtropical South America to Uruguay, northern Argentina, and possibly Chile; also in southern Lesser Antilles and reported from Jamaica.

Systematics.—The following subspecies are tentatively recognized: *lilium* (most of South America, including Trinidad); *angeli* (Dominica in Lesser Antilles); *luciae* (St. Lucia in Lesser Antilles); *paulsoni* (St. Vincent in Lesser Antilles); *parvidens* (México southeastward to Colombia); *zygomaticus* (Martinique in Lesser Antilles). The taxa *angeli* and *paulsoni*, originally named as species, are here listed as subspecies of *lilium* following Koopman (1968) and Jones and Phillips (1970, 1976).

Sturnira thomasi de la Torre and Schwartz, 1966

Distribution.—Known only from Guadeloupe, Lesser Antilles.

Systematics.—*S. thomasi* is tentatively recognized here as a valid, monotypic species because it differs in several ways from other named Antillean populations of *Sturnira*. It is related to *lilium* and ultimately may prove best regarded as a subspecies of that species.

Sturnira tildae de la Torre, 1959

Distribution.—Originally named from Trinidad, this species now is known to be widely distributed in northern and central South America, south at least to Mato Grosso, Brazil, and Amazonian Perú.

Systematics.—*S. tildae* is a monotypic species.

Sturnira magna de la Torre, 1966

Distribution.—Known only from Amazon drainage in Colombia, Ecuador, and Perú.

Systematics.—*S. magna* is a monotypic species.

Sturnira mordax (Goodwin, 1938)

Distribution.—Recorded only from Costa Rica.

Systematics.—*S. mordax* is a monotypic species described originally as the sole representative of the genus *Sturnirops*, possibly valid as a subgenus (see Davis *et al.*, 1964).

Sturnira bidens (Thomas, 1915)

Distribution.—Known only from near Tambo, Colombia, the type locality at Baeza, Ecuador, and cloud forests of eastern Peruvian Andes.

Systematics.—*S. bidens* is a monotypic species and for many years was placed in the genus *Corvira*. Gardner and O'Neill (1969) reduced *Corvira* to subgeneric status under *Sturnira*.

Sturnira nana Gardner and O'Neill, 1971

Distribution.—Known only from the type locality, Huanhuachayo, Ayacucho, Perú.

Systematics.—*S. nana* is a monotypic species in the subgenus *Corvira* (Gardner and O'Neill, 1971).

Sturnira aratathomasi Peterson and Tamsitt, 1968

Distribution.—Southwestern Colombia and Ecuador west of Andes.

Systematics.—*S. aratathomasi* is a monotypic species.

Sturnira ludovici Anthony, 1924

Distribution.—Western (Sinaloa) and eastern (Tamaulipas) México southeastward through Central America at least to Colombia, Venezuela, Ecuador, and Perú; limits of range poorly understood owing to confusing systematic picture (see below).

Systematics.—Two subspecies presently recognized in the literature are *ludovici* (central México to South America) and *occidentalis* (western México). However, several named kinds of *Sturnira* (including *hondurensis*, *bogotensis*,

and *oporophilum*) related to *ludovici*, but not currently recognized in literature, may, in fact, be valid species or subspecies.

Sturnira erythromos (Tschudi, 1844)

Distribution.—Presently recorded only from eastern slope of Andes in Perú, but probably widely distributed in northern South America.

Systematics.—*S. erythromos* is currently regarded as a monotypic species.

Genus URODERMA Peters

Uroderma bilobatum Peters, 1866

Distribution.—Southern México (Veracruz and Oaxaca), Central America, South America as far south as southern Perú and adjacent Bolivia, and southeastern Brazil.

Systematics.—Currently recognized subspecies (Davis, 1968; Baker and McDaniel, 1972) include: *bilobatum* (eastern Bolivia, Brazil, the Guianas, and Venezuela); *convexum* (Pacific versant of Middle America from Nicaragua southeastward to adjacent South America); *davisi* (Pacific versant of Middle America from Chiapas to El Salvador and probably Honduras); *molaris* (Caribbean versant of Middle America from Veracruz to Costa Rica); *thomasi* (Ecuador, Perú, northwestern Bolivia); *trinitatum* (Trinidad).

Uroderma magnirostrum Davis, 1968

Distribution.—Chiapas southeastward in Pacific versant of Middle America to Panamá, and northern and central South America east of Andes (reported from northern Bolivia, Brazil, Colombia, eastern Perú, eastern Ecuador, and Venezuela).

Systematics.—*A. magnirostrum* is a monotypic species.

Genus VAMPYROPS Peters

Vampyrops infuscus Peters, 1881

Distribution.—Colombia south to Perú and Brazil.

Systematics.—*V. infuscus* is a monotypic species.

Vampyrops vittatus (Peters, 1860)

Distribution.—Known to occur at intermediate elevations (900 to 2600 meters) from Costa Rica south to Perú and east to Venezuela.

Systematics.—*V. vittatus* is a monotypic species.

Vampyrops dorsalis Thomas, 1900

Distribution.—Known from intermediate elevations in Costa Rica, Panamá, Colombia, Ecuador, Perú, and questionably from Venezuela.

Systematics.—This species is in need of systematic review, but probably is polytypic, with disjunct populations occurring above 900 meters from eastern Panamá south to Perú and east into Venezuela. We follow Gardner and Carter (1972) and Carter and Rouk (1973) in our treatment of *V. dorsalis.*

Vampyrops aurarius Handley and Ferris, 1972

Distribution.—Known only from the Guiana Highlands of Venezuela.

Systematics.—*V. aurarius* is recognized provisionally as a valid species, but may prove to be a synonym of *V. dorsalis.*

Vampyrops nigellus Gardner and Carter, 1972

Distribution.—Recorded only from Colombia and Perú, but probably occurs also in Ecuador.

Systematics.—*V. nigellus* is considered to be a monotypic species.

Vampyrops brachycephalus Rouk and Carter, 1972

Distribution.—Known from Colombia, Venezuela, Guyana, Amazonian Brazil, Ecuador, and Perú.

Systematics.—*V. brachycephalus* is here considered as monotypic and to include *V. latus* and *V. l. saccharus* of Handley and Ferris.

Vampyrops helleri Peters, 1867

Distribution.—Southern México south through Middle America and northern South America to Perú, Bolivia, and Brazil; also found on Trinidad.

Systematics.—As pointed out by Rouk and Carter (1972), certain differences exist between specimens of *helleri* from México south through Middle America and those in Perú, but too few specimens are available to interpret these differences. The name *incarum* Thomas, 1912, would apply to Peruvian specimens and probably other Amazonian material should the differences prove to be of subspecific import. *V. zarhinus* is considered to be a synonym of *V. helleri*, and the holotype to have come from Panamá.

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

Distribution.—Reported from Central (Mato Grosso) and eastern (Bahía) Brazil south to Uruguay, Paraguay, Bolivia, and northern Argentina (Chaco). Although recorded by several authors from localities in western South America, these reports evidently refer to other species of bats.

Systematics.—*V. lineatus* is a monotypic species as presently understood, but appears closely allied to *V. recifinus*, with which it may be conspecific.

Vampyrops recifinus Thomas, 1901

Distribution.—Known from the Brazilian state of Pernambuco and purported to occur in those of Bahía and São Paulo.

Systematics.—Provisionally recognized as a monotypic species closely related to *V. lineatus*, from which it may not be distinct even at the subspecific level.

Genus VAMPYRODES Thomas

Vampyrodes caraccioloi (Thomas, 1889)

Distribution.—Southern México (Oaxaca, Veracruz) southeastward through Central America to South America as far south as northern Brazil and Amazonian Perú.

Systematics.—Two subspecies are recognized, following Handley (1966): *caraccioloi* (Trinidad and Tobago, and adjacent regions of northeastern South American mainland); *major* (México to Perú, *ornatus* a synonym). Some recent authors have regarded *major* as a species distinct from, but closely related to, *caraccioloi*.

Genus VAMPYRESSA Thomas

Vampyressa pusilla (Wagner, 1843)

Distribution.—Southern México (Veracruz), Central America, northern and central South America south at least to southeastern Brazil and Perú.

Systematics.—Goodwin (1963), who reviewed the genus *Vampyressa*, recognized three subspecies (*pusilla*, *thyone*, and *venilla*). Later, Peterson (1968), in his synopsis of the genus, listed only two (regarding *venilla* as indistinct from *thyone*). Handley (1966) did not recognize subspecies in *V. pusilla*. The species *nattereri*, named by Goodwin (*op. cit.*), is here regarded as a synonym of *pusilla* following Peterson (*op. cit.*).

Vampyressa melissa Thomas, 1926

Distribution.—Known only from eastern slope of Andes in Perú.

Systematics.—*V. melissa* is a monotypic species, which together with *V. pusilla* constitutes the subgenus *Vampyressa*.

Vampyressa nymphaea Thomas, 1909

Distribution.—Reported from Nicaragua, Costa Rica, Panamá, and western Colombia.

Systematics.—*V. nymphaea* is a monotypic species representing, along with *V. brocki*, the subgenus *Metavampyressa*.

Vampyressa brocki Peterson, 1968

Distribution.—Presently known only from Guyana and Colombia.

Systematics.—*V. brocki* is a monotypic species.

Vampyressa bidens (Dobson, 1878)

Distribution.—Ecuador, Perú, Colombia, northern Brazil, and Guyana.

Systematics.—*V. bidens* is a monotypic species and the sole representative of the subgenus *Vampyriscus*, which has been used in the generic sense by some recent authors.

Genus CHIRODERMA Peters

Chiroderma doriae Thomas, 1891

Distribution.—Eastern Brazil (Minas Gerais).
Systematics.—*C. doriae* is a monotypic species.

Chiroderma improvisum Baker and Genoways, 1976

Distribution.—Known only from the Lesser Antillean island of Guadeloupe.
Systematics.—*C. improvisum* is a monotypic species known only from the holotype.

Chiroderma villosum Peters, 1860

Distribution.—Southern México (Oaxaca and Veracruz) south to Perú, Bolivia, and Brazil.
Systematics.—Two subspecies are recognized, *villosum* (Trinidad and adjacent Venezuela south to Perú and Brazil) and *jesupi* (México south through Central America to northern Colombia).

Chiroderma salvini Dobson, 1878

Distribution.—Western México (Chihuahua) south to Colombia and Ecuador.
Systematics.—Two subspecies currently are recognized, *salvini* (Puebla, México, south to northern South America) and *scopaeum* (western México from Chihuahua south to Guerrero).

Chiroderma trinitatum Goodwin, 1958

Distribution.—Panamá east to Trinidad and south to Perú, Bolivia, and Brazil (Mato Grosso).
Systematics.—Two subspecies are recognized, *trinitatum* (Trinidad and Amazonian South America south to Perú and Brazil) and *gorgasi* (Darién, Panamá, east to Venezuela).

Genus ECTOPHYLLA H. Allen

Ectophylla alba H. Allen, 1892

Distribution.—Known only from Nicaragua, Costa Rica, and western Panamá.
Systematics.—*E. alba* is a monotypic species.

Ectophylla macconnelli Thomas, 1901

Distribution.—South America (reported from Amazonian Ecuador and Perú, Bolivia, Brazil, Colombia, Venezuela, Guyana, and Trinidad) and reported from Costa Rica and Panamá in North America.

Systematics.—Two subspecies usually are recognized, *macconnelli* of mainland South America and *flavescens* in Trinidad. For many years, *E. macconnelli* was regarded as representing the monotypic genus *Mesophylla*, which name still is used by some as a subgenus (but see Starrett and Casebeer, 1968).

Genus ARTIBEUS Leach

Artibeus cinereus (Gervais, 1855)

Distribution.—South America from Trinidad and Tobago, Colombia, and Venezuela southward to Bolivia; also reported from the Lesser Antillean island of Grenada.

Systematics.—Probable subspecies include: *cinereus* (Grenada, Trinidad and Tobago, the Guianas, and adjacent parts of Venezuela and northeastern Brazil); *anderseni* (central Brazil and adjacent Bolivia); *bogotensis* (Colombia and eastern Venezuela); *pumilio* (Amazonian Perú and Ecuador, Mato Grosso, Brazil, and adjacent regions); *solimoesi* (recently described from Codajas, Amazonas, Brazil); *A. glaucus* and *A. watsoni* are closely related species.

Artibeus glaucus Thomas, 1893

Distribution.—West of Andes in northwestern South America, south at least to central Perú.

Systematics.—See comments under *A. watsoni* below. Davis (1970*a*) regarded both *A. glaucus* and *A. watsoni* as species distinct from, albeit closely related to, *A. cinereus.* Additional study may show that all three represent the same species (*cinereus*), the situation thought to prevail prior to Davis' study. *A. rosenbergi* may be synonymous with *glaucus* or may be recognizable at the subspecific level.

Artibeus watsoni Thomas, 1901

Distribution.—Southern México southeastward through much of Central America to adjacent parts of South America.

Systematics.—*A. watsoni* was recognized by Davis (1970*a*) as a monotypic species closely related to *A. glaucus*, with which it may prove to be conspecific, and to *A. cinereus.*

Artibeus phaeotis (Miller, 1902)

Distribution.—Lowlands of eastern (north to Veracruz) and western (north to Sinaloa) México southeastward through Central America at least to eastern Perú in South America.

Systematics.—Subspecies (Davis, 1970*a*) include: *phaeotis* (Caribbean versant from Veracruz to South America); *nanus* (Pacific versant from Sinaloa to Oaxaca); *palatinus* (Pacific versant from Chiapas to Costa Rica).

Artibeus toltecus (Saussure, 1860)

Distribution.—Western (north to Sinaloa and Durango) and eastern (north to Tamaulipas) México southeastward at low and moderate elevations to northwestern South America.

Systematics.—Recognized subspecies (Davis, 1969) include *toltecus* (eastern México through Central America to South America) and *hesperus* (Pacific versant of western México south to Nicaragua); the subspecific name *ravus* may be applicable to South American populations.

Artibeus aztecus Andersen, 1906

Distribution.—Disjunct populations at moderate to relatively high elevations in central México (Sinaloa and Nuevo Leon south to Guerrero), Guatemala, and adjacent parts of Chiapas and Honduras, and Costa Rica and western Panamá.

Systematics.—Three subspecies (Davis, 1969) are recognized as occurring in the three distributional regions listed above—*aztecus*, *minor*, and *major*, respectively.

Artibeus hirsutus Andersen, 1906

Distribution.—Western México from central Sonora southward to Morelos and Guerrero.

Systematics.—*A. hirsutus* is a monotypic species.

Artibeus inopinatus Davis and Carter, 1964

Distribution.—Presently known only from El Salvador, Honduras, and Nicaragua.

Systematics.—*A. inopinatus* is a monotypic species closely related to *A. hirsutus*.

Artibeus concolor Peters, 1865

Distribution.—Colombia, Venezuela, the Guianas, and adjacent parts of Brazil and Perú.

Systematics.—*A. concolor* is a monotypic species.

Artibeus jamaicensis Leach, 1821

Distribution.—From eastern (as far north as southern Tamaulipas) and western (as far north as Sinaloa) México south through Central America, Colombia, Ecuador, Perú, Bolivia, and Brazil to Mato Grosso; also widely distributed in the Antilles.

Systematics.—Infraspecific variation in *A. jamaicensis* is well understood only in North America (Davis, 1970*b*; Jones and Phillips, 1970). Currently recognized subspecies are: *jamaicensis* (Greater Antilles, except Cuba, and Lesser Antilles south to St. Vincent); *fraterculus* (western Ecuador); *parvipes* (Cuba, southern Bahamas); *paulus* (Pacific versant of Middle America from Chiapas to Costa

Rica); *planirostris* (Brazil and adjacent regions); *richardsoni* (Caribbean versant of Middle America, from Chiapas southeastward to Panamá and adjacent South America); *trinitatus* (Grenada, in the Lesser Antilles, and Trinidad and Tobago); *triomylus* (western México from Sinaloa to Oaxaca); and *yucatanicus* (eastern México and Yucatán Peninsula).

The *jamaicensis* complex currently is under study by several investigators. It is evident that two or more species ultimately will be recognized from among "*jamaicensis*-like" bats. For example, *fraterculus* may represent a distinct species, and we are aware of an undescribed species from Amazonian Ecuador, Perú, and adjacent areas.

Artibeus lituratus (Olfers, 1818)

Distribution.—Widespread in Neotropical Middle and South America, from México south to northern Argentina; also occurs on southern islands of Lesser Antilles.

Systematics.—Infraspecific relationships are poorly understood at present. A provisional list of subspecies is: *lituratus* (southeastern Perú, Bolivia, southern Brazil, Paraguay, and northern Argentina); *fallax* (Venezuela and the Guianas south through the lower Amazon of Brazil); *hercules* (southern Colombia, Ecuador, and Perú); *intermedius* (mainland North America and northern Colombia); and *palmarium* (southern Lesser Antilles, Trinidad and Tobago, and adjacent South America).

Genus ENCHISTHENES Andersen

Enchisthenes hartii (Thomas, 1892)

Distribution.—Eastern (north to Tamaulipas) and western (north to Jalisco) México southeastward through Central America to eastern Andean slope in Perú. Additionally, an isolated specimen has been reported from Tucson, Arizona (Irwin and Baker, 1967).

Systematics.—*E. hartii* is a monotypic species. The genus *Enchisthenes* is regarded by some authorities as indistinct from *Artibeus*.

Genus ARDOPS Miller

Ardops nichollsi (Thomas, 1891)

Distribution.—Lesser Antilles from St. Eustatius southward to St. Vincent.

Systematics.—Five subspecies (Jones and Schwartz, 1967) are recognized: *nichollsi* (Dominica); *annecteus* (Guadeloupe); *koopmani* (Martinique); *luciae* (St Lucia and St. Vincent); *montserratensis* (Montserrat and St. Eustatius).

Genus PHYLLOPS Peters

Phyllops falcatus (Gray, 1839)

Distribution.—Cuba.

Systematics.—*P. falcatus* is a monotypic species. It and *P. haitiensis* evidently are closely related and possibly represent a single species. Also, a related species, *P. vetus*, is known only as a fossil from Cuba.

Phyllops haitiensis (J. A. Allen, 1908)

Distribution.—Hispaniola.

Systematics.—*P. haitiensis* is a monotypic species. See remarks above.

Genus ARITEUS Gray

Ariteus flavescens (Gray, 1831)

Distribution.—Jamaica.

Systematics.—*A. flavescens* is a monotypic species.

Genus STENODERMA É. Geoffroy St.-Hilaire

Stenoderma rufum Desmarest, 1820

Distribution.—Puerto Rico and Virgin Islands.

Systematics.—Three subspecies (Jones *et al.*, 1971*a*) are as follows: *rufum* (St. John and St. Thomas, Virgin Islands); *anthonyi* (fossil, Puerto Rico); *darioi* (Puerto Rico).

Genus PYGODERMA Peters

Pygoderma bilabiatum (Wagner, 1843)

Distribution.—Reported from Surinam, southeastern Brazil, Paraguay, and adjacent Argentina; limits of range unknown.

Systematics.—*P. bilabiatum* is a monotypic species. The reported occurrence of this species in North America has been shown to be erroneous (Koopman, 1958).

Genus AMETRIDA Gray

Ametrida centurio Gray, 1847

Distribution.—Northern South America (Venezuela, Trinidad, the Guianas, and Brazil; also reported from Bonaire Island).

Systematics.—According to Peterson (1965), who synonymized *A. minor* with *A. centurio*, the latter is a monotypic species.

Genus SPHAERONYCTERIS Peters

Sphaeronycteris toxophyllum Peters, 1882

Distribution.—Northwestern South America in Colombia, Venezuela, and Amazonian Perú, south to Bolivia.

Systematics.—*S. toxophyllum* is a monotypic species.

Genus CENTURIO Gray

Centurio senex Gray, 1842

Distribution.—Western (north to Sinaloa) and eastern (north to Tamaulipas) México southeastward to Panamá, and Trinidad; probably also in northern South America.

Systematics.—Two subspecies (Paradiso, 1967), *senex* (North America) and *greenhalli* (Trinidad), are recognized.

SUBFAMILY PHYLLONYCTERINAE

Genus BRACHYPHYLLA Gray

Brachyphylla cavernarum Gray, 1834

Distribution.—Puerto Rico and Lesser Antilles, south to St. Vincent and Barbados.

Systematics.—Two subspecies are recognized, *cavernarum* (Puerto Rico to St. Vincent) and *minor* (Barbados). Members of the genus *Brachyphylla* are here placed tentatively in the subfamily Phyllonycterinae following Silva Taboada and Pine (1969).

Brachyphylla nana Miller, 1902

Distribution.—Cuba and Hispaniola (known also from fossilized cave deposits on Jamaica).

Systematics.—Two subspecies, *nana* on Cuba and *pumila* on Hispaniola, currently are recognized.

Genus EROPHYLLA Miller

Erophylla bombifrons (Miller, 1899)

Distribution.—Hispaniola and Puerto Rico.

Systematics.—Two subspecies currently are recognized, *bombifrons* (Puerto Rico) and *santacristobalensis* (Hispaniola).

Erophylla sezekorni (Gundlach, 1861)

Distribution.—Cuba, Jamaica, and the Bahamas.

Systematics.—Four subspecies currently are recognized, as follows: *sezekorni* (Cuba); *mariguanensis* (southern Bahamas); *planifrons* (northern Bahamas); *syops* (Jamaica).

Genus PHYLLONYCTERIS Gundlach

Phyllonycteris poeyi Gundlach, 1861

Distribution.—Cuba and Hispaniola.

Systematics.—There are two nominal subspecies, *poeyi* on Cuba and *obtusa* (known only from skeletal remains) on Hispaniola.

Phyllonycteris major Anthony, 1917

Distribution.—Puerto Rico.

Systematics.—Known only from cave deposits and probably extinct, *P. major* is a monotypic species.

Phyllonycteris aphylla (Miller, 1898)

Distribution.—Known only from Jamaica.

Systematics.—*P. aphylla* is a monotypic species placed in a distinct subgenus (*Reithronycteris*).

Subfamily Desmodontinae

Genus Desmodus Wied-Neuwied

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

Distribution.—Eastern (north to Tamaulipas) and western (north to Sonora) México southward through Middle America and much of South America to Uruguay, northern Argentina, and central Chile; known also from Cuba as a fossil and from Texas in fossilized cave deposits.

Systematics.—Probably there are two recognizable extant subspecies—*rotundus* (southern South America north in Andes to Ecuador) and *murinus* (North American segment of range of species south to Amazon basin in South America). A postglacial fossil subspecies (*puntajudensis*) recently has been described from Cuba.

Genus Diaemus Miller

Diaemus youngii (Jentink, 1893)

Distribution.—Rare; recorded from scattered localities from Tamaulipas, México, southward to southern Brazil and Bolivia.

Systematics.—*D. youngii* is currently regarded as a monotypic species.

Genus Diphylla Spix

Diphylla ecaudata Spix, 1823

Distribution.—Southern Texas southward through eastern México, Central America, and South America at least as far as Perú and southern Brazil.

Systematics.—Two subspecies are recognized (Ojasti and Linares, 1971), *ecaudata* (South America and eastern Panamá) and *centralis* (western Panamá to Texas).

Key to Subfamilies and Genera of Phyllostomatidae

Subfamilies

1. Single upper incisor and upper canine enlarged and bladelike ..... *Desmodontinae*
   Upper incisor(s) and canine not enlarged and bladelike 2

2. Noseleaf rudimentary, without distinct upright process; tail present ... *Phyllonycterinae*
   Noseleaf usually well developed; tail absent if noseleaf rudimentary 3
3. Tongue elongate, with conspicuous bristlelike papillae on anterodorsal surface; first upper premolar usually distinctly separated from canine and rarely in contact with second upper premolar (first upper premolar sometimes in contact with canine in *Monophyllus*, but distinctly separated from second upper premolar) ..... *Glossophaginae*
   Tongue not elongate, lacking conspicuous bristlelike papillae; first upper premolar in contact with canine and usually with second upper premolar 4
4. Zygomatic arch incomplete ..... *Carolliinae*
   Zygomatic arch complete 5
5. Molars dilambdodont (distinct W-shaped pattern of lophs on occlusal surface) ..... *Phyllostomatinae*
   Molars lacking dilambdodont pattern ..... *Stenoderminae*

Phyllostomatinae

1. One lower incisor 2
   Two lower incisors 4
2. Two lower premolars ..... *Mimon*
   Three lower premolars (second small to minute) 3
3. Second lower premolar crowded to lingual side of toothrow, first and third lower premolars usually in contact ..... *Chrotopterus*
   Second lower premolar not crowded from toothrow, first and third lower premolars not in contact ..... *Tonatia*
4. Two lower premolars ..... *Phyllostomus*
   Three lower premolars (second sometimes crowded to lingual side of toothrow) 5
5. Rostrum as long as braincase ..... *Vampyrum*
   Rostrum shorter than braincase 6
6. Second lower premolar large, subequal in size to first and third premolars 7
   Second lower premolar small to minute, much smaller than first and third premolars 8
7. Auditory bullae large, greatest diameter much exceeding distance between them ..... *Macrotis*
   Auditory bullae small, greatest diameter less than distance between them ..... *Micronycteris*
8. Second lower premolar displaced lingually from toothrow; first and second lower premolars in contact or nearly so 9
   Second lower premolar not displaced lingually from toothrow; first and second lower premolars usually not in contact 10
9. Greatest length of skull less than 20 mm. ..... *Macrophyllum*
   Greatest length of skull more than 20 mm. ..... *Trachops*
10. Dorsal profile of rostrum strongly convex; deep depression present between orbits ..... *Lonchorhina*
    Dorsal profile of rostrum not convex; no depression between orbits ..... *Phylloderma*

Glossophaginae

1. Permanent lower incisors lacking 2
   Two pairs of permanent lower incisors, usually well developed 8
2. Premolars 3/3 ..... *Anoura*
   Premolars 2/3 3
3. Molars 2/2 ..... *Lichonycteris*
   Molars 3/3 4
4. Pterygoids highly modified, expanded at base and inflated in appearance; pterygoid wings long and in contact, or nearly so, with auditory bullae 5
   Pterygoids normal, not expanded at base or inflated in appearance; pterygoid wings short and not in contact with auditory bullae 7
5. First and second upper incisors separated by distinct gap; upper premolars low, barely exceeding height of molars ..... *Choeroniscus*
   First and second upper incisors in contact, or nearly so; upper premolars distinctly higher than molars 6
6. Rostrum distinctly longer than postrostral part of cranium; upper molars essentially equal in size, all with a distinct metastyle ..... *Musonycteris*
   Rostrum about equal in length to postrostral part of cranium; third upper molar somewhat smaller than first two and lacking a distinct metastyle ..... *Choeronycteris*
7. Upper molars lacking mesostyle; lower molars long and narrow; known only from Middle America ..... *Hylonycteris*
   Mesostyle present on all upper molars; lower molars only moderately compressed; known only from Brazil and Venezuela ..... *Scleronycteris*
8. Molars 2/2 ..... *Leptonycteris*
   Molars 3/3 9
9. Zygomatic arch complete, first upper incisor not markedly enlarged and spatulate ... 10
   Zygomatic arch incomplete, first upper incisor enlarged and spatulate 11
10. Evident gap between upper premolars and between them and adjacent teeth; tail relatively long and extending beyond posterior border of uropatagium ..... *Monophyllus*
    Upper premolars usually in contact and filling space between canine and first molar; tail short and not extending beyond posterior border of uropatagium ..... *Glossophaga*
11. Rostrum elongate, longer than postrostral part of cranium; postcanine maxillary teeth reduced in size and with evident gaps between them ..... *Platalina*
    Rostrum not elongate, no longer than postrostral part of cranium; postcanine maxillary teeth of normal size, last premolar and molars in contact (or nearly so) 12
12. First upper premolar smaller than second and laterally compressed ..... *Lonchophylla*
    First upper premolar essentially same size as second, not laterally compressed (triangular in outline) ..... *Lionycteris*

Carolliinae

1. Tail present; upper premolars essentially equal in size ..... *Carollia*
   Tail absent; first upper premolar much smaller than second ..... *Rhinophylla*

Stenoderminae

1. Molars 2/2 2
   Molars 2/3 or 3/3 7
2. Upper dental arcade semicircular, rostrum less than half as long as braincase ..... *Centurio*
   Upper dental arcade not semicircular, rostrum more than half as long as braincase ... 3
3. Rostrum inflated, nearly cuboid in form ..... *Pygoderma*
   Rostrum not inflated or cuboid in form 4
4. Posterior margin of external nares with marked, lyre-shaped emargination ..... *Chiroderma*
   Posterior margin of external nares lacking lyre-shaped emargination 5
5. Second upper molar markedly larger than first; upper premolars separated from each other and adjacent teeth by evident gaps ..... *Ectophylla* (part)
   Second upper molar essentially equal in size to, or smaller than, first; no gaps between anterior upper cheekteeth 6
6. Posterior margin of external nares more or less straight; second upper molar much smaller than first and differing in form ..... *Artibeus* (part)
   Posterior margin of external nares broadly V-shaped; second upper molar resembling first in size and form ..... *Vampyressa* (part)
7. Molars 2/3 8
   Molars 3/3 12
8. Palate short, posterior border having deep U-shaped emargination that reaches level of first molar ..... *Ariteus*
   Palate long, posterior border having shallow emargination that falls far short of level of toothrow 9
9. First upper incisor markedly bifid, less than twice size of second incisor ..... *Artibeus* (part)
   First upper incisor not bifid or only weakly so, more than twice size of second incisor 10
10. Second upper molar noticeably larger than first; upper premolars separated from each other and from adjacent teeth by evident gaps ..... *Ectophylla* (part)
    Second upper molar equal in size to, or smaller than, first; no gaps between anterior upper cheekteeth 11
11. Incisors 2/1 or 2/2; height of first incisor greater than height of first premolar; greatest length of skull less than 22 ..... *Vampyressa* (part)
    Incisors 2/2; height of first incisor much less than height of first premolar; greatest length of skull more than 24 ..... *Vampyrodes*
12. Upper dental arcade expanded laterally to form semicircular arc 13
    Upper dental arcade not expanded laterally, U-shaped in occlusal view 14
13. Orbital space wider than long; interorbital constriction less than 5 ..... *Ametrida*
    Orbital space longer than wide; interorbital constriction more than 5 ..... *Sphaeronycteris*
14. Palate short, posterior palatal emargination reaching level of first upper molar 15
    Palate of medium length or long, posterior border variously emarginate but never to level of toothrow 17

15. Palatal emargination broadly V-shaped ..... *Phyllops*
Palatal emargination deeply U-shaped 16

16. Well-developed V-shaped ridge from sagittal crest to anterior margin of orbits, forming deep rostral depression ..... *Stenoderma*
V-shaped ridge from sagittal crest to anterior margin of orbits lacking, rostrum normal ..... *Ardops*

17. Upper molars distinctly grooved longitudinally, the first two subquadrate in outline and lacking well-developed cusps; first upper incisor approximately half as high as canine ..... *Sturnira*
Upper molars lacking longitudinal groove, the first two not subquadrate in outline and possessing well-developed cusps; first upper incisor much less than half as high as canine 18

18. First upper incisor less than twice size of second and resembling it in shape; upper incisors in contact and filling space between canines 19
First upper incisor more than twice size of second and differing from it in shape; evident gaps present between upper incisors 20

19. First upper incisor deeply bifid; m3, if present, minute and peglike ..... *Artibeus* (part)
First upper incisor not bifid; m3 relatively large and well developed ..... *Enchisthenes*

20. Crowns of first upper incisors parallel, deeply bifid; lower incisors in contact ..... *Uroderma*
Crowns of first upper incisors converge distally, not deeply bifid; lower incisors separated by distinct gaps ..... *Vampyrops*

Phyllonycterinae

1. Tail not extending beyond edge of uropatagium ..... *Brachyphylla*
Tail extending beyond edge of uropatagium 2

2. Zygomatic arch complete; second and third lower molars distinctly cuspidate ..... *Erophylla*
Zygomatic arch incomplete; second and third lower molars not distinctly cuspidate ..... *Phyllonycteris*

Desmodontinae

1. First lower incisors in contact; interfemoral membrane with distinct fringe of moderately long hairs ..... *Diphylla*
First lower incisors not in contact; interfemoral membrane without fringe of hair 2

2. Lower incisors not bifid; wing white from middle of proximal phalanx to tip ..... *Diaemus*
Lower incisors bifid; wing usually pigmented to tip (if white-tipped, white does not extend proximally to first phalanx) ..... *Desmodus*

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ZOOGEOGRAPHY

KARL F. KOOPMAN

Of the nine families of bats in the Western hemisphere, three (Emballonuridae, Vespertilionidae, Molossidae) are found also in the Old World. Of the six endemic New World (and chiefly Neotropical) families, the Phyllostomatidae is by far the largest grouping. The Noctilionidae, Furipteridae, and Thyropteridae have only two species each, the Natalidae probably only six species, and the Mormoopidae eight species (see Smith, 1972). The Phyllostomatidae, however, have 136 species as recognized in the classification in this volume.

Except for a few areas (West Indies, southeastern Brazil, northern México) even the Pleistocene fossil record of bats for the Neotropical region is poor. To my knowledge the only pre-Pleistocene record of bats in the Neotropical region is of *Notonycteris* (a phyllostomatid) from the Miocene of Colombia. This shows that the Phyllostomatidae were in South America by at least that time. In the Miocene, South America was still an island continent separated from other continents by ocean barriers. Judging by present diversity in South America, it is likely that the Phyllostomatidae was the first chiropteran family to reach South America during its long period of isolation, and may even have originated as a family on that continent. The other five families more or less confined to the Neotropical region have too few species for anything very definite to be said about their area of origin (see Koopman, 1970). While it is thus probable that South America was the primary center of phyllostomatid evolution, it is clear that both Middle America and the West Indies have been important secondary centers.

In the following sections, after a short discussion of distribution of the subfamilies, the various special regions of South America, Middle America, and the West Indies will be taken up in turn with a discussion of the phyllostomatids found within each of them It should be emphasized that oceanic straits as well as high mountains and cold temperate lowland areas (such as Patagonia) constitute formidable barriers for the Phyllostomatidae.

DISTRIBUTION OF MAJOR PHYLLOSTOMATID GROUPS

Of the six subfamilies in to which the Phyllostomatidae are currently divided, all but the Phyllonycterinae are widely distributed in South and Middle America. The phyllonycterines are endemic to the West Indies, which also have phyllostomatines, glossophagines, and stenodermines. Vampires are known in the fossil record of Cuba, but there are no certain records of carolliines in the West Indies as defined here. Several genera of glossophagines and stenodermines are confined to the Antilles.

On the mainland, many genera and even species are distributed over a large part of the total range of the family. Others, particularly in the Glossophaginae (and to a lesser extent the Stenoderminae), have restricted ranges (for example,

Platalina). It should also be mentioned that the Sturnirini (all now included in the genus *Sturnira*) are strongly concentrated in the northern Andean region with relatively few species far away from it. For futher information on distribution of individual species, the reader is referred to the preceding article in this volume and the appendix of this paper.

Regional Bat Faunas

South America

Patagonian subregion.—This is that portion of South America south of the tropical forests. It has never been precisely defined but would certainly include, for our purposes, all of Chile and Uruguay, also all of Argentina except small portions of the northeast and northwest. The high Andes and altiplano of western Bolivia and southern Perú also would be included as well as dryer areas of western Paraguay, southern Bolivia, and extreme southeastern Brazil. Although there are several species of bats that are mostly confined to the Patagonian region, all are vespertilionids. A few species of phyllostomatids, the main range of which lies farther north, do reach the Patagonian subregion to a limited degree, but only six species really penetrate the subregion. Of these, only one, *Desmodus rotundus*, reaches any distance southward—to central Argentina and even central Chile. While it is possible that this may in part reflect the man-made availability of cattle as food, this is by no means certain. *Sturnira lilium* also reaches central Argentina, but an old record from Chile is apparently erroneous. Of the other four species, *Chrotopterus auritus*, *Glossophaga soricina*, and *Artibeus lituratus* range no farther than northern Argentina, whereas *Vampyrops lineatus* has recently been recorded from Uruguay.

Eastern Brazilian highlands and coast.—The dry chaco zone of northern Argentina, western Paraguay, and southeastern Bolivia continues in modified form as the caatinga, a belt of scrub forest (really a savanna), which reaches the Atlantic coast a little to the west of easternmost Brazil. This isolates the mountain and coastal forests of eastern Brazil, eastern Paraguay, and northeastern Argentina from those of the Amazon basin. As a result, there are a number of mammals, particularly primates and rodents, that are confined to this eastern area. However, out of 36 species of phyllostomatids known from the region, only four (*Tonatia brasiliense*, *Vampyrops recifinus*, *Chiroderma doriae*, and possibly *Lonchophylla mordax*) are, as at presently recognized, endemic to it. In view of the fact that bats are able to fly across short stretches of unfavorable habitat, however, this is not surprising. There are, on the other hand, some 42 species of phyllostomatids in the Amazon basin that are not known from the eastern Brazilian highlands and coastal area, although some may eventually be found there.

Amazon Basin.—This represents perhaps the real heartland of the Neotropical region. It includes the entire Amazon drainage of Brazil and also includes northeastern Bolivia (with an extension along the eastern face of the Andes into northwestern Argentina), the eastern lowlands of Perú and Ecuador, the Amazon and Orinoco drainages of Colombia and Venezuela, and also the Guianas. Some

74 species of phyllostomatids are known from this area, 14 of which apparently are endemic. However, the list of endemics (*Micronycteris behni*, *M. daviesi*, *Lonchorhina orinocensis*, *Tonatia carrikeri*, *Phyllostomus latifolius*, *Scleronycteris ega*, *Choeroniscus inca*, *Lichonycteris degener*, *Rhinophylla fischerae*, *Vampyrops infuscus*, *V. aurarius*, *Vampyressa brocki*, *V. bidens*, and *Artibeus concolor*) includes several species that are poorly known or of dubious validity. Four other species (*Mimon bennetti*, *Phyllostomus elongatus*, *Rhinophylla pumilio*, and *Pygoderma bilabiatum*) are shared only with the eastern Brazilian area. More taxonomic work undoubtedly will change considerably the figures both for total number and number of endemics.

Eastern slopes of the northern Andes.—The upper forested slopes on the eastern side of the Andes from Colombia to Bolivia, while ecologically continuous with the Amazonian lowlands to the east, are environmentally distinctive to the extent that many lowland species extend only to a limited extent up these slopes, whereas other species are confined to higher elevations. Unfortunately the altitudinal distributions of phyllostomatids are not well known in most of this Andean belt and, at present, it is only about Perú that much can be written. I have chosen to ignore species that do not occur above about 1000 meters but include as endemics all species that are confined to elevations above 500 meters. Using these criteria, some 25 species are known from the upper slopes of the eastern Andes, and three of these (*Mimon koepkeae*, *Sturnira nana*, and *Vampyressa melissa*) are endemic. There would be more endemic species (such as *Sturnira erythromos* and *S. bidens*) if higher elevations of the internal Andean valleys of Colombia were included.

Northern coast and islands.—I would define this area on the mainland as extending from the northern end of the Cordillera Occidental (just east of the Gulf or Uraba) east along the coast to the Paria Peninsula in northeastern Venezuela. In Venezuela, it would include only a rather narrow coastal strip including the mountains directly to the south, but in Colombia would extend up the river valleys between the cordilleras, but not west of the Cordillera Occidental nor east of the Cordillera Oriental. The boundaries are most difficult to draw in Colombia. Here the higher elevations in the internal Andean valleys are perhaps better placed with eastern slope highlands. The lowlands of the Cauca Valley, on the other hand, are almost equally well placed with lowlands of the Pacific coast. However, in the absence of a great deal more detailed distributional information, I have been unable to draw a better boundary. A number of islands are also included, chiefly Aruba, Curaçao, Bonaire, Margarita, Trinidad, Tobago, and Grenada. I have published previously on the bat faunas of these islands (Koopman, 1958), but a number of species have been recorded since. I previously (Koopman, 1959) treated Grenada and the Grenadines as part of the West Indies, but, as explained in the Lesser Antillean section, I believe these islands are better placed here. Perhaps the greatest significance of this northern coast and island area is that a number of the species occurring there have affinities with Central America (and sometimes the West Indies) rather than with the Amazon Basin. Some 64 species are known from this area. Although only *Leptonycteris*

curasoae and the poorly known *Tonatia venezuelae* and *Vampyrops oratus* (included in *V. dorsalis* in the preceding annotated list) are endemic, there are several Central American species (*Micronycteris schmidtorum*, *Lonchophylla concava*, *Anoura cultrata*, and *Centurio senex*) that in South America (aside from the Pacific coast of Colombia) are known only from this northern coast and island district.

Pacific coast of Perú.—This is a relatively narrow coastal strip lying between the Andes and the sea. On the north, it grades into the Pacific coastal region of Colombia and Ecuador (which tends to be considerably wetter) and to the south is continuous with the dry Atacaman Desert of Chile. At the northern end, the region supports a fair-sized bat fauna including a high percentage of endemics, but this fauna becomes progressively impoverished to the south with increasing aridity. Only nine species of phyllostomatids are known from coastal Perú, but two of these (*Lonchophylla hesperia* and *Platalina genovensium*) are endemic. Four of the species do not occur along the coast south of northwestern Perú (*Lonchophylla hesperia*, *Uroderma bilobatum*, *Vampyrops helleri*, and *V. vittatus*). Two (*Anoura geoffroyi* and *Artibeus jamaicensis*) reach central Perú, and two (*Glossophaga soricina* and *Platalina genovensium*) southern Perú. There is one species, not a phyllostomatid (*Amorphochilus schnabeli*), that has a distribution along the coast from Ecuador to northern Chile, and it is probable that the ninth species of phyllostomatid (*Desmodus rotundus*), which occurs widely in coastal Perú, has reached central Chile by the same route.

Pacific coast of Colombia.—The narrow strip of Colombia, Ecuador, and extreme southeastern Panamá between the Cordillera Occidental and the Pacific ocean is zoogeographically and to some extent historically more a part of Central America than of South America. Much of it is also exceedingly wet and for these reasons it represents a minor center of endemism. Some 50 species of phyllostomatids are known from this Pacific coastal strip of Colombia. Only *Choeroniscus periosus* and *Rhinophylla alethina* are endemic, but *Glossophaga commissarisi*, *Vampyressa nymphea*, *Artibeus toltecus*, and the dubiously distinct *Mimon cozumelae* and *Artibeus watsoni* are otherwise known only from Central America.

Middle America

Central America.—Although originally a portion of the North American continent when it was separated by water from South America, Central America has undergone extensive mutual faunal interchange with South America as a result of similar environments. However, there is a fair amount of endemism and there are some taxa that do not occur in South America, but are shared with tropical México west of the Isthmus of Tehuantepec. (That part of México east of the Isthmus is here considered part of Central America.) Some 68 species of phyllostomatids are known from Central America, four of which (*Anoura werckleae*, *Sturnira mordax*, *Ectophylla alba*, and *Artibeus inopinatus*) are endemic. There are four other species (*Glossophaga alticola*, *Hylonycteris underwoodi*,

Carollia subrufa, and *Artibeus aztecus*) that are not considered endemics because they have invaded tropical México (but do not occur in South America).

Tropical México west of the Isthmus of Tehuantepec.—Above the Isthmus of Tehuantepec, tropical México becomes split into Atlantic and Pacific segments separated by the Mexican plateau. The number of species in both northeastern and northwestern México declines as the various tropical habitats successively wane and disappear. Tropical México is here considered to end in southern Sonora and southern Tamaulipas. Some 29 species of phyllostomatids have a significant distribution above the Isthmus, but only *Musonycteris harrisoni* and *Artibeus hirsutus* are endemic.

Subtropical Nearctica.—This represents the impoverished northern margin of phyllostomatid distribution just as the Patagonian subregion does in the south. It includes the southwestern United States, Baja California, and northern Sonora in the west; southern Texas, Coahuila, all but the southern tip of Nuevo Leon, and northern Tamaulipas in the east. If the Arizona record of *Enchisthenes harti* and the Texan record of *Diphylla ecaudata* are rejected as accidental, then, according to my reckoning, only four species (*Macrotus californicus*, *Choeronycteris mexicana*, *Leptonycteris nivalis*, and *L. sanborni*) penetrate into Nearctica. In view of the extensive invasion of the Patagonian subregion both east and west of the Andes by *Desmodus rotundus*, it would seem most surprising that it hardly penetrates Nearctica. McNab (1973) has shown, however, that in both North and South America, the distributional limits coincide quite closely with the 10° winter isotherm.

West Indies

Greater Antilles.—For purposes of phyllostomatid distribution, I include in this region the essentially oceanic islands from the Bahamas, Cuba, and Jamaica to the Virgin Islands. Most of the bats in this area have come from Middle America, and the number of species decreases markedly from Cuba and Jamaica eastward. Excluding the dubious Jamaican records of *Vampyrum spectrum*, *Carollia perspicillata*, and *Sturnira lilium*, and the dubious Bahamian record of *Lonchorhina aurita*, some 19 species of phyllostomatids are represented, although five of these (*Tonatia bidens*, *Monophyllus plethodon*, *Phyllops vetus*, *Phyllonycteris major*, and *Desmodus rotundus*) are known only as fossils. Of the 19 species, 12 are endemic, and all of these belong to endemic West Indian genera. Two of the nonendemic species (*Monophyllus plethodon* and *Brachyphylla cavernarum*) also belong to endemic West Indian genera, being shared only with the Lesser Antilles. Thus only five mainland species (*Macrotus waterhousii*, *Tonatia bidens*, *Glossophaga soricina*, *Artibeus jamaicensis*, *Desmodus rotundus*) represent recent invaders of the Greater Antilles from the mainland.

Lesser Antilles.—These are the essentially oceanic islands in the West Indies, extending from Saba and Anguilla in the north to St. Vincent and Barbados in the south. Earlier, I (Koopman, 1959) included Grenada and the Grenadines, in this grouping, but in view of the fact that Grenada has none of the charac-

teristic West Indian endemics, but does have several mainland species (both bats and other mammals) lacking on St. Vincent and the islands farther north, it seems preferable to exclude Grenada and the Grenadines from the true West Indies. When the Lesser Antilles are defined in this way, and excluding the dubious record of *Carollia* from Redonda, only eight species of phyllostomatids are known. Only two (*Sturnira thomasi* and *Ardops nichollsi*) are endemic, but two others (*Monophyllus plethodon* and *Brachyphylla cavernarum*) are (or were) shared only with the Greater Antilles, leaving only four that also occur on the mainland (*Glossophaga longirostris*, *Sturnira lilium*, *Artibeus jamaicensis*, and *A. lituratus*). It is probable that the Lesser Antilles are of considerably more recent origin than the Greater Antilles and have been colonized relatively recently from South America and the Greater Antilles.

Conclusions

South America would seem to be the major area of differentiation, if not origin, of the Phyllostomatidae. An original colonization in mid-Tertiary, perhaps Oligocene, would appear most likely. The Amazon Basin, in the broad sense, has the greatest number of species today, a number of them endemic, and could well have been the major center of diversification. However, other areas must have been colonized at a relatively early date because even the peripheral West Indies have an endemic subfamily. However, dispersal beyond the limits of the tropics has obviously been difficult as seen in the small number of species that occur today in the Nearctic region and Patagonian subregion. This does not mean that the distribution always has been as restricted to the north and south; it is known, for example, that the tropics were more extensive in the middle Cenozoic. The only definite fossil evidence of wider former distribution of phyllostomatids, however, is the Pleistocene occurrence of *Desmodus* in Florida and northern California, where no phyllostomatids occur today.

Local differentiation of faunas within the tropics as a result of barriers to dispersal and regional ecological differences proves of greater interest than does the decrease in numbers of species as the margins of the tropics are approached. The Andes, the dry chaco and caatinga belts of Brazil, the grasslands (llanos) of north-central Venezuela, and the water gaps in and around the West Indies all have acted as partial barriers to phyllostomatid dispersal. Climatic alterations and eustatic changes have, however, altered the effectiveness of these barriers with time. Thus during interpluvials, the caatinga barrier must have, at least in part, disappeared, whereas during glacial periods, Central America extended out toward Jamaica.

In western South America, the Andes have given rise to marked ecological differences over relatively short distances. In Perú, the higher subtropical and temperate slopes of the Andes support a clearly different fauna from that of the Amazonian lowlands. Except for a few passes in northern Perú, these temperate forested slopes are separated from the dry Pacific coastal belt. Proceeding northward into Colombia, the coastal zone changes from dry in southern Peru to extremely wet in northern Colombia. As a result, different faunas have developed

ecologically distinct from one another and geographically isolated from the eastern slopes. The complexity of the Andes in Colombia produces a series of phyllostomatid faunas that defy, at present, any precise analysis. One fact is evident. Much more locality data from critical areas will have to be accumulated before the distributional patterns of South American phyllostomatids can be understood fully.

Acknowledgments

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Appendix: Taxonomic Notes

A number of unpublished records (mostly specimens in the American Museum of Natural History) extend known distributions or otherwise modify the taxonomic basis for the above account of phyllostomatid zoogeography. They are listed here by species, with whatever discussion seems appropriate.

Micronycteris schmidtorum.—To my knowledge, the only record of this species from South America consists of seven specimens (AMNH 130715-20, 130725) collected from Río Tocuyo, Lara, Venezuela, in March 1938. This places *M. schmidtorum* in the northern coastal region.

Micronycteris brachyotis.—The basis for the inclusion of Amazonian Brazil in the distribution rests on a single specimen (AMNH 94601) collected from Igarape Brabo (on the Rio Tapajoz), Para, Brazil, in May 1931.

Micronycteris sylvestris.—The inclusion of eastern Perú in the distribution rests on a single specimen (AMNH 214316) from Cordillera Vilcabamba, west side, 890 m., Cuzco, Perú, which was obtained in late June or early July 1966.

Tonatia bidens.—Although I (with E. E. Williams) originally described *T. saurophila* as a separate species, I am now convinced after seeing more material of both *saurophila* and mainland *bidens*, that the former is best considered only a subspecies of the latter.

Tonatia carrikeri.—The Bolivian record is a single specimen (AMNH 209322) collected from: Río Itenez, Beni, opposite Costa Marques, Brazil.

Tonatia nicaraguae-minuta.—Both species were described originally in the same paper (Goodwin, 1942). While *nicaraguae* has page priority over *minuta*, this has no standing under the present rules. Against this, the first person to combine the two nominal species (Handley 1966*b*:761) clearly synonymized *nicaraguae* with *T. minuta*. The holotypes of both named forms are in the American Museum. The type of *nicaraguae* is immature, has a broken and somewhat decalcified skull, and is the only specimen from its locality. The holotype of *minuta* is adult, has a skull in good condition, and is one of a series of six from the same locality. I am therefore inclined to call the combined species *Tonatia minuta*. To my knowledge, the only definite published localities in South America, outside the type locality in Amazonian Peru, are in Trinidad. However, the two specimens from the Rio Tapajoz, Para, Brazil, referred to *brasiliense* by Goodwin (1942:207) are similar to *minuta* and may be referable to it. Until the taxonomic status of *brasiliense* and *venezuelae* is settled, however, this will remain uncertain.

Mimon crenulatum.—The Bolivian record is based on a single specimen (AMNH 209323) from the mouth of the Río Baures, Beni, Bolivia.

Mimon koepkeae.—Comparison of a specimen (AMNH 233222) from Estera Rohuana, 1900 m., Ayacucho, Perú, with numerous specimens of *M. crenulatum* from Perú and other parts of South America, convinces me that *koepkeae* is only a Peruvian highland subspecies of *M. crenulatum.*

Trachops cirrhosus.—The Bolivian records are from five localities in the department of Beni (AMNH 209348-52, 210679-84).

Lonchophylla mordax.—This species is known definitely only from eastern Brazil if *concava* is treated as a separate species. Records from Bolivia and Amazonian Brazil should be reinvestigated. All small *Lonchophylla* I have seen from these areas have been *L. thomasi.*

Lonchophylla thomasi.—The Bolivian records are from two localities in the department of Beni (AMNH 209358, 210688). The species also is known from two localities in the state of Para, Brazil (AMNH 95493, 95495, 95772, 97271-72).

Rhinophylla fischerae.—The Brazilian record is based on four specimens (AMNH 94555-58) from Rio Tapajoz, Caxiricatuba, Para, Brazil.

Vampyrops dorsalis.—In my opinion, the species as listed here is a complex of more than one species. A specimen of *oratus* (AMNH 235560) from Rancho Grande, Aragua, Venezuela, is much smaller than specimens of *dorsalis* from the Pacific coast of Colombia or from the eastern slope of the Andes in Perú.

Vampyrops nigellus.—Comparison of *nigellus* (represented by many specimens from eastern Perú) with *lineatus* (represented by many specimens from Paraguay, Mato Grosso in Brazil, and Bolivia) convinces me that the two are conspecific.

Vampyrops helleri.—There are numerous specimens from Bolivia in the American Museum of Natural History, the southernmost being from *ca.* 54 km. S mouth of Río Chapare, Santa Cruz.

Chiroderma villosum.—There are numerous specimens of *C. villosum* from Bolivia in the American Museum of Natural History, the southernmost being from Buenavista, Santa Cruz.

Chiroderma trinitatum.—The Bolivian record is based on four specimens (AMNH 209519-21, 210810) from three localities in the northern part of the department of Beni.

Ectophylla macconnelli.—The Bolivian record is based on six specimens (AMNH 209577-81, 215025) from three localities in northern Beni.

Enchisthenes harti.—The Peruvian records are based on numerous specimens from high elevations (1660 to 3540 m.) in the departments of Huánuco, Ayacucho, and Cuzco.

Sphaeronycteris toxophyllum.—The Bolivian record is based on three specimens (AMNH 209739-41), each from a different locality in northern Beni.

Diaemus youngii.—The Bolivian record is based on seven specimens (AMNH 209742-46, 215026) from three localities in northern Beni.

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CHIROPTERAN EVOLUTION

JAMES DALE SMITH

One of the most intriguing problems in vertebrate evolution is the evolution and diversification of the mammalian order Chiroptera. Among vertebrates, bats share with birds and possibly the reptilian pterosaurs (the latter may have been adapted to gliding rather than true flight) the unique ability of sustained flight. Whereas the pelvic appendages of birds have remained relatively unchanged for terrestrial locomotion and only the pectoral appendages modified for flight, bats have become totally committed, in an anatomical sense, to a strategy for flight. The difference in the mode of adaptation to flight by birds and bats no doubt reflects two quite different selective regimes involving bipedal and quadrupedal ancestry, respectively. Bats apparently became adapted for an aerial existence in order to exploit an aerial insectivorous food source. On the other hand, birds initially may have developed flight to pursue a predacious mode of life, to escape predators, for dispersal, or a combination of these (Ostrom, 1974). Admittedly, aerial insectivory has been important in the adaptation and diversification of birds, but this particular feeding strategy has not been the central focus in their speciation.

Although bats are a remarkably successful group and comprise the second largest mammalian order, they remain one of the least known groups in terms of a fossil record. The delicacy of the chiropteran skeleton and the cave and forest-dwelling habit of bats have apparently contributed to the paucity of fossils. The antiquity of the Chiroptera is confirmed by *Icaronycteris* from the early Eocene of Wyoming and France (Russell *et al.*, 1973; includes description and comparisons of *Icaronycteris*? *menui*); *Palaeochiropteryx* and *Archaeonycteris* from the early Eocene of Austria; *Cecilionycteris* from the middle Eocene of Germany; *Ageina* from the early Eocene of France; and the extant genus *Hipposideros* from the middle Eocene of Europe. By the Oligocene and Miocene, six chiropteran families (Pteropodidae, Rhinolophidae, Emballonuridae, Phyllostomatidae, Vespertilionidae, and Molossidae) are represented in the geologic record. Unfortunately, most of the fossilized remains of bats are extremely fragmentary with the exception of *Icaronycteris index*, which is beautifully preserved.

Martin (1972) compiled a synopsis of late Pliocene and Pleistocene bats (including phyllostomatids) from North America and the Antilles. For the most part, his list includes extant species or extinct species that are clearly related to living taxa. Paula Couto (1938) reported numerous Pleistocene fossil bats from Brazil but these, too, were extant species or related thereto. Two vespertilionids, *Miomyotis floridanus* and *Suaptenos whitei*, were described by Lawrence (1943) from the early Miocene of Florida, and, more recently, Sutton and Genoways (1974) described *Ancenycteris rasmusseni* from late Miocene deposits in Gallatin County, Montana. Galbreath (1962) described *Oligomyotis casementi* from Middle Oligocene deposits in Logan County, Colorado. In addition to these fos-

sils, which clearly are assignable to the Chiroptera, there are a number of fragmented insectivore remains that are suggestive of a chiropteran grade, but that can only be categorized as "*incertae sedis*" (Simpson, 1945; Russell and Sigé, 1970).

The development of flight by bats (which has involved nearly all major organ systems) was primarily concerned with providing a delivery system for the feeding apparatus. Based on dental morphology of extant species as compared with that of early fossils, it is generally assumed that aerial insectivory was the initial impetus for chiropteran evolution. Subsequent diversification has been associated with the further partitioning and specialization of this generalized feeding strategy into carnivory, piscivory, foliage gleaning, frugivory, nectarivory, and sanguivory. [For convenience, I have selected the trophic categories described by Wilson (1973) in this discussion; I realize that these, in themselves, represent generalized strategies that could be further partitioned.]

It is the goal of this chapter to consider the evolution of the Phyllostomatidae. This family has commanded the interest of students of chiropteran evolution because it represents one of the most, if not the most, diverse families in terms of feeding strategy—all categories except piscivory being represented within the context of the family. Furthermore, although ranking third in number of species (136, as compared to 285 for vespertilionids and 150 for pteropodids), the phyllostomatids exceed all other families of bats in number of genera (49, Koopman and Jones, 1970; and Jones and Carter, this volume). Lastly, the adaptive radiation of phyllostomatids apparently has been confined to the tropical regions of the New World. Before proceeding further with a discussion of the phyllostomatids, I believe it is relevant and important to consider some of the overall aspects of chiropteran evolution.

Evolutionary Impetus of the Chiropteran Grade

Because of the meager fossil record for bats, students of chiropteran evolution have been forced to extrapolate the past history of the order based on features of living species. For the most part, anatomical features of the flight mechanism and dental morphology have been utilized in this endeavor, whereas the ecological role, in terms of feeding strategy and niche diversity, mostly has been overlooked. The primary emphasis of chiropteran biology has been descriptive and it is only recently that there has been a shift to synthesizing this information in terms of faunal and ecological complexity. The problem is further aggravated by the paucity of information relating to world ecosystems in the late Mesozoic and early Cenozoic. However, to arrive at a reasonable interpretation of the evolution of the Phyllostomatidae as well as that of the Chiroptera as a whole, one must at least be aware that their adaptive radiation progressed as an integral part of developing global ecological complexity.

Based on known fossils, the chiropteran grade was fully established in the early Eocene. Reasonable conjecture might project the origin of the group back as far as the early Paleocene or perhaps even into the late Cretaceous. At that point in geologic time, the angiosperm radiation was in its initial stages (Axelrod,

1952, 1970). Also, by the close of the Cretaceous, the anthophilous insect orders Coleoptera, Diptera, and quite probably the Lepidoptera (principal food resources of insectivorous bats) were well established in an evolutionary and ecological sense (Leppik, 1957, 1960; Baker and Hurd, 1968). In addition, eutherian and metatherian mammals were differentiated and both were expanding into numerous terrestrial niches.

If tooth morphology is any indication, most of the terrestrial niches, open to mammals, were geared to insectivory or some form of carnivory, although generalized herbivory would certainly have been within the functional potential of these small vertebrates. It is not difficult to visualize the chiropteran ancestry as having taken the form of small arboreal insectivores that may have possessed gliding membranes.

The argument for an arboreal ancestor as opposed to a strictly terrestrial ancestor seems obvious in light of the fact that all volant mammals normally launch from trees or heights above the ground. The transition from gliding to a movable wing could have progressed by way of elongation of the digits and interconnected membranes to increase the surface area of the patagium. The patagial arrangement possessed by living Dermoptera may resemble an early stage through which the chiropteran ancestor passed. It seems reasonable to suspect that digital elongation would have reached a point of diminishing returns in that further progression would have produced an ungainly and clumsy structure that necessitated movement as a wing rather than use as a fixed gliding device. [It should be noted here that birds and the recently described giant pterosaur (Lawson, 1975*a*, 1975*b*) apparently achieved greatly elongated wings by fusion and elongation of nondigital elements or elongation of a single digit with broad-based articulations, respectively.] Having successfully traversed this critical point in wing development, apparently by simply utilizing the existing dorsal and ventral thoracic musculature to drive the wing (Vaughan, 1970*a*, 1970*b*, 1970*c*), bats were well on their way to occupying an aerial insectivorous niche. Further refinements of the wing probably related to such parameters as maneuverability and speed.

The arguments to support the conjectured insectivory of the chiropteran ancestor may be regarded as open to question. As noted above, this general assumption is based on the morphology of the dental arcade of known fossil bats. The primitive tribosphenic dentition of eutherian-metatherian mammals was modified in the earliest bats to a dilambdodont condition with a marked W-shaped ectoloph. This configuration, which allows an increase in the number of shearing facets on the postcanine dentition, is generally associated with insectivory (or carnivory) in living bats as well as in living insectivores such as shrews and moles. The point to be made here is that whereas an arboreal habit seems requisite for the development of chiropteran flight, insectovory, in and of itself, does not. Surely, niche partitioning would have played as integral a part in the various mammalian adaptive radiations in the late Cretaceous or early Paleocene as it has in contemporary ecosystems.

With this in mind we might ask the question, why do animals occupy an arboreal niche to begin with? If living forms are any indication, we might con-

sider spatial segregation of such parameters as nesting and roosting sites, escape from terrestrial (nonarboreal) predators, and the utilization of such food resources as insects or other small organisms gleaned from branches and foliage, seeds, fruits, flowers, and the like. All of these variables would have been important to the chiropteran ancestor, and, certainly, the utilization of various food items (omnivory) would have been well within the potential of their tribosphenic dentition.

The foregoing discussion points out the evolutionary impetus for the chiropteran grade. It is relevant to our consideration of the evolution of the Phyllostomatidae (a group that exploits many feeding strategies) because it establishes the rationale and potential of the arboreal niche with regard to chiropteran evolution. Although insectivory, in the form of foilage gleaning or perhaps aerial insectivory, may have been important to the chiropteran ancestor, certainly opportunistic carnivory or even frugivory (utilization of fruits, seeds, and flowers) would have been possible. The latter is especially important considering the degree of dental specialization and other anatomical departures from the chiropteran norm seen in living pteropodids (apparently exclusive frugivores and the only bats other than phyllostomatids to utilize this food resource). On this basis alone and without a great deal of conjecture it would be possible to postualte diphyly, or at least an early dichotomy, for bats with respect to the two distinct lineages—Megachiroptera (Pteropodidae) and Microchiroptera (all other living families of bats).

Phylogenetic Relationships of the Chiroptera

Judgements as to the phylogeny and evolution of major groups of bats have been mostly intuitive and based on features exhibited by living species. Hill (1974), in his description of the new bat family Craseonycteridae, warned of the inherent difficulties and dangers of this practice. With respect to bats, the problem historically has involved the assessment of the degree of specialization of the flight mechanism and the dental arcade; other systems most certainly could be added in this consideration, but, to date, few have been examined.

Whether rightly or wrongly, if we are to proceed with an interpretation of chiropteran phylogeny based on living taxa and the meager sample of fossil representatives, we must establish an inference as to the nature of the prototype. The recent description of *Icaronycteris index* from the early Eocene of Wyoming (Jepsen, 1966, 1970; Russell and Sigé, 1970; Segall, 1971) has provided chiroptologists with a tantalizing insight into the prospective chiropteran prototype. *Icaronycteris* along with *Paleochiropteryx*, *Archaeonycteris*, *Cecilionycteris*, and *Ageina* establishes the nature of a world-wide paleochiropteran grade in early to middle Eocene times.

Cranially, the Paleochiroptera resembled tupaiids in general shape, although the braincase may not have been as inflated. The facial portion of the cranium was long and tapered distally. The premaxillaries of *Icaronycteris* appear to have been fused, although Jepsen (1970) claimed they were not united at the midline. The zygomatic plate was broad and the zygoma were well developed. There is no

indication of a postorbital bar on any of the paleochiropteran fossils. The dental formula was i 2-3?/3 c 1/1 p 3/3 m 3/3. The incisors were well developed and the premolars exhibited a reduction in size from posterior to anterior. The molars were typically tribosphenic and dilambdodont, with a W-shaped ectoloph and small hypocone on the upper teeth. The lower molars had well-developed talonids. All molar cusps and associated commissures were high and contributed to the complex of shearing facets so characteristic of insectivore dentitions.

The wing of paleochiropterans was fully developed, but primitive in most aspects. The globular head of the humerus was the most prominent feature of the proximal portion of this bone and the greater tuberosity was not particularly enlarged and did not extend proximal of the head of the humerus. Contrary to Jepsen (1966), I doubt that there was a "secondary articulation" established between the greater tuberosity and the supraglenoid region of the primitive, yet chiropteran, scapula (Smith, 1972). Distally, the humerus was rather primitive, with a short medial process and generalized trochlear and capitular surfaces. The radius appears to have been typically chiropteran, and, judging from the distal articulation of the humerus, there were no special locking facets present in the elbow region; disjointing stresses developed during flight in this region were probably prevented by muscular and ligamentous binding. The ulna of *Icaronycteris* was not fused with the proximal portion of the radius and, albeit reduced in size, it appears to have been nearly complete, resembling the condition found in megachiropterans (Pteropodidae). The first digit (thumb) of *Icaronycteris* was large and apparently free of the patagium, and the second digit terminated with a claw, again resembling the Megachiroptera. Although some phalangial elements are missing from all available fossils, the wing apparently was broad, of low aspect, and without any special tip modifications (Findley *et al.*, 1972). The degree of sacral fusion to the pelvic region in paleochiropterans was somewhat less than that which occurs in either the Megachiroptera or Microchiroptera. The head of the femur was large and globular and set between the flangelike greater and lesser trochanters. *Paleochiropteryx* had a well-developed calcar, whereas the remaining paleochiropterans apparently did not, although this absence may be an artifact of preservation. The tail was long and slender in *Icaronycteris* and *Paleochiropteryx*. I suspect that *Archaeonycteris* also possessed a long tail.

The paleochiropteran grade, as exemplified by the Eocene fossils, was primitive and generalized in most respects. There is little doubt that these bats were insectivorous, but their capacity for acoustic orientation remains questionable (Segall, 1971). With further refinements in the wing, for speed and maneuverability, and specialization of the cochlear region, for acoustic orientation, the Microchiroptera are easily derived from the paleochiropteran grade as characterized above. I suspect that such divergence occurred in the Paleocene.

The question concerning the relationship of the Megachiroptera and the paleochiropteran grade is not so easily resolved. Meschinelli (1903) described *Archaeopteropus transiens* from the early Oligocene of Italy. Meschinelli, along with Andersen (1912), Revilliod (1922), and Dal Paiz (1937), regarded *Arch-*

aeopteropus as representing the oldest member of the Megachiroptera. This assignment is based primarily upon similarities of wing morphology, because Revilliod (1922), Russell and Sigé (1970), and Slaughter (1970) have pointed out that the dentition of *Archaeopteropus*, which is badly fragmented, more closely resembles that of the Microchiroptera in appearance. I suspect that *Archaeopteropus* represents a further differentiation of the paleochiropteran grade and perhaps is not at all related to the Megachiroptera. The distinctness and marked departure of megachiropteran dentition from that of the Microchiroptera, as well as from known Tertiary fossils, suggests to me that this group of bats had their origin much earlier in the paleochiropteran grade or perhaps, as noted above, separately from an insectivorous ancestral stock.

It is important to point out the rationale for weighting dental morphology, in deference to wing morphology, at this level of interpretation of chiropteran evolution. Since the Oligocene, there appears to have been relatively little variation in the dental morphology of the Microchiroptera; the greatest departure from the basic dilambdodont condition is seen in the phyllonycterine and desmodontine phyllostomatids. The reduction and modification of the dentition in these two subfamilies seems to be the predictable consequence of a highly specialized feeding strategy and in both cases the dental pattern is traceable to the "primitive" dilambdodont condition (Slaughter, 1970). The degree and consistency of difference of the megachiropteran dentition as well as the apparent total absence in living or fossil taxa of any dentition remotely similar to the dilambdodont condition, further suggests a rather lengthy separation from the paleochiropteran ancestor. [Slaughter's (1970:77, fig. 1) argument for a single divergence of the Microchiroptera and Megachiroptera from a paleochiropteran prototype based on supposed similarity of the dentitions of *Archaeopteropus*—see comment above—and *Harpyionycteris* is weak.] On the other hand, marked differences in wing morphology might not be expected. The retention of a "primitive" wing by megachiropterans may simply reflect the adequacy of this structure to the habit of these bats; whereas, the wing of microchiropterans has been modified to provide greater maneuverability or speed, thereby facilitating further partitioning of the insectivorous niche. Therefore, with regard to the Microchiroptera, the departure from the paleochiropteran prototype had to do more with refining the wing for maneuverability and speed and with less emphasis on modifying the dental morphology. Among the Microchiroptera, the phyllostomatids illustrate the greatest diversity in dental modification and this appears to have taken place since the Oligocene as will be discussed beyond.

The Microchiroptera, no doubt, have their origin within the paleochiropteran grade. Twenty-one genera (age and geographic location in parenthesis) occur as Tertiary fossils and are assignable to the following six living families (Revilliod, 1922; Stirton, 1931; Lawrence, 1943; Simpson, 1945; Galbreath, 1962; Russell and Sigé, 1970; Slaughter, 1970; Smith, 1972; Sutton and Genoways, 1974): Emballonuridae—*Vespertiliavus* (Eocene-Oligocene, Europe); Rhinolophidae—*Palaeophyllophora* (Eocene-Oligocene, Europe), *Paraphyllophora* (Eocene-Miocene, Europe), *Palaeonycteris* (Oligocene, Europe), *Rhinolophus* (Eocene-Recent, Europe), *Pseudorhinolophus* (Eocene-Oligocene, Europe), *Hipposideros*

(Eocene-Recent, Europe); Megadermatidae—*Necromantis* (Eocene, Europe), *Miomegaderma* (Miocene, Europe), *Provampyrus* (Eocene-Oligocene, Africa); Phyllostomatidae—*Notonycteris* (Miocene, South America); Vespertilionidae—*Stehlinia* (Eocene-Oligocene, Europe), *Nycterobius* (= *Revilliodia*) (Eocene-Oligocene, Europe), *Samonycteris* (Miocene? Pliocene, western Asia), *Suaptenos* (Miocene, North America), *Miomyotis* (Miocene, North America), *Ancenycteris* (Miocene, North America), *Oligomyotis* (Oligocene, North America), *Myotis* (Oligocene-Recent, Europe), *Simonycteris* (Pliocene, North America); Molossidae—*Tadarida* (= *Nyctinomus*) (Oligocene-Recent, Europe). In addition, there are several genera of such fragmentary remains that familial assignment is not possible at this time. From this, it is evident that most of the major families of Microchiroptera were well established at least by middle Oligocene or Miocene.

It seems to be generally agreed upon that the majority of the Microchiroptera originated in the Old World. This thesis is supported by the middle Tertiary occurrence of the Emballonuridae, Rhinolophidae, Megadermatidae, Vespertilionidae, and Molossidae in European deposits. With the exception of the Megadermatidae, which apparently has no living representative in the Palearctic (temperate Eurasia), all of the above-listed families have differentiated in, and presently occur in, all major zoogeographic regions of the Old World. It is noteworthy that the differentiation of these five families, as well as the remaining five in the Old World (Rhinopomatidae, Craseonycteridae, Nycteridae, Myzopodidae, and Mystacinidae), has proceeded along the theme of insectivory or, in several cases, carnivory or piscivory (for example, *Megaderma*, *Macroderma*, and, perhaps, *Cardioderma*). Of these 10 Old World families, only three (Emballonuridae, Vespertilionidae, and Molossidae) also have adaptively radiated in the New World, the emballonurids being confined there to the Neotropics.

Although it has not been precisely stated, an emballonuroidlike ancestry generally has been accepted as the base for the Microchiroptera (Fig. 1A). Seemingly, this hypothesis is based more on the apparent antiquity of the group rather than any particular set of primitive characteristics. Certainly, the long and slender free tail of *Rhinopoma* is reminiscent of a condition noted in several paleochiropterans. However, the trend toward facial shortening by reduction in size and number of premolars, rostral inflation, unfused and unique form of the premaxillaries, trend toward complicated osseous processes on and posterior to the dorsonasal plate, complicated basisphenoidal pits, and specializations of the humerus (both proximally and distally) suggest a somewhat more specialized state for these bats than would be expected for an ancestral group. A further corollary of the hypothesis is that the New World noctilionids, mormoopids, and phyllostomatids evolved from an Old World emballonuroid migrant. The Neotropically endemic natalids, thyropterids, and furipterids apparently were derived somewhat later from a vespertilionoid stock, which in turn had evolved from the emballonuroid complex.

Until the discovery of *Icaronycteris index* (Jepsen, 1966), which verified the existence of a world-wide paleochiropteran grade, the foregoing hypothesis would not have been totally untenable. With *Icaronycteris*, more light is shed, albeit dim, on the question of early chiropteran phylogeny, and it now becomes

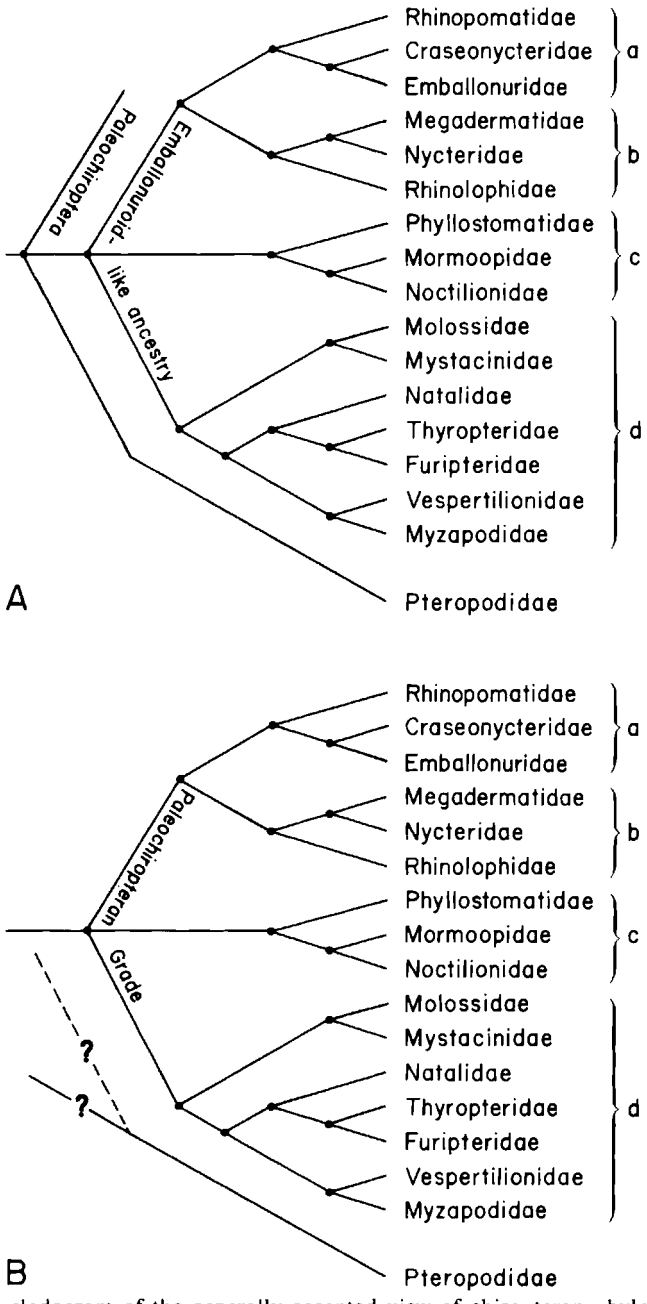

FIG. 1.—A, cladogram of the generally accepted view of chiropteran phylogeny with the Microchiroptera derived from a common emballonuroidlike ancestry. B, an alternative proposal for chiropteran evolution with several microchiropteran lineages being derived, independently, from a world-wide paleochiropteran grade and the Megachiroptera (Pteropodidae) derived either separately from an insectivorous stock or early from the paleochiropteran grade. a, Emballonuroidea; b, Rhinolophoidea; c, Phyllostomatoidea; d, Vespertilionoidea.

possible to suggest an alternative to an exclusively emballonuroid ancestry of the Microchiroptera, at least in the New World. This alternative hypothesis would be to recognize a paleochiropteran grade as a source from which several lineages of Microchiroptera adaptively radiated (Fig. 1B).

In the consideration of the phylogeny of the New World bats, especially noctilionids, mormoopids, and phyllostomatids, the above proposition is of paramount importance. The discovery of *Notonycteris magdalenesis* (Savage, 1951, from the late Miocene of Colombia) indicates that phyllostomatids were well established in an evolutionary sense in the late Tertiary. The oldest emballonuroids from the Quercy fauna (Eocene-Oligocene of Europe) were not markedly dissimilar from modern species of that family. The amount of time involved to account for the magnitude of anatomical differentiation of the phyllostomatids from an emballonuroidlike ancestor, a migrant from the Old World, seems to shift unduly the whole evolutionary sequence of the Microchiroptera to a much earlier and as yet undocumented age. It is equally plausible to suggest a separate and independent radiation of these three unique New World families from the paleochiropteran grade present in the early to middle Tertiary of the New World.

In further support of the alternative hypothesis, a consideration of the overall anatomical adaptation to a particular feeding strategy is relevant. With regard to the Microchiroptera, some varied modes of insectivory (or carnivory) apparently were the initial impetus for the differentiation of the various families. I think it is important to note that it is only in the New World tropics that alternative microchiropteran feeding strategies such as frugivory, nectarivory, and sanguivory developed.

It could be argued that, in the Old World, the various frugivorous, nectarivorous, and other similar niches were already occupied by the Megachiroptera. This, of course, is entirely possible, but it is not consistent in an evolutionary sense to invoke an adaptive potential for an emballonuroidlike ancestor in the New World (where alternative feeding niches apparently were available) and not to consider the same potential as likely in the Old World tropics. Therefore, it seems reasonable to expect that alternative feeding strategies would have been expressed, even in a minor way, in the adaptive radiation of Old World microchiropterans. Yet, the oldest microchiropteran fossils from the Old World now available for interpretation as well as the entire Old World microchiropteran complex, are specialized for insectivory or a related feeding strategy.

The argument for ecological competitive exclusion of the Microchiroptera by the Megachiroptera for frugivorous and nectarivorous feeding niches in the Old World also seems weak. If behavior of living representatives of both groups and the mode by which food resources are partitioned is any indication of past history, then, indeed, the availability of alternative feeding niches to Microchiroptera in the Old World tropics is to be expected. This thesis is proposed on the basis that the nonacoustically orienting megachiropterans, facultatively, utilize the food resources (fruits, flowers, nectar, and pollen) during the twilight (crepuscular) period, thereby leaving these resources available during the nocturnal hours for acoustically orienting microchiropterans.

Smith (1972), in considering the phylogenetic relationships of the Mormoopidae, suggested that the Phyllostomatidae, Mormoopidae, and Noctilionidae were intimately related to the extent that they might have been derived from common ancestry. This relationship is supported on the basis of similar cranial and postcranial skeletal morphology as well as on similarities of the soft anatomy. The anatomical similarities of the phyllostomatids with these two families is especially pronounced if one considers the subfamily Phyllostomatinae. With regard to the three families, the phyllostomatids are the most divergent, with the mormoopids being somewhat intermediate between noctilionids and phyllostomatids in this regard (Fig. 1). This divergence simply may be a reflection of the diversity in feeding strategies utilized by the latter.

Relationships within the Phyllostomatidae

The adaptive radiation of the Phyllostomatidae apparently was a response to exploit the various frugivorous niches in the New World tropics. One subfamily, the Desmodontinae, developed the unique feeding strategy of sanguivory. In addition to these specialized strategies, some members of the family, particularly the phyllostomatines, pursue the more typical chiropteran feeding strategy of insectivory and, in several instances, carnivory and omnivory. The family as currently understood is divided into six (perhaps seven) subfamilies: Phyllostomatinae, Glossophaginae, Carolliinae, Phyllonycterinae, Stenodermatinae (here including the Sturnirinae), and Desmodontinae. This classification is traditionally based mostly on dental morphology.

The phylogenetic relationships within the family are complex and are not well understood at this time. Part of the confusion may be due to similar, but unrelated, adaptations to similar feeding strategies. The phyllostomatines are generally considered to represent the most primitive of phyllostomatid subfamilies. The dental arcade of these bats shows the least amount of modification when compared to other subfamilies. Slaughter (1970) suggested the prototypic dentition of the phyllostomatids would have had a formula of i 2/2, c 1/1, p 2/3, m 3/3, which is found in most living members of the subfamily. The upper molars had well-pronounced and W-shaped ectolophs, a characteristic of insectivorous, piscivorous, and carnivorous bats. As in noctilionids and mormoopids, the W-shaped ectoloph on the upper molars of phyllostomatines extends at least half the width of the tooth and the protocone-hypoconal shelf is not particularly broadened. In addition, P3 and p3 probably were not much reduced in size in the prototyptic dentition.

In comparing *Notonycteris magdalenensis* with other phyllostomatines, Savage (1951) recognized several groups of genera within the subfamily. He distinguished these primarily on the configuration of the cusps on the cheekteeth. In one group, he included *Notonycteris*, *Chrotopterus*, and *Vampyrum*, which he found to differ strikingly from *Phyllostomus*. Walton and Walton (1968) and Smith (1972) also noted several groups of genera within the phyllostomatine bats based on various postcranial characteristics. In their *Macrotus* type, Walton and Walton (1968) included Savage's (1951) *Notonycteris-Chrotopterus-*

Vampyrum group; their second group was typified by *Phyllostomus*. Smith's groupings differed somewhat in composition, with *Micronycteris*, *Lonchorhina*, and *Macrotus* allied in one group and a *Phyllostomus* group including *Phyllostomus*, *Trachops*, *Phylloderma*, and presumably *Mimon*, *Tonatia*, *Chrotopterus*, and *Vampyrum*. Slaughter (1970) arranged the phyllostomatines in a slightly different fashion based on dentition. His most primitive group is represented by *Macrotus*; another group included *Phyllostomus*, *Lonchorhina*, and *Mimon*, whereas a third was composed of *Trachops* and *Vampyrum*. In his systematic study of the genus *Sturnira*, de la Torre (1961) proposed yet another association of phyllostomatine genera. He grouped *Vampyrum*, *Chrotopterus*, and *Trachops* as related lineages, but in his phylogeny he indicated their individual separation rather early in the evolution from an ancestral type. In another group, he placed the genera *Macrotus*, *Micronycteris*, *Tonatia*, *Mimon*, and *Phyllostomus*. Cytological, serological, and host-parasite data provide further contradictory results (Baker, 1967; Gerber, 1968; Wenzel *et al.*, 1966). From the foregoing, it is apparent that there are, at least, several lineages of phyllostomatines, although the number and constitution of each is not well understood at this time.

The chronology of the phyllostomatid radiation, is not known. Taking *Notonycteris* as a reference point, we might presume that the phyllostomatids have been evolving since the early Miocene or perhaps late Oligocene. From the phyllostomatine complex, the remaining subfamilies of phyllostomatids have adaptively radiated. The next group to be considered is the Glossophaginae, by virtue of the fact that they have been recently examined by Phillips (1971) from an evolutionary point of view.

The glossophagines are small to medium-sized phyllostomatids with a reduced dentition, noticeably elongated nose, and extensible tongue—all adaptations for a soft-fruit and nectar feeding strategy. These bats can be considered as ecological equivalents of hummingbirds and perhaps have been influenced by similar selective factors, resulting in hovering flight, elongated rostral regions, and other unique features. Several genera (*Glossophaga*, *Leptonycteris*, and *Anoura*) also may include insects and other animal matter in their diets. Phillips (1971) investigated the dentition of glossophagines and noted that they, too, appear to comprise several distinct lineages. One of these groups is composed of *Glossophaga*, *Monophyllus*, *Leptonycteris*, *Anoura*, *Lonchophylla*, *Lichonycteris*, *Lionycteris*, *Hylonycteris*, *Scleronycteris*, and *Platalina*. This group seems to be related to the *Micronycteris-Macrotus* group of the phyllostomatines. Phillips' second group included *Choeronycteris*, *Choeroniscus*, and *Musonycteris* and appears to be allied with the *Phyllostomus* group. These two groups were characterized by Phillips on the basis of dental and basicranial features. Again, other evidence suggests contradictory arrangements. Baker (1967) indicated a closer karyotypic affiliation of *Leptonycteris* and *Glossophaga* with *Phyllostomus*, *Trachops*, and *Macrotus*, whereas *Choeronycteris* and *Choeroniscus* were found to resemble *Carollia*. On the other hand, Gerber (1968), reporting on immunologic and electrophorectic comparisons, suggested that *Choeronycteris* was

more closely related to *Phyllostomus* than to *Anoura*, *Leptonycteris*, and *Glossophaga*; the latter were considered by him to be more closely allied to *Carollia*, *Artibeus*, and *Sturnira*.

Walton and Walton (1968) did not recognize a dichotomy within the Glossophaginae; however, de la Torre (1961) did, but the composition of his two groups differs with the groupings of other investigators. He included *Lionycteris*, *Glossophaga*, *Lonchophylla*, and *Platalina* in one group and *Monophyllus*, *Anoura*, *Leptonycteris*, and *Choeronycteris* in the second. In addition, he derived the glossophagines, as well as the remaining subfamilies, from a prephyllostomatine ancestor. In my examination of the Mormoopidae (Smith, 1972), I found that the glossophagines, generally, more closely resemble the *Micronycteris-Macrotus* line. Furthermore, the distal end of the humerus suggested some affinity between glossophagines and the Carolliinae.

The phylogenetic relationships of the remaining phyllostomatid subfamilies is even less well documented than those of the above-mentioned subfamilies. As noted above, Phillips (1971), Gerber (1968), Smith (1972), and Slaughter (1970) suggested affinities between the Glossophaginae and Carolliinae, which, in turn, may be related to a *Micronycteris-Macrotus* lineage; Walton and Walton (1968) associated the Carolliinae with a *Phyllostomus* lineage.

All of the above investigators seem to agree that the Sturnirinae (here considered in the Stenoderminae) is allied with the Glossophaginae-Carolliinae line. Walton and Walton (1968) placed the sturnirines in association with the glossophagines, but derived this complex from their *Phyllostomus* type. Earlier, de la Torre (1961) placed the sturnirines in close association with the *Vampyrops*-like stenodermines, and argued against the separation of *Sturnira* (including *Corvira* and *Sturnirops*) as a separate subfamily (an arrangement also adopted by Jones and Carter, this volume). Slaughter (1970) agreed with de la Torre's proposition, but pointed out the relative uniqueness of sturnirine dentition.

The genus *Brachyphylla* has had a varied history of taxonomic affiliation. Some previous investigators (for example, H. Allen, 1898; G. M. Allen, 1939) have associated *Brachyphylla* with the Phyllonycterinae, whereas Gray (1866) erected a separate tribe for the genus. Dobson (1878) and Miller (1907) and most recent workers have treated this genus as a primitive member of the Stenoderminae. Silva-Taboada and Pine (1969), however, presented a strong case for relating *Brachyphylla* with the phyllonycterines based on osteological and behavioral characteristics, and host-parasite specificity. Slaughter (1970) alluded to a similarity between this genus and *Sturnira*, and proposed that these two genera, as well as the Glossophaginae and Stenoderminae, were collectively involved with some, as yet unclarified, common ancestor. He concluded by noting that *Sturnira* and *Brachyphylla* appeared to be equally distinct from the stenodermines.

Miller (1907) associated the endemic (and probably autocthonous) Antillian subfamily Phyllonycterinae with the Stenoderminae and most recent investigators have preserved this association. On the other hand, Slaughter (1970) suggested that with little dental modification, the glossophagines could have given rise to this group. Walton and Walton (1968) allied the phyllonycterines most closely with their *Macrotus*-type group.

The Stenoderminae represent the primary frugivorous members of the family. Adaptive radiation in this subfamily apparently has proceeded along the lines of partitioning this abundant and diverse food resource. The relationship of stenodermines with other phyllostomatids is difficult to ascertain. Slaughter (1970) noted their dental similarity with the Glossophaginae but he also mentioned similarities with *Macrotus* and *Phyllostomus*. The humerus of stenodermines is much more generalized than that possessed by glossophagines and more closely resembles that observed in the *Phyllostomus* line (Smith, 1972). I suspect the stenodermines differentiated rather early from the phyllostomatine stock and perhaps from the *Phyllostomus* lineage.

Within the subfamily Stenoderminae, there appear to be at least two, perhaps three, lineages. One of these groups is typified by the generally long-faced *Vampyrops, Uroderma, Vampyressa, Chiroderma, Ectophylla, Mesophylla* and *Vampyrodes*, whereas the other is represented by the shorter-faced *Artibeus* and *Enchisthenes* along with the Antillean endemics, *Stenoderma, Ariteus, Ardops*, and *Phyllops*. If not included in the latter group, the genera *Centurio, Sphaeronycteris, Pygoderma*, and *Ametrida* might be considered as comprising yet a third group based on their rather uniquely modified dental arcade. These groupings are more or less reinforced by karyotypic data (Baker, 1970, 1973; Greenbaum *et al.*, 1975) and cranial and dental morphology (Starrett and Casebeer, 1968; Slaughter, 1970).

The final subfamily to be considered is the Desmodontinae. Perhaps because of their sanguivorous food habits and unique dental characteristics, the vampires have been considered by many investigators to represent a separate and distinct family, although related to the Phyllostomatidae. However, evidence presented by several recent workers (Griffin and Novick, 1955; Forman *et al.*, 1968; Machado-Allison, 1967; Smith, 1972) strongly suggests inclusion of the vampires as a subfamily within the Phyllostomatidae. The actual affinities of this subfamily are, nevertheless, obscure. Slaughter (1970) suggested that the desmodontines may have taken their origin from within the Carolliinae, possibly from an ancestor intermediate to *Carollia* and *Rhinophylla*.

From the foregoing account, it is obvious that there is a great deal of uncertainty and contradictory evidence associated with the evolution and phylogeny of the phyllostomatids—more, perhaps, than with any other chiropteran family. Whereas in most other families, evolution has proceeded as variations on a basic insectivorous theme, the evolution of the phyllostomatids has included this basic trend as well as adaptations to other feeding strategies such as nectarivory, frugivory, and sanguivory. Although there is some indication that each subfamily has had its own "feeding specialty," there apparently has been considerable overlap, which has led to widespread convergence within the family. Without additional fossil material from the Miocene and Pliocene, the degree to which such convergence has occurred will remain highly uncertain. A tentative phylogeny for the Phyllostomatidae is represented in Fig. 2. It is proposed simply as a point of departure for future investigations into the relationships of this family.

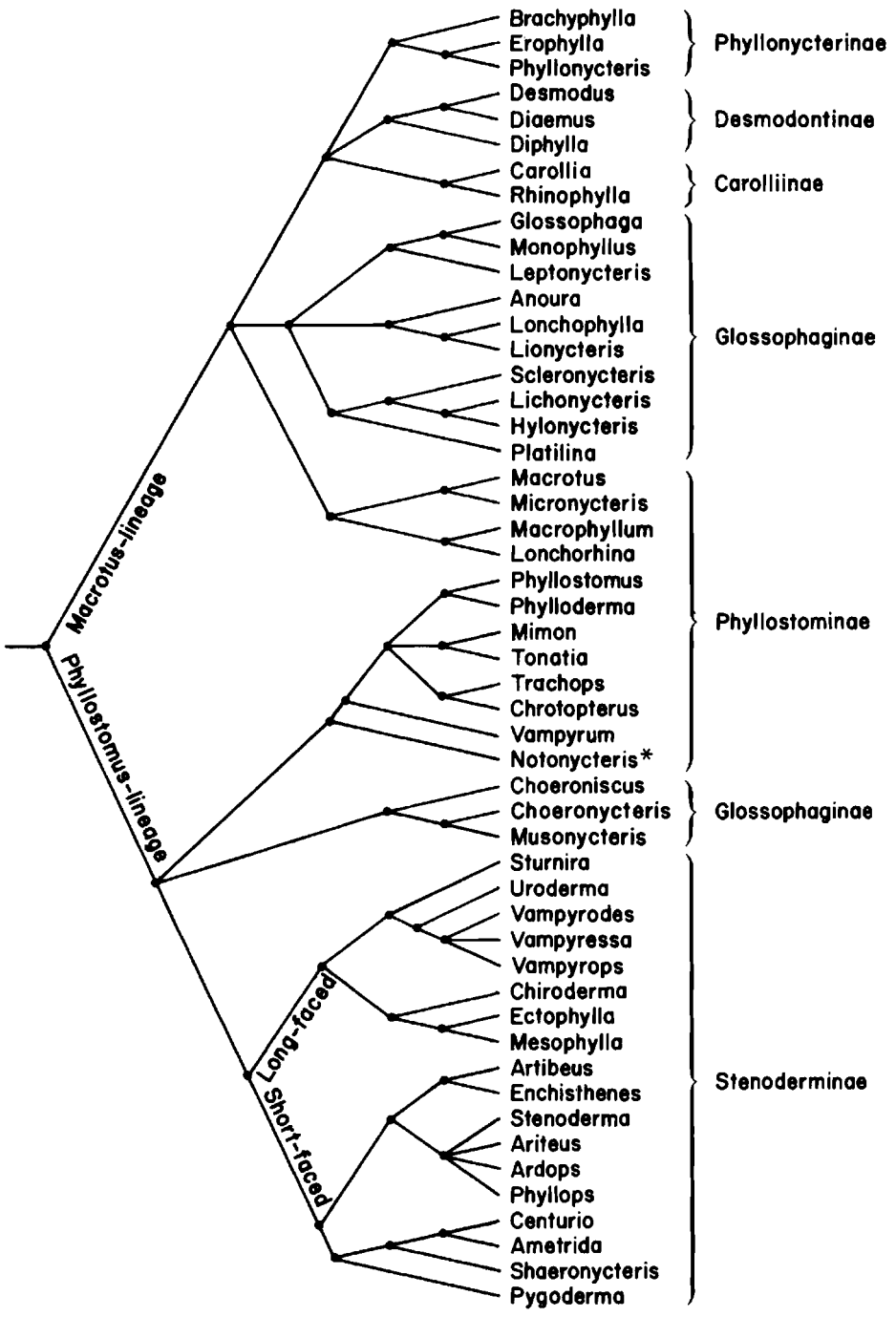

FIG. 2.—A cladogram showing a tentative phylogeny of the Phyllostomatidae. Because much of the evidence up to this time is contradictory and confusing, this phylogeny is proposed as a point of departure for future investigations. An asterisk indicates an extinct taxon.

Fossil Record of the Phyllostomatidae

The paleontological record of the family Phyllostomatidae is limited primarily to the late Pleistocene (LP) and sub-Recent (SR), although one fossil has been recovered from the Miocene (M). Most of the known fossils are representatives of extant species († indicates an extinct taxon). No doubt, modern quarry techniques for recovering small, delicate specimens and exploration in tropical regions will add to the following list.

Subfamily Phyllostomatinae

Macrotus californicus Baird

United States (*Texas*): cave in Terlingua district (LP), Cockerell, 1930.

Macrotus waterhousii Gray

Bahamas: Little Exuma Island (LP), Koopman, 1951; Great Exuma Island (LP), Koopman *et al.*, 1957.

Cuba: Daiquiri Cave (LP), Anthony, 1919; Camaguey Cave (LP), Koopman and Ruibal, 1955, Jagüey Cave (LP), Silva-Taboada, 1974.

Jamaica: Dairy Cave (LP), Portland Cave (LP), Williams, 1952.

Haiti: Cave near St. Michel (SR), Diquini (SR), Miller, 1929.

Puerto Rico: Cueva de Clara (LP), Choate and Birney, 1968.

†*Tonatia saurophila* Koopman and Williams

Jamaica: Wallingford Cave (LP), Dairy Cave (LP), Koopman and Williams, 1951.

Mimon cozumelae Goldman

Mexico (*Yucatán*): Spikul Cave (SR), Hatt *et al.*, 1953.

Phyllostomus discolor (Wagner)

Venezuela (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Phyllostomus hastatus (Pallas)

Venezuela (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

†*Notonycteris magdalenesis* Savage

Colombia (*Huila*): Univ. California Paleo. Loc. V4517, vicinity of Villavieja (M), Savage, 1951.

Chrotopterus auritus (Peters)

Mexico (*Yucatán*): Lara's Cave (SR), Spikul Cave (SR), Hatt *et al.*, 1953

Subfamily Glossophaginae

Glossophaga soricina (Pallas)

Mexico (*Yucatán*): Loltun Cave (SR), Coyok Cave (SR), Hatt *et al.*, 1953.
Venezuela (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Monophyllus redmani Leach

Cuba: Masones Cave (LP), Jagüey Cave (LP), Silva-Taboada, 1974; Camaguey Cave (LP), Koopman and Ruibal, 1955.

Jamaica: Portland Cave (LP), Williams, 1952.

HAITI: Diquini (SR), Miller, 1929.

PUERTO RICO: Cueva Catedral (LP), Anthony, 1918; Cueva Monte Grande (LP), Reynolds *et al.*, 1953; Cueva de Clara (LP), Choate and Birney, 1968.

†*Monophyllus plethodon frater* Anthony

PUERTO RICO: Cueva Catedral (LP), Anthony, 1917; Cueva de Clara (LP), Cueva del Perro (LP), Choate and Birney, 1968.

Leptonycteris nivalis (Saussure)

MEXICO (*Nuevo León*): San Josecito (LP), Jones, 1958.

Subfamily Phyllonycterinae

Brachyphylla cavernarum Gray

PUERTO RICO: Cueva Catedral (LP), Anthony, 1918; Reynolds *et al.*, 1953.

Brachyphylla nana Miller

CUBA: Daiquiri Cave (LP), Anthony, 1919; Camaguey Cave (LP), Koopman and Ruibal, 1955; Masones Cave (LP), Jagüey Cave (LP), Silva-Taboada, 1974.

JAMAICA: Dairy Cave (LP), Koopman and Williams, 1951; Portland Cave (LP), Williams, 1952.

HAITI: Cave near Atalaye (SR), Miller, 1929

Erophylla sezekorni (Allen)

BAHAMAS: Great Exuma Island (LP), Koopman *et al.*, 1957.

CUBA: Camaguey Cave (LP), Koopman and Ruibal, 1955; Masones Cave (LP), Jagüey Cave (LP), Silva-Taboada, 1974.

JAMAICA: Dairy Cave (LP), Portland Cave (LP), Williams, 1952.

Phyllonycteris major Anthony

PUERTO RICO: Cueva Catedral (LP), Cueva del Perro (LP), Choate and Birney, 1968.

Phyllonycteris poeyi Gundlach

CUBA: Daiquiri Cave (LP), Anthony, 1919; Camaguey Cave (LP), Koopman and Ruibal, 1955; Masones Cave (LP), Jagüey Cave (LP), Silva-Taboada, 1974.

HAITI: Crooked Cave (LP), Cave near Port-de-Paix (LP), Cave at Diquini (LP), Miller, 1929.

Phyllonycteris aphylla (Miller)

JAMAICA: Wallingford Cave (LP), Dairy Cave (LP), Koopman and Williams, 1951; Portland Cave (LP), Williams, 1952.

Subfamily Stenoderminae

Uroderma bilobatum Peters

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Vampyrops helleri Peters

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Chiroderma salvini Dobson

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Artibeus jamaicensis Leach

MEXICO (*Yucatán*): Lara's Cave (SR), Has Cave (SR), Loltun Cave (SR), Coyok Cave (SR), Spikul Cave (SR), Chacaljas Cave (SR), Hatt *et al.*, 1953.

CUBA: Daiquiri Cave (LP), Anthony, 1919; Camaguey Cave (LP), Koopman and Ruibal, 1955.

HAITI: Cave near St. Michel (SR), Diquini (SR), Miller, 1929.

PUERTO RICO: Cueva Monte Grande (LP), Anthony, 1918; Cueva de Clara (LP), Cueva del Perro (LP), Choate and Birney, 1968; Reynolds *et al.*, 1953.

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Artibeus cinereus Miller

MEXICO (*Yucatán*): Coyok Cave (SR), Hatt *et al.*, 1953.

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Enchisthenes harti (Thomas)

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Sphaeronycteris toxophyllum Peters

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

Phyllops falcatus (Gray)

CUBA: Daiquiri Cave (LP), Anthony, 1919; Camaguey Cave (LP), Koopman and Ruibal, 1955.

Phyllops haitiensis (J. A. Allen)

HAITI: Cave near St. Michel (SR), Cave near Atalaye (SR), Diquini (SR), Miller, 1929; Cave near EnCafe (SR), Miller, 1930.

†*Phyllops vetus* Anthony

CUBA: Daiquiri Cave (LP), Anthony, 1919.

Ariteus flavescens (Gray)

JAMAICA: Dairy Cave (LP), Williams, 1952.

†*Stenoderma rufum anthonyi* Choate and Birney

PUERTO RICO: Cueva de Clara (LP), Cueva del Perro (LP), Choate and Birney, 1968.

Subfamily Desmodontinae

Desmodus rotundus (Wagner)

UNITED STATES (*Texas*): Cave in Terlingua district (LP), Cockerell, 1930.

MEXICO (*Yucatán*): Loltun Cave (SR), Hatt *et al.*, 1953.

CUBA: Cueva Lamas (LP), Koopman, 1958.

VENEZUELA (*Aragua*): Cueva de Quebrada Honda (SR), Linares, 1968.

†*Desmodus rotundus puntajudensis* Woloszyn and Mayo

CUBA: Centenario de Lenin, Loma del Medio, Punta Judas, NE coast of Las Villas (SR), Woloszyn and Mayo, 1974 (these authors were uncertain about assigning Koopman's, 1958, specimen from Cueva Lamas to this taxon).

†*Desmodus stocki* Jones

UNITED STATES (*California*): Potter Creek Cave (LP), Hutchinson, 1967; (*Florida*): Reddick (LP), Gut, 1959, and Olsen, 1960; Arredondo (LP), Martin, 1972.

MEXICO (*Nuevo León*): San Josécito Cave (LP), Jones, 1958; (*México*): Tlapacoya (LP), Alvarez, 1972.

†*Desmodus* sp.

VENEZUELA (*Monagas*): Cueva del Guacharo (LP), (Clayton Ray and Omar Linares, personal communication)

[Paula Couto (1938) reported *Schizostoma* (= *Micronycteris*), *Lophostoma* (= *Tonatia*), *Vampyrus* (= *Chrotopterus*, *Tonatia*, or *Vampyrum*), *Phyllostoma* (= *Phyllostomus*), *Tylostoma* (= *Mimon crenulatum*), *Carollia*, *Lonchoglossa* (= *Anoura*), *Glossophaga*, *Chiroderma*, *Sturnira*, *Vampyrops*, *Artibeus*, *Desmodus*, "*etc.*," from Pleistocene cave deposits of Brazil. I have not included these in the above listing because he did not designate species and their determination would be difficult from the generic list that he presented. No locality information other than Brazil was given. In addition, there is a vague reference to phyllostomatid genera cited by Peter Lund and Herluf Winge from Brazilian Pleistocene caves.]

?Phyllostomatidae *incertae sedis*

Univ. California Mus. Paleo. No. 54572, ant. two-thirds of right p2 from UCMP loc. V-5847 in Big Cat Quarry, Cuyama Valley Badlands, Santa Barbara Co., California. *Age.*—early Clarendonian. James (1963) noted that this tooth was in the size range of *Phyllostomus*, *Chrotopterus*, *Vampyrum*, and *Notonycteris*, but admitted that generic assignment was impossible and familial assignment was conjectural.

UCMP No. 82144, left lower canine; UCMP No. 80324, edentulous and incomplete right dentary, from UCMP loc. V-6761 Branch Canyon Formation, Santa Barbara Co., California. *Age.*—Hemingfordian. Hutchison and Lindsay (1974) noted that these specimens resembled *Pteronotus* (family Mormoopidae), *Lonchorhina*, and *Macrophyllum*, but deferred generic assignment.

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COLLECTING TECHNIQUES

MERLIN D. TUTTLE

Phyllostomatids exhibit an unusual diversity in roosting and foraging behavior. Hence, while several collecting methods (such as mist-netting and trapping) are exceptionally versatile, even these fall far short of capturing all species under all circumstances. Because each technique results in selective capture of certain species while practically excluding others, faunal analyses should be based upon the widest possible variety of collecting methods. By contrast, ecological and behavioral studies of one or a few species should employ only those techniques best adapted to obtaining desired data while, at the same time, minimizing disturbance to the population.

This chapter provides information on means of locating phyllostomatids and their roost sites, and discusses those collecting techniques that have proven to be effective. For a summary of other methods not mentioned here see Greenhall and Paradiso (1968:8-15).

MATERIALS

Many materials for collecting bats may be placed in one of two categories—those employed at roosts and those used along flyways or at places where bats forage. However, other materials are useful in both kinds of situations and will be discussed first; equipment used primarily for specialized collecting will be dealt with later.

An electric headlight is essential for most types of collecting. The best light I have been able to find is the Justrite Headlight (obtainable from Justrite Manufacturing Co., 2061 N Southport Avenue, Chicago, Illinois 60614). This light has an adjustable beam and space to store spare bulbs behind the headlight reflector. A good power source is the alkaline Eveready battery, no. 520. A canvas battery holder can be carried on an army pistol belt.

Several kinds of holding cages have been described (Greenhall and Paradiso, 1968:20-21), but I have found it more convenient to hold captured bats in bags made of nylon army mosquito netting with tie strings near the top. Muslin bags may also be used. However, muslin is bulky and much heavier to carry, rots easily in tropical environments, and bats cannot be seen without opening the top of the bag.

Mist nets are the most versatile devices for collecting bats. They can be purchased from the following suppliers: Bleitz Wildlife Foundation, 5334 Hollywood Boulevard, Hollywood, California 90027; Eastern Bird Banding Association, Biology Department, Indiana University of Pennsylvania, Indiana, Pennsylvania 15701; Northeastern Bird Banding Association, 37 Old Brook Road, West Hartford, Connecticut 06117; and W. B. Davis, P. O. Box 3522, Bryan, Texas 77801. They are available in widths of 6, 9, 12, and 18 meters by 1.2 or

2.4 meters high, and are constructed of 30 to 70-denier thread in 25 to 36 millimeters or longer mesh. Various colors are available, but black seems to be most efficient for night use. The most versatile nets for catching bats have four shelves, are 6 or 12 meters wide and 2.4 meters high, and are constructed of 50 or 70-denier thread with 36-millimeter mesh (Handley, 1968:15-16). One should always sample one or a few nets from a given supplier before ordering more. It is wise to check each one for the following possible defects: 1) improperly threaded shelf strings, which cause uneven distribution of netting; 2) shelf strings that have become untied and must be rethreaded; 3) shelf strings of unequal length; 4) inadequate amount of netting between shelf strings; and 5) netting that is not soft and pliable. Also, the loops at the ends of each shelf string should be made of cotton because nylon loops tend to become untied easily.

A recently developed double-framed trap has been used under a wide range of conditions and has proven successful in capturing many temperate and tropical bats (Tuttle, 1974*a*). The bats collide with fine vertical wires and fall unharmed into a large canvas receptacle from which they are unable to escape. This trap is easily carried by one man, can be assembled or broken down in 45 minutes, and is particularly useful in studies that require rapid handling of large samples. At present these traps are not produced commercially, but a complete description with specifications for construction has been published (Tuttle, 1974*c*). Several earlier and less versatile traps also have been described (Constantine, 1958, 1962, 1969).

Other important items are a machete and gloves. In tropical areas, a machete with a 15 to 18-inch blade (and a belt sheath) is an efficient tool for clearing netting and trapping sites, for preparing poles for nets, and for chopping into roosts in small holes. A pair of leather gloves should be used when catching roosting bats by hand and for handling captured specimens.

Handling of Nets and Traps

Mist-netting and trapping are the two most effective methods known for collecting a variety of bats. Much of their success, however, is dependent upon knowledge of how and where to use them. Operational details are dealt with here, whereas factors influencing where and when to use nets will be discussed later.

Mist Nets

Preparatory to setting a mist net, appropriate poles must be obtained. In tropical rain forests, one rarely experiences difficulty in finding adequate saplings that can be cut into lengths of two and a half to three meters. These should be straight, stiff, and about five centimeters in diameter at the base. All twigs should be removed. A machete may be used to sharpen the larger end of each pole. Work in relatively dry areas may require carrying a supply of poles; telescoping aluminum poles and adjustable metal pole clamps are convenient.

When a suitable netting site has been found, a machete is used to remove sufficient vegetation and debris so that the net will not become tangled. At the same time, it is important not to remove too much vegetation, thus leaving the

net exposed and conspicuous. The goal is to allow barely enough space for the collector to pass freely along both sides without endangering the net, but no more. At windy sites, extra space should be allowed for billowing of the net.

In most tropical areas, poles can be driven into the ground by repeated jabbing and twisting. When several have been cut, it is best to select the heaviest pole with the hardest, sharpest point to make holes for the rest. Depending on the rigidity of the poles, holes should be angled so that erected poles lean slightly outward. This allows for bending from the inward pull of the net. When a pole is limber or inadequately anchored in the ground, guy lines can be used to hold it in place. In rocky river beds, it may be necessary to provide additional support by piling large rocks against the bases of the poles.

Before the first pole is finally secured, the loops of one end of the net are placed in proper sequence over the upper end. When a new net is first unpacked, the main loops, which fit over the poles, usually will be gathered in the center in two bunches in the correct order. It is important that these be separated carefully to avoid initial confusion. Next, an outside loop is found and the rest of the loops on that end are arranged in appropriate sequence over a finger, from which all are slipped over the end of the pole. The pole is firmly secured, and the net is unfolded until it is pulled tight to mark the spot where the second pole is to be placed. At this point, one person may hold the net off the ground while another prepares the hole. If alone, refold the net before making the hole, unfolding it only when ready to secure the second pole. Before slipping the loops over the pole, it is necessary to check the top shelf string to be sure that the net is not twisted, with the loops in reverse sequence. When possible, nets should be set and adjusted before dark, but they should not be opened on the poles until it is time to use them.

In the evening, when collectors tend their nets, they should be equipped with a headlight, a good battery, spare bulbs, holding bags, a pair of gloves, insect repellent, and spare string to repair broken shelf strings and to guy leaning poles. In some areas they may also wish to carry a gun; poisonous snakes, caiman, crocodiles, and large cats may be attracted to the squeals of trapped bats.

Nets should not be left unattended for long, and must be guarded almost constantly when set over trails and around villages where domestic animals and humans are likely to pass. Even in the absence of other problems, bats themselves will soon destroy an unattended net. Such large species as *Chrotopterus auritus*, *Phyllostomus hastatus*, or *Vampyrum spectrum* can completely ruin a net and escape in as little time as a minute. Also, the longer a bat struggles in the net the more difficult it is to remove. As a result, a netter should be careful not to set too many nets, as more bats may be caught than can be removed, leading to loss of both bats and nets.

As soon as possible after a bat strikes the net, the collector should grasp it with a gloved hand and determine from which side it entered. It should be held firmly in the gloved left hand (for a right-handed person) while the ungloved right hand is used to extricate the bat from the open side of the pocket, starting with the head. I usually try to remove netting from the bat's mouth first to pre-

vent further damage to the net, and then work back, freeing the wings and finally the feet. However, the reverse is sometimes more convenient.

Each net must be readjusted at regular intervals so that the bag does not move along the shelf strands, leaving tight places where bats bounce off or bunched places that they more easily detect. If rain or fog causes water droplets to collect, these should be shaken from the net as soon as possible. Also, leaves, twigs, and insects should be removed quickly before they tangle a net. Badly tangled sticks can be removed most easily if first they are broken into small pieces; large beetles should be disarticulated.

Even when one is careful, an occasional large bat will succeed in chewing through a shelf string and, as a result, a large section of net ceases to function. If possible, broken shelf strands should be rethreaded in daylight, but two experienced netters can accomplish the job in a few minutes at night. The net loops immediately above and below the broken string should be spread as far apart as possible and raised until the track of the broken string is roughly at eye level. A piece of woven nylon fishline of about the same diameter as the original string and a meter long should be tied to the end of the longest string so that this leader can be threaded easily without tension. The shelf string then is carefully threaded through about every fourth mesh along the original track. When the ends meet, one person holds the two strings to release tension (or an end loop is removed from its pole) while the other ties the splice in place (including a small piece of leader) so that the repaired shelf string is the same length as before. Holes in the mesh are not easily repaired, and after enough accumulate the net should be discarded or cut into smaller pieces.

A net should not be closed until all insects, twigs and other debris have been removed, after which all of the loops are pushed together near the upper ends of the poles. In areas where human interference is not a problem, nets may be left "closed" on the poles until the following night, but when they are removed it is important to keep the loops in order. I usually follow Handley's (1968:17) method of tying a piece of white string about 40 centimeters long to the top loop of each end. Before removing a net from its poles, the string at each end is threaded through the rest of the loops and tied. Next the loops are removed from one pole, and the net is folded by reaching out about a meter at a time to grasp the net, folding it back to the first hand again and again as one walks toward the other pole. Finally, the loops are removed from the other pole, tied, and the net is folded and stored in a small bag.

Traps

Traps generally are not broken down between settings, but if this is necessary, as for shipping, they are reassembled in the following manner. Each frame is assembled separately and bolted to the other using four threaded rods. The legs are bolted in place and the trap righted before the angled rods and wires are bolted to the top of each frame and carefully unrolled. The threaded rods for adjusting wire tension are extended as far as possible, and the botton angled rods are bolted to the bottom on each frame. Finally the threaded rods at the top are tightened to adjust wire tension.

Proper adjustment of trap frames and wires is essential. Much depends on the speed and angle of approach by bats. The trap should be vertical and perpendicular to the flight path. Traps are generally most effective when adjusted so that the two parallel sets of vertical wires are roughly seven and a half centimeters apart, although this distance may need to be varied for different conditions and kinds of bats. During initial testing of crude trap designs, I succeeded in capturing an impressive number of phyllostomatids (Tuttle, 1974*a*). However, all subsequent trap modifications were designed to increase vespertilionid captures, without consideration of phyllostomatids, and the wire spacing was increased from two centimeters to two and a half centimeters. A spacing of two centimeters or less, combined with increased elasticity of the springs, might prove advantageous for phyllostomatids. Regardless of spacing, the tautness of the wires should be proportional to the speed of the bats. Normally, wires should be adjusted so that they are barely tight. When bats escape by bouncing off the trap, wires should be loosened; when bats pass completely through the trap, both frames should be tightened. Captured bats are easily removed with gloved hands, and should be sorted into separate bags to avoid placing carnivorous species with other bats. Several thousand can be handled in an hour. Even though large numbers of bats do not damage traps, one must be constantly vigilant lest bats rapidly accumulate and suffocate before removal. Whenever a trap begins to catch more bats than can be removed conveniently, it can be turned sideways, carried out of the flight path, or covered on one side with a small canvas.

Capture Techniques

Roosts

Little is known about the ecological requirements of phyllostomatid bats, and there is a paucity of information available on roosting behavior. I selected 28 sources from which information pertaining to roosting habits was taken (Table 1). Pine (1972) was used as the sole source of material on *Carollia* due to prior confusion in identification. Walker (1964) is cited only when original observations could not be found. Sources are numbered (see parenthetical numbers in Literature Cited), and numbers of references cited appear in the appropriate places in Table 1. Species for which I was unable to find information on roosting habits are not included.

Early literature emphasized discovery of new species and seldom mentioned how or where bats were collected. Recently, the use of mist nets has enhanced knowledge of overall distribution and provided much ecological data. Nevertheless, netting has been so convenient that few researchers have been forced to look for roosting bats. Searches for roosts have been limited to a few obvious types of places. As a result, roosts in caves, houses, hollow trees, or culverts are often reported whereas those in foliage and other less evident places are not, leaving the roosting habits of even some common species unknown. With this bias in mind, I will provide suggestions for finding the types of roosting sites that have proven most productive.

Caves.—Caves may provide roosting sites for more different species of phyllostomatids than any other kind of shelter. Most caves are located in limestone,

TABLE 1.—*Known roosting sites of phyllostomatid bats. Numbers identify citations from the literature (see right-hand margin of cited literature); those in parentheses in the table indicate the observation or identity of species is in question.*

Species	In caves or tunnels	In hollow trees or logs	In buildings	In culverts or bridges	In or under large leaves or palm fronds	In foliage or under branches	Under overhanging roots or stream banks	In rock crevices	In hollow termite nests	Under fallen logs
Micronycteris brachyotis	8,12	8,12								
Micronycteris daviesi		27								
Micronycteris hirsuta		8,12,27	12	8						
Micronycteris megalotis	1,8,10[1] 28	8,10,12	8,12, 14,16	8,10, 12,20			1,27			11
Micronycteris minuta		8								
Micronycteris nicefori	8	8,U	12							
Micronycteris schmidtorum	28	16								
Micronycteris sylvestris	10,28	8								
Macrotus californicus	31			30						
Macrotus waterhousii	5,9,18, 26,28		5,9,26							
Lonchorhina aurita	4,8,12,16, 21,28			28						
Lonchorhina orinocensis								U		
Macrophyllum macrophyllum	4,12,28			29						
Tonatia bidens		8								
Tonatia carrikeri		1								
Tonatia nicaraguae									8	
Tonatia sylvicola		(27)							12, 22,27	
Mimon bennettii		1								
Mimon cozumelae	10,12,28			28						

TABLE 1.—*Continued.*

Mimon crenulatum		8,12,U	8						
Phyllostomus discolor	U[2]	8							
Phyllostomus elongatus		27							
Phyllostomus hastatus	8,12,27	8,12, 22,27	1,8, 12,27		8			27	
Trachops cirrhosus	1,4,10 12,16,28	8	12	28					
Chrotopterus auritus	6,10,28								
Vampyrum spectrum		8,14	14						
Platalina genovensium	21								
Glossophaga alticola	5								
Glossophaga commissarisi	18								
Glossophaga longirostris	1,8		1,8						
Glossophaga soricina	5,8,10,12, 18,28	8,12	8,10, 12,28	8,12,20, 27,28					
Lonchophylla concava	12								
Lonchophylla robusta	12								
Lonchophylla thomasi						14			
Monophyllus plethodon	25								
Monophyllus redmani	2,9,25								
Anoura caudifera	22	22							
Anoura geoffroyi	8,16,18, 21,27,28								
Musonycteris harrisoni					(28)[3]				
Choeronycteris mexicana	5,18		16,28			5			
Choeroniscus inca									23
Hylonycteris underwoodi	10,28			19					
Leptonycteris nivalis	5,6,10,28		29						
Leptonycteris sanborni	18			18					
Carollia brevicauda	20	20		20					
Carollia castanea	20	20				20			
Carollia perspicillata	20	20	20	20	20				
Carollia subrufa	20	20	(20)	20			20		

TABLE 1.—*Continued.*

Sturnira lilium	8,28	1,8,28	8	19,28				
Brachyphylla cavernarum	2		3					
Brachyphylla nana	26							
Uroderma bilobatum			4		1,4,8,12, 14,28			
Vampyrops dorsalis						24[4]	24	
Vampyrops helleri	28	8	8	28	8	24		
Vampyrops infuscus	24		24					
Vampyrops lineatus						29		
Vampyrops vittatus	(27)[5]						24	
Vampyrodes caraccioloi					8	8,13		
Vampyressa pusilla						11		
Chiroderma trinitatum	8							
Ectophylla macconnelli					22			
Artibeus aztecus	6,18,28							
Artibeus cinereus					8,13			1
Artibeus hirsutus	5,18,28		5					
Artibeus inopinatus			7					
Artibeus jamaicensis	2,8,9,10, 12,16,28	8,12, 18,28	8,10,12, 16,28	19	5,8,28	1,8,28	10[6]	
Artibeus lituratus	8,28	8	8	19	8,14	8		10
Artibeus phaeotis	28							
Artibeus toltecus	6,16		16		28			
Artibeus watsoni					15			
Ardops nichollsi						17		
Phyllops haitiensis			29			29		
Phyllops falcatus			29					
Centurio senex					28	8		
Sphaeronycteris toxophyllum	29[7]							
Erophylla bombifrons	2							
Erophylla sezekorni	9,26							
Phyllonycteris aphylla	9							
Phyllonycteris poeyi	26							

TABLE 1.—*Continued.*

Desmodus rotundus	5,8,10 12,18,28	8,10, 12,28	8,10, 12,28	8,28	10,28
Diaemus youngii	8,28	8			
Diphylla ecaudata	10,28				

U, author's unpublished observations (except *P. discolor* by James W. Bee).
[1]in an agouti burrow.
[2]in cavelike ruins.
[3]Villa's speculation.
[4]in Spanish "moss."
[5]recorded as *V. infuscus*, herein considered as conspecific with *V. vittatus*.
[6]beneath aerial roots of a strangler-fig on a tree trunk.
[7]data on specimen label indicates taken from cavity in ground.

and geological maps often prove helpful in locating potential areas of caverns. Natives generally can provide information about the larger caves, but many smaller caves also harbor bat colonies of great interest. To find these, one should scout particularly along bases of cliffs and in the area of sink holes, although any major limestone outcropping is worth checking.

Once a cave is located, it is important to understand that it may contain solitary as well as colonial species, and that either type may be encountered barely within the cave, in well-lighted areas. In fact some species, such as *Micronycteris megalotis*, are rarely found beyond the twilight zone. Solitary bats roosting near cave entrances are the most difficult to collect. One must approach and enter the cave slowly, with minimal noise. Each depression in the ceiling or hole in the wall should be approached cautiously, and care should be taken not to shine a harsh beam of light directly inside a potential roost. Also, before looking, listen. If several bats are together, they often can be heard in places where they would not otherwise be noticed. Species forming large colonies, however, generally prefer the inner areas of caves and can be heard or smelled well in advance. In addition to advertising their location, such bats also tend to be slower to fly and therefore easier to collect than are solitary kinds.

Hollow trees.—Many more tropical bats probably use hollow trees for roosting than is yet suspected. Table 1 indicates that 44 per cent of the species known from caves also have been found roosting in hollow trees. Although hollow trees may be found almost anywhere, I have been most successful in locating them in lowlands where flooding occurs. River banks and lagoons, therefore, frequently provide the best areas.

It has been my experience that common colonial bats such as *Carollia*, *Phyllostomus*, and *Saccopteryx* are most frequently found in large conspicuous cavities, whereas the rarer, often solitary, species tend to be found in hollows so small that they are rarely noticed. Openings of any size, origin, and location should be investigated. Many holes as little as five centimeters in diameter lead to cavities containing bats. Several species of *Micronycteris* are particularly attracted to such places, where they can be found singly or in groups of up to a dozen. I once collected a small colony of *Micronycteris megalotis* in a hollow tree reachable only by way of an animal burrow 50 centimeters in diameter, and several times found *Phyllostomus hastatus* roosting 10 to 15 meters above ground in hollow horizontal branches only 20 to 25 centimeters in diameter. Some phyllostomatids will actually "burrow" into soft decaying wood. I once found several *Mimon crenulatum* roosting together in a woodpecker hole 12 centimeters in diameter, in the dead trunk of a palm tree; the cavity was nearly completely full of rotting wood. Handley (1966:761) also took this species in a rotting tree stump. Undoubtedly, a number of other less commonly observed phyllostomatids occupy cavities that are equally difficult to find.

Buildings.—Although an impressive number of species has been recorded from buildings, the only phyllostomatids that I commonly found in buildings in Perú and Venezuela were *Carollia perspicillata* and, less frequently, *Phyllostomus hastatus* and *Glossophaga soricina*. The latter was found mostly in cellars and other structures that were made of concrete. Otherwise, particularly in towns,

one is much more likely to encounter molossids and vespertilionids; nearly every old church houses these.

Local inhabitants usually can give directions to at least a few houses where bats roost. Often, one can simply inspect for staining around places where the bats enter roosts, and they sometimes can be smelled or heard. Tile roofs, attics, and cavities between walls all are likely to be used as roosting sites, and any place that is dark or dimly lit and protected from frequent disturbance should be checked. In Perú, abandoned Indian huts with roofs thatched of palm frequently sheltered *Carollia* and *Phyllostomus.*

Culverts and bridges.—For overall convenience there is no better place to look for bats than in culverts and under bridges. The oldest structures are the most productive, particularly those with entrances or undersides largely obscured by vegetation. Under bridges, if bats are not initially seen or heard, one should cautiously proceed to check between cross braces, and particularly in expansion joints. For a detailed description of how to find roosts at bridges, see Davis and Cockrum (1963).

Large leaves.—At least 11 species have been found roosting under large leaves (Table 1), primarily those of the banana, *Heliconia,* and various species of palms. Of these, only one, *Phyllostomus hastatus,* is not a stenodermine. The best known users of large leaves are *Artibeus cinereus, A. watsoni,* and *Uroderma bilobatum.* According to Goodwin and Greenhall (1961:254, 262), these "tent-makers" roost in small colonies "under the cut leaves of palm trees and on the under side of banana leaves" where they make a "series of cuts across the pleated surface of a leaf, causing half of the leaf to bend at an angle to form a protected retreat." On Barro Colorado Island, *A. watsoni* chose the fronds of *Geonoma decurrens* and *G. binervia* (Ingles, 1953:267), whereas on Trinidad, *Uroderma bilobatum* preferred carat palm (*Sabal glaucescens*) leaves (Goodwin and Greenhall, 1961:254).

The only instance known to me in which a phyllostomatid definitely has been found roosting inside an unfurling leaf was reported by Starrett and de la Torre (1964:58). They collected two *Carollia perspicillata* in banana leaves where *Thyroptera tricolor* also roosted. The dead fronds that collect around trunks of palm trees also provide shelter for many bats, but these sites have received little attention. I have watched molossids and vespertilionids emerging from such places, and suspect that phyllostomatids also may utilize them.

Other foliage.—Although a number of stenodermines have been found in dense foliage or vines, they are usually encountered only by accident in these places because the abundance of such habitat makes it unnecessary for them to concentrate in large groups. Those I have encountered seemed to prefer places that were well shaded and protected from above by the foliage. Roosts may sometimes be recognized by chewed pulp, seeds, and other debris dropped by the bats.

Miscellaneous.—Some phyllostomatids frequent root ledges and rock crevices; *Tonatia* forms small colonies in hollow termite nests. *Micronycteris megalotis* was once found by accident in an agouti burrow about 26 centimeters in diameter (Hall and Dalquest, 1963:222), and Allen (1939:73) reported *Tonatia* from a rabbit burrow. Such sites, though difficult to locate, may be interesting and productive.

How to Collect at Roosts

In addition to the more general equipment already discussed, a bee smoker, hand net, and .22-caliber pistol are essential for collecting at many roosts. In the discussion that follows, it is assumed that at least two persons will be working together. In all collecting at roosts, it is vital to avoid alarming bats with unnecessary noise, vibration, or light.

Hand netting.—A hand net ideally should have a sturdy hoop about 40 centimeters in diameter attached to a 1.2-meter aluminum handle. If needed, additional sections of telescoping aluminum can be purchased for extending the handle to five meters. The bag should be made of nylon army mosquito netting, at least 75 centimeters deep, rounded at the bottom, and sewn at the top to heavy cloth fitting over the hoop. A piece of heavy plastic 18 centimeters wide should hang freely around the inside of the hoop, preventing climbing bats from escaping.

Hand nets are most frequently used at roosts in hollow trees, animal burrows, rock crevices, or caves. At a hollow tree, careful inspection should be made to determine the number and size of openings from which bats could escape. Each potential exit then should be covered with a net or somehow blocked. Many bats can be frightened into attempting to leave by pounding on the tree trunk with a rock. If that fails, a limber stick of appropriate length may be cut, leaving small branches and foliage intact at one end. This can be carefully inserted and twirled near the bats. If bats remain stubborn in their refusal to come out, a bee smoker can be used. A length of flexible tubing may be attached, if needed, to direct the smoke to a specific place. Emerging bats are caught in the hand nets, from which they are transferred to holding bags.

Hand-netting in caves is much more difficult. Especially near the entrance, each depression or crevice should be approached cautiously, with the headlight not aimed beyond the reach of the net. Frequently, an extra section of handle is required so that bats can be reached quickly before they become alarmed. When a colony is heard, the roosting bats should be approached by sound rather than by sight, with the headlight aimed at the floor just ahead. Speed is crucial inasmuch as many bats will fly as soon as possible after sighting an approaching light. Most collectors find it easier to wait until evening when emerging bats can be trapped or netted at the cave entrance.

Shooting.—Bats can be shot at roosts with a .22-caliber pistol and long rifle dust shot. Although such pistols frequently are bored smooth to improve the shot pattern, I have never found that to be necessary. The acceptable collecting range is roughly four to nine meters. For greater range, one can use a .32 or .410-caliber auxillary barrel and dust shot in a 16-gauge shotgun. The most frequent problem is that of shooting at too short a range, thus damaging specimens.

Shooting is best employed when collecting at sites that are easy to see from a distance and difficult to approach without alarming bats. Examples of such places are foliage roosts, cavities in cliff faces, overhanging roots, large caves, culverts, and bridges. A pistol also can be used in large hollow trees and in small caves, but there is danger of damaging the ears of the collector. Whenever

other options are available, shooting should be avoided, as some specimens may be damaged while others, which escape, may be needlessly injured.

Netting.—Nets can be effective in capturing bats emerging from roosts not easily covered by a hand net, and are especially important at bridges where small colonies may be difficult to approach. At a culvert, for example, one person tends the net, which is set to block one end, while another frightens the bats from the opposite end. Damaged nets can be cut to make one or more small nets, two to three meters long, which are handy at culverts. When not in use, short nets are easily rolled onto an aluminum pole.

Mist nets also may be employed in front of such roosting sites as buildings and caves during evening emergence. Frequently, bats occupying these places cannot be reached or forced to exit before their natural departure. When colonies are small, mist nets can be quite convenient; when large numbers are involved, however, nets often entangle hundreds of bats at a time and are ruined long before bats can be extricated.

Trapping.—Traps are particularly useful at entrances to caves containing large colonies. They may be set anywhere along the flight path of emerging bats, but the best place is often some distance from a roost entrance—for example, where bats normally enter foliage that can assist in obscuring the trap from detection. Prior observation of emergence patterns permits optimal trap placement. Frequently, however, traps simply can be set directly in front of a point of emergence or in a cave entrance; the area around the trap may be partially blocked with brush or netting.

Foraging Sites

At least a few foraging bats can be found almost anywhere at night in the tropics; however, some places are far more productive than others. The few examples presented here may be intuitively obvious; many additional possibilities become apparent only with experience. Often the best places are discovered only by careful observation at twilight or at night while searching with a headlight. Searches at night should include frequent pauses with the light turned off, listening for the sounds of falling fruit, flying bats, and the squabbling that occurs at major feeding sites.

Trails.—Most forest trails at least a meter in width are likely to be used by bats, particularly when the surrounding vegetation is both tall and dense. In the tropics, the best trails are those that lead from villages to gardens or plantations. While these trails are especially productive places for collecting frugivorous species, others connecting pastures or leading to livestock sheds are more likely to be used by vampires. The widest trails, especially short sections between clearings, are better for foraging insectivores.

Forest edges.—Bats forage and fly along the edges of most forested areas, but edges of small clearings within forests are best for collecting phyllostomatids, except when there are feeding or watering places in larger open areas nearby.

Streams.—Streams provide natural flyways, especially where surrounding forest is dense. Slow-flowing streams, three to 10 meters in width, seem to have

the most traffic. Swift mountain streams and large rivers frequently are less productive of phyllostomatids and, in the latter case, pose difficulties in collecting.

Ponds.—Isolated ponds in areas where there are no other sources of available water often attract bats in spectacular numbers and variety in the dry season. Other watering places, sometimes only a few centimeters in diameter, appear to be highly attractive to some stenodermines, even in the rainy season and in places where other water is abundant (Tuttle, 1974*b*). These sites are often well known to local native hunters who visit them in order to hunt tapirs (*Tapirus terrestris*), which also are attracted in unusual numbers.

Feeding sites.—Many phyllostomatids are best collected in proximity to their feeding places. Glossophagines visit many flowering trees and shrubs, the best of which may be found by watching hummingbirds; certain plants that attract these birds during the day are equally attractive to bats at night. Flowering banana and cashew trees are well worth checking.

Bats of the subfamilies Carolliinae and Stenoderminae are most commonly collected near fruiting trees or shrubs. Wild figs attract a variety of these bats in large numbers, and gardens containing fruiting bananas, guavas, papayas, or mangos also are excellent attractions. Especially in virgin forest, fruit-eating birds and monkeys often provide clues to additional food sources.

Vampires frequently are numerous around the borders of villages when chickens, dogs, or pigs are present. *Desmodus* is encountered most frequently near cattle or horses, whereas *Diaemus* and *Diphylla* are more likely to be found near poultry. The presence of vampires is easily confirmed by the presence of dried blood on the head and shoulder regions of livestock, or on perches where poultry roost at night.

Feeding areas of phyllostomatines seem to be more generalized and unpredictable, but I have nearly always succeeded in collecting *Phyllostomus discolor*, *P. elongatus*, and *P. hastatus* on small banana plantations in forested areas. Goodwin and Greenhall (1961:240) reported *P. hastatus* flying in groups of up to 100 to feed on the seeds of spacaia nut trees (*Lecythis zabucajo*), and that *Micronycteris megalotis* was attracted to fruiting guava trees (*op. cit.*, 228). I have most frequently collected other phyllostomatines such as *Chrotopterus*, *Mimon*, *Phylloderma*, *Tonatia*, and *Trachops* in natural clearings beneath a dense canopy of virgin lowland forest, where they appeared to be foraging. Such areas are found where undergrowth has been eliminated by wet-season flooding.

Highland passes.—A surprising number and variety of phyllostomatids can be collected as they fly through low places along ridges. These are most easily found along roads that follow ridges. At elevations between 1400 and 2800 meters, I have commonly collected such interesting genera as *Chiroderma*, *Enchisthenes*, and *Vampyrops*.

How to Collect at Foraging Sites

Shooting.—Though shooting at dusk or later with a shotgun and number 12 shot is an excellent method for collecting many emballonurids, noctilionids, vespertilionids, and molossids, this method seldom works well for obtaining

phyllostomatids. For shooting to be practical, bats must fly high enough to be seen against the horizon while there is still adequate light, and there should be relatively bare ground or water below so that downed specimens can be found. The foraging habits of only a few phyllostomatids fit these requirements. Some of the larger species, such as *Phyllostomus hastatus*, can be shot at dusk from a small boat as they attempt to cross rivers enroute to their feeding sites. They float and can be scooped from the river in a hand net. Large frugivorous species sometimes can be spotted with a headlight and shot while feeding.

Netting and trapping.—Many phyllostomatids have been collected efficiently only in mist nets and traps. Whereas nets have been used almost exclusively since the late 1950's, the potential of traps has received widespread attention only recently. Either nets or traps can be set at almost any place where bats are expected to fly, although they are not equally practical under all circumstances. Traps are especially convenient whenever large numbers of bats must be handled rapidly. They are not easily damaged by bats or other animals and do not require frequent attention unless exceptionally large numbers are being caught. Nets can be raised into the forest canopy, but the procedure is difficult and costly (Humphrey *et al.*, 1968). Traps, however, can be set easily in dense foliage on the ground or hoisted into the canopy without danger of becoming tangled. They are unaffected by wind, whereas a net must be set exactly perpendicular to even a light breeze or the netting quickly blows to one end, making the net virtually inoperable. The main disadvantages of traps are that they are much heavier than nets, and cover a smaller area.

Either nets or traps may be set at any of the previously discussed kinds of places, but much of the success in using these devices depends on the collector's ability to camouflage them. Many feeding sites involve flowering or fruiting trees where nets or traps are set as close in front of a tree as possible, or immediately beneath the lowest branches. Sometimes, however, nearby openings or trails used by approaching bats provide easier collecting sites. Along trails and streams, nets and traps should be set in the narrowest places, preferably where there are natural obstructions, such as fallen trees, that block all but a small space. Traps are particularly effective at such sites. Hanging vines, overhanging limbs, and sharp turns provide additional concealment. At ponds and small clearings, where larger areas must be covered, nets are more easily used and should be set around the edges parallel to the vegetation. Around native gardens and other similar sites, I frequently have strung as many as 10 12-meter nets end to end, alternating the loops from two nets on each pole, but such an array of nets must be manned by several people. If traps are to be used at these places, they must be set either where vegetation forces natural funneling of the bats or where artificial blocking at the sides can achieve the same end. Often the sides can be blocked by tying a strong line to the top of the trap on each side, running the lines to nearby trees. Leafy vegetation is then cut and hung from the lines. This is especially effective at the approaches to ponds or where traps are set over streams. At low passes along mountain ridges, nets are preferable, and several may be set end-to-end just below the crest where they blend with the steep hillside.

Effectiveness at all places will be increased by frequent changes of position to counter learning behavior of bats.

When choices are available, nets and traps should be set in the darkest places and at times when there is little or no moon. Usually, the first and last two hours of the night are most productive, but a few species are more likely to be caught at other times.

Techniques for luring bats.—There are two methods that have considerable potential for attracting bats to collecting sites. Many bats can be attracted to nets or traps when other bats are induced to call in distress. In general the smallest species make the best "callers." Often, the distress cries of a small bat will attract large species in addition to others of its own size, whereas a large species, such as *Phyllostomus hastatus*, calls its own kind while frightening most others away. On several occasions I have achieved excellent results by hanging a bag containing 20 to 30 quarreling bats of several species on the side of a bat trap in a place where no bats had been caught previously. I predict that taped recordings may someday prove invaluable for luring bats into nets and traps.

The less tested of the two techniques is the use of bait. At one locality in Perú, *Carollia* was so persistent in searching out my rat traps baited with banana that even those set beneath dense vegetation or fallen logs caught them. Although this was unusual, *Carollia* often was attracted to ripening stalks of bananas in native huts. I also have taken *Rhinophylla pumilio* in a banana-baited rat trap. Fruit, caged animals, or even caged insects could be hung behind traps set in places where bats would be forced to approach from the opposite side. It is quite possible that some glossophagines could be attracted to hummingbird feeders. Many phyllostomatids probably could be lured into baited bat traps.

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CARE IN CAPTIVITY

ARTHUR M. GREENHALL

In the past 50 years only about a dozen articles have appeared that dealt solely with care of bats in captivity. With the exception of the spectacular flying foxes and the vampire bats, maintenance of bats either as experimental animals or as zoological park exhibits has been neglected. Interest in bats as laboratory animals increased after 1953, mostly stimulated by discovery in the United States of rabies in insectivorous bats (Constantine, 1970). As it became evident that public health relationships existed between bats and man, attempts increased to study live bats under controlled conditions.

Valuable sources of the information included in this chapter have been unpublished manuscripts or papers in press. I have also included some personal observations where appropriate. I have reviewed most of the available literature, but despite active research interest, published information is woefully lacking for captive Chiroptera, particularly the Phyllostomatidae. Little or nothing is known about the care of insectivorous phyllostomatids. However, because a number of vespertilionids and molossids have been raised successfully on artificial diets, I have described diets, cage systems, and techniques for their husbandry, as a potential guide for the care of insect-eating phyllostomatids.

Phyllostomatid bats present a number of unusual maintenance problems. What these problems are, and how they have been or may be solved, is the topic of this chapter. This information is intended primarily for those who maintain bats in captivity for research or educational purposes and not for someone simply interested in keeping bats as pets.

TRANSPORTATION

Transportation of bats to the laboratory or zoo should be carefully planned. Because phyllostomatids are mainly tropical, transport time should be minimal, and the shipper must be aware that weather conditions may change rapidly from the hot lowlands to the cool uplands or from tropical to temperate latitudes. It is often possible to arrange for commercial carriers to take special intransit precautions with the animals being shipped. I have had excellent cooperation from airlines and shipping companies in keeping my bats away from extreme heat or cold or other potentially stressful situations.

Bats may be transported in metal cans, wire cages, light-weight wooden boxes, or in cardboard or plastic cartons. Most bats, unlike many other mammals, will not attempt to gnaw out of containers, but they can squeeze through incredibly small holes and cracks. Bats generally travel better individually than in groups, with each animal placed in a single compartment or in a light cloth bag within a rigid container. Vampire bats and carnivorous species should not be grouped with bats of other species. Care must be taken to avoid exposing bats to the sun, to provide proper ventilation, and to control temperature and humidity. Food

and water must be provided for long trips. All persons wishing to transport bats should be aware of the rules and regulations governing the national and international shipment of live animals.

On arrival, the shipping containers in which the animals are received should be either incinerated or thoroughly cleaned and sterilized to minimize contamination by disease organisms or parasites. If permanent living quarters are unavailable, cleaned temporary cages, such as those used for shipping, could suffice. The physical condition of every bat should be assessed upon arrival.

The Laboratory Environment

Temperature and Relative Humidity

Among the more important factors influencing the successful maintenance of bats are temperature and relative humidity. If possible, these should be controlled automatically. Under natural conditions bats are exposed to daily fluctuations of temperature and relative humidity; however, little is known about the optimum conditions for captive tropical bats. Nevertheless, a temperature of 20 to 25°C and a relative humidity of 70 to 75 per cent seems satisfactory for many species. Low humidities can be injurious to the wing membranes (Racey, 1972).

Uwe Schmidt (personal communication) maintains his animal room at a constant temperature of 27°C and a relative humidity between 65 and 75 per cent. This is satisfactory for *Phyllostomus discolor*, *Carollia perspicillata*, *Artibeus lituratus*, and *Desmodus rotundus*. Rasweiler and de Bonilla (1972:659) and Rasweiler and Ishiyama (1973:56-57) maintained their laboratories at temperatures between 21 and 28°C and a relative humidity between 55 and 92 per cent, which proved satisfactory for *Glossophaga soricina*, *Anoura caudifer*, *Phyllostomus discolor*, *Carollia perspicillata*, *Artibeus lituratus*, and *Sturnira lilium*. My bat laboratory in Trinidad was not air-conditioned. The daily temperature ranged between 21.1 and 29.4°C, and the relative humidity between 55 and 95 per cent, conditions undoubtedly suitable for *Glossophaga soricina*, *Phyllostomus discolor*, *P. hastatus*, *Vampyrum spectrum*, *Carollia perspicillata*, *Vampyrops helleri*, *Artibeus jamaicensis*, *A. lituratus*, and *Desmodus rotundus* in that many of these bats lived in the laboratory for several years.

The Desmodontinae do well under a variety of laboratory conditions. Wimsatt and Guerriere (1961:450) maintained *Desmodus rotundus* in an air-conditioned laboratory at temperatures between 20 and 25°C and a relative humidity between 30 and 65 per cent, which approximated temperatures and humidities previously recorded in México. They also observed that vampires in the laboratory tolerated higher relative humidities and short exposures to lower temperature, but that their tolerance of temperature above 25°C was poor. In Trinidad, Greenhall (1965*b*:442) kept *Desmodus* and *Diaemus* in a laboratory at temperatures between 21 and 29°C and an average daily relative humidity of 75 per cent. The colony of *Desmodus* and *Diaemus* studied by Dickson and Green (1970:38) in London was kept in quarters held at a constant temperature of 24°C during the

day but which cooled naturally to 21° during the night. The relative humidity was fairly constant at about 50 per cent. At an elevation of 2545 meters, where vampires do not normally occur in México, Schmidt and Greenhall (1972:243) attempted to maintain a laboratory temperature of between 25° and 30°C and a relative humidity above 55 per cent for *Desmodus*. At this elevation there were problems in controlling an acceptable temperature and relative humidity. Power failures, aggravated by the lack of a standby generator for emergency use, complicated matters. We normally used thermostatically controlled electric heaters and infrared heat lamps to maintain the temperature and cool mist electric humidifiers to control relative humidity. Uwe Schmidt (personal communication) reported *Desmodus* thrived in his animal room in Germany, which was maintained at a constant temperature of 27°C and a relative humidity of between 65 and 75 per cent.

Daily fluctuation in temperature and relative humidity can be monitored with a hygrothermograph. The thermograph readings should be calibrated with an accurate minimum-maximum thermometer; the hydrograph with a wet and dry-bulb hygrometer.

Ventilation.—There is practically no information on the importance of ventilation and circulation of air in laboratories housing bats. Pye (1967) cautions that many bat species are sensitive to draughts and overventilation should be avoided. In my experience, bats in poorly ventilated laboratories appear restless.

Light

Light appears to be an important factor in regulating the daily activities of bats (DeCoursey and DeCoursey, 1964). Uwe Schmidt (personal communication) claimed that a colleague investigating daily bat activity found that *Phyllostomus discolor*, *Carollia perspicillata*, and *Artibeus lituratus* died when kept continuously in total darkness for 10 days. Illumination is automatically controlled in many laboratories and 13 hours of light and 11 hours of darkness has been found to be satisfactory for *Phyllostomus discolor*, *Sturnira lilium*, and *Artibeus lituratus* (Rasweiler and Ishiyama, 1973), *Glossophaga soricina*, *Anoura caudifer*, and *Carollia perspicillata* (Rasweiler and de Bonilla, 1972), *Desmodus rotundus* and *Diaemus youngii* (Dickson and Green, 1970), and *Desmodus rotundus* (Schmidt and Greenhall, 1972). Many of the same phyllostomatids, except *Diaemus*, have been displayed successfully in a large simulated South American cave and tropical rain forest exhibit at the New York Zoological Park where, by varying the intensities of white, blue, green, and occasionally red light, the activity patterns of the bats were reversed. Vampire bats kept by Wimsatt and Guerriere (1961) were subjected to low-intensity illumination from light entering through two glass-brick windows and glass panel in a door. The bat cage itself further reduced the light because only the front was made of transparent material. Electric lights were turned on in the bat room only briefly when the cages were cleaned or the animals were being attended. No effort was made by the investigators to control the light regime because wild vampires are found in roosts receiving varying intensities of light.

Housing

The size and type of cage should reflect the requirements of the particular bats kept and the purposes of the investigators. The size of a cage or other enclosure and the number of animals to be housed should be planned carefully. Some phyllostomatids adapt readily to captivity even when confined in small cages. Overcrowding should be avoided to minimize injuries and possible death from bickering and fighting among the captives.

The size of the cage should be such that the bats can either fly freely or not fly at all. Injuries or health deterioration may result if bats attempt to fly in cages that are too small. Bats that can hover, such as species of the Glossophaginae and Carolliinae, may be kept in fairly small cages. The minimum cage space should be sufficient to permit bats to flex their wings and ensure that they can adequately perform their grooming activities (Racey, 1972).

Materials and construction.—Almost any material such as wood, metal, glass, plastic, and so forth may be used to construct a cage, but care must be taken in selection of material. Wood will eventually rot as a result of repeated soaking by bat urine. The urine also may have a corrosive effect on certain metals and the reingestion of any corrosive by-products could be dangerous (Pye, 1967). Zinc and galvanized steel were compared by Racey (1970) and zinc, although more expensive, was preferred because it was more resistent to corrosion. Wimsatt *et al.* (1973) constructed their new vampire bat cages using stainless steel and plexiglass.

Any paint used should be free of lead and nontoxic to mammals. Three Australian fruit bats, *Pteropus*, died of lead poisoning at the National Zoological Park, Washington, D.C. (Zook *et al.*, 1970). The source of lead was believed to be leaded paint that peeled from the walls of the cage and accidentally fell on fruit that was subsequently ingested by the bats.

Inasmuch as bats can squeeze through incredibly small spaces and cracks, cage doors and corner joints must be carefully constructed.

Perches.—Bats generally roost high in their cages and descend to the cage floor to feed and drink. The sides or walls, therefore, must be roughened or lined with a wire mesh or a "ladder" so as to permit easy descent. Bats that hang pendantly from tree branches, such as *Artibeus* and *Centurio*, should have their roosts provided with suitable perches (branches or roughened wooden dowling) so that they may hang comfortably. According to Pye (1967), heavy pteropids are apt to suffer from excessive curvature of the claws if they must continuously hang from wire. This might apply as well to large phyllostomatids such as *Phyllostomus hastatus*, *Vampyrum spectrum*, and *Artibeus lituratus*.

Special Considerations for Caging

Space will not permit detailed descriptions of the various cages used to maintain bats. I have selected a few that either have special features or have been proven practical. Those interested in the details of construction and illustrations should refer to the literature cited and Appendicies 1 to 8. It should be pointed out that a cage system designed for one kind of bat may not be suited to other bats.

Insectivorous Bats

The cage used by Krutzsch and Sulkin (1958) for rabies research with *Tadarida brasiliensis* was designed as a "safety cage," and incorporated features to reduce the hazard of working with infected animals. These features included two slots, one for access from outside the cage to the feeding shelf and the other for the removal of dead bats; a sliding floor plate allowing for the transfer of live bats from one cage to another; and lock screws preventing the accidental opening of the hinged door and floor plate. The cages were constructed of materials able to withstand repeated sterilization by autoclaving.

Racey (1970) successfully kept vespertilionids for reproductive studies in cages modified from Jewell's (1964) design for small mammals. Zinc was used for construction. All internal vertical surfaces were lined with plywood in which horizontal grooves were cut that enabled bats to climb and hang with ease. These cages may be hosed with high-pressure water jets and scrubbed clean. If required, the plywood can be removed and replaced after the cage is sterilized. Division of the cage into a roosting box and a feeding area is not essential, but, given a choice, bats will roost in the box if the depth is adequate.

Nectarivorous Bats

Rasweiler and de Bonilla (1972) and Rasweiler (1973) maintained a variety of pollen-eating and nectar-eating phyllostomatids, and also *Carollia*, for reproductive studies. Bats were handled daily, requiring an efficient cage system noninjurious to them and yet conducive to their reproductive activities. The cages used, which served best for *Glossophaga* and *Carollia*, should be suitable for any phyllostomatid that can hover or fly within a confined space and will accommodate about 20 bats (see Appendix 1).

One end of each cage is completely enclosed with plywood and forms a roosting box, with an opening for passage to and from the feeding area. Immediately above the food dishes, thin sheets of galvanized iron are wired to the under surface of the roof to discourage roosting and the fouling of food by feces. The cage floor consists of two galvanized iron pans, which are covered with newspaper or dried clay chips.

Frugivorous and Omnivorous Bats

Another cage made of wood and wire, for medium-sized phyllostomatids such as *Phyllostomus discolor*, *Artibeus lituratus*, and *Sturnira lilium*, was devised by Rasweiler and Ishiyama (1973:57) and would also be satisfactory for *Phyllostomus hastatus*. It will hold about 10 large bats or 15 small bats and has a removable roosting box (see Appendix 2). It is a modification of the Wimsatt vampire bat cage (Appendix 3).

Sanguivorous Bats

A variety of cages—ranging from elaborate and costly metal, plastic, and wooden containers to inexpensive, disposable cartons, jars, and cans—have been

used to house vampire bats. Some zoological parks have provided cages with realistic cavelike interiors for public display of the bats.

There are some problems unique to keeping vampires in captivity, such as a regular blood supply for food, removal of their adhesive feces, and potential risk to human health. Another is the corrosive effect on some metals by the copious urine and tarlike excreta. Also, the unusual agility of *Desmodus rotundus* requires constant alertness by attendants in order to prevent their escape.

Wimsatt *et al.* (1973:251-253) designed a cage (Appendix 3) in which vampires have reproduced and one that has several advantages over previous cages. They described it as follows. "The principal innovations include: 1) a removable animal compartment (in which the bats preferentially roost); 2) a plastic-backed absorbent floor paper that is pulled through the front of the cage from a roll mounted on the back side (the soiled portion is then cut off and discarded); and 3) a plexiglass sliding front wall that is removable from above, and in the center of which is mounted a hinged door with latching bar. Only the roosting compartment and lower side walls beneath it are lined with stainless wire mesh; this discourages bats from roosting elswehere in the cage and the mesh on the lower wall assists their ascent to the roosting compartment. Because all but the front of the cage is of opaque construction and the only opening from the cage to the roosting box is from beneath, the interior of the roosting compartment is quite dark, even when the laboratory lights are turned on. The bats are thus sheltered from view (and viewing), which appreciably lessens the disturbance potential of activities outside the cage. Adequate ventilation is provided by a few holes high in the side walls, in the plexiglass front panel, and in the hinged door of the roosting compartment and its plexiglass insert. . . . The latter are especially important if more than a few animals are confined in the smaller compartment for periods exceeding a few minutes." The construction cost is high (about $400 for one cage in 1972), but the expense is partially compensated for by the durability of the cage, which, if handled with reasonable care, is practically indestructible. A home-made cage of smaller dimensions, made of aluminum instead of stainless steel, costs less than $100.

The cage described above, which is also claimed to be suitable for gregarious molossids such as *Molossus ater*, was modified by Rasweiler and Ishiyama (1973) to house frugivorous phyllostomatids. The basic cage design can be followed for constructing larger or smaller cages, and cheaper materials can be utilized. Metal has obvious advantages over wood or other nondurable materials that would not survive repeated washing and sterilization. Wimsatt *et al.* (1973:253) noted: "While the cages have no 'built-in' temperature or humidity controls their solid, draught-free construction minimizes the effects of normal fluctuations in these parameters in the ambient environment. Ideally, however, they should be placed in a room where reasonable temperature and humidity control is achievable."

At less expense, Dickson and Green (1970:39-40) adapted translucent polypropylene rat cages for *Desmodus* and *Diaemus* that housed five vampire bats each (Appendix 4).

Schmidt and Greenhall (1972:242-243) designed a flight cage in México for observing and photographing interactions between vampires and prey without disturbing either bats or prey. This enclosure contained a roosting cage hung on the wall of one end of the cage. A glass-fronted observation area was constructed at the other end so that bat activities could be photographed through the glass window (Appendix 5). The roosting cage contained two panels forming three interconnecting compartments and permitted the bats to orient themselves according to their social hierarchy.

Rexford D. Lord (personal communication) stated that bats do not adapt well to cages originally intended for laboratory rodents. He has designed a practical flight cage for *Desmodus* (Appendix 6).

Disposable Cages

Some investigators have reduced cage costs by housing bats in inexpensive, easily disposable, cylindrical cardboard containers such as those used for packaging ice cream. These are converted by removing a circular section of the lid and replacing it with a piece of window screen, from which a bat may hang. Food and water dishes are placed on the bottom of the container or water bottles and hoppers may be attached to the outside with tubes inserted through holes cut in the side of the container—Constantine, 1952:396; Tesh and Arata, 1967: 106-107 (Appendicies 7, 8); Barbour and Davis, 1969.

Lord (1971) used a four-liter cylindrical oil can for vampire bats, modified as were the ice cream cartons described above. The cans are inexpensive and easily cleaned or discarded.

Wide-mouthed glass jars also have been used to house bats. A wire mesh ladder hooked over the edge of the jar will enable the bat to climb down for food and water (Mohos, 1961; Davis and Luckens, 1966; Barbour and Davis, 1969).

Greenhall *et al.* (1971) used square-shaped glass jars with metal lids for vampire bats. The jars were placed on their sides with the tops facing forward. The lid had either its center removed and replaced with 1.3-centimeter wire mesh or had holes made directly into the metal top with a can opener. These holes were just large enough to allow the base of the food hopper to be inserted in the lid. If wire mesh was used, a hole large enough to accommodate a food hopper was created in the wire. A piece of 1.3-centimeter mesh was bent into a semicircle to form a bridge and placed inside the jar. This shape permitted a bat either to rest on top of the bridge or to hang underneath. Paper napkins, placed below the bridge to absorb urine and feces, were replaced daily. Pairs of bats were kept together for more than a year and a number of young were born and reared. These glass jars were inexpensive, readily available, and easily serviced and sterilized. They were ideal for rabies studies because infected bats could be clearly and safely observed without risk. For rabies investigations, I prefer the transparent containers to those that are opaque, because visibility is a safeguard for the investigator or caretaker.

Safety Cage

The recapture of escaped bats can be a time-consuming and frustrating task. To solve this problem Rasweiler and de Bonilla (1972) devised an ingenious walk-in safety cage made of wire mesh over a frame, which can be moved up to the front of each large cage or bank of cages containing bats. Escaped bats are restricted to the walk-in cage and are easily recaptured. These authors suggested that, where space is at a premium or cost is a consideration, something similar, but collapsible, could be constructed from mosquito netting.

Miscellaneous Cages

Useful descriptions of other cages are available for *Phyllostomus hastatus* (Dunn, 1933; Beecher, 1971), *Vampyrum spectrum* (Greenhall, 1965*b*, 1968; Bradbury, 1970), and *Desmodus rotundus* (Flores *et al.*, 1971; Bullard and Shumake, 1973).

SANITATION

Cage Floor Protection

Whatever type of cage is used, it must be easy to clean. Various investigators have their own preferences for cage floor protection and the type of material used will depend on the bat, its food, and the nature of its feces and urine. Absorbent materials such as paper towels and napkins, as well as newspapers, are satisfactory for most bat sanitation, whether the bats have dry fecal pellets (insectivores) or moist fecal pellets (those that eat nectar, fruit, or blood). Rasweiler (1976) pointed out that paper, particularly if dry, should be carefully positioned and slightly dampened if necessary, to prevent it from flapping about when the bats fly. *Glossophaga* and *Carollia* are easily frightened from food and water receptacles by moving and noisy paper (Pye, 1967).

Sawdust, wood shavings, and dried clay chips, such as those used for cat litter, also will absorb urine and moist feces, but may prove a nuisance when used for the larger fruit-eating bats and vampires, which tend to be sloppy feeders. Fruit-eating bats often scatter pieces of fruit about their cages and vampire bats, fed from open dishes, may spit drops of blood. Absorbent materials may adhere to the bodies, wings, and feet of these bats inasmuch as they tend to crawl and walk on the floor of cages more than do other species.

Due to the sticky tarlike consistency of vampire bat excreta and the corrosive effects of the urine on metal, cage sanitation has always been a special problem with vampire bats. Wimsatt *et al.* (1973) devised a novel sanitation system consisting of a roll of absorbent, plastic-backed paper, mounted on a bracket at the rear of the cage. As the floor paper becomes soiled, it is pulled forward from the roll through the cage and the dirty paper cut off and discarded. Dickson and Green (1970) lined the floor of their polypropylene cages with absorbent disposable cardboard trays similar to those used in markets to package meat and poultry. Because the method of feeding and watering involves no blood spillage or fouling, it is necessary to change the trays only twice a week. The cages, however, are changed every two weeks for cleaning and disinfecting.

I have used different types of floor covering for vampire cages. In small cages or glass jars, I prefer absorbent paper napkins, but I have also used blotting paper. In walk-in cages I prefer thin plastic sheeting spread over the walls and floor. The sheeting may be attached to the walls by scotch tape or laid directly on the floor. If the floor covering tends to shift, a weighted object will prevent this. Rexford D. Lord (personal communication) also used plastic sheeting. This material is easily cleaned with hot water and can be replaced with fresh plastic as required. I do not care for clay chips or sawdust in vampire bat cages inasmuch as the material will adhere to any moist portion of a bat's body.

Disinfectants and Deodorants

If cleaning and disinfecting has been done carefully, there usually is little need for a deodorant. Occasionally, however, it may be necessary to mask an odor that cannot be eliminated. According to Walker (1942:313), an excellent deodorant not known to be harmful to any animal, unless possibly reptiles, is a solution of "about 4 ounces of oil of pine to a gallon of water." Disinfectants and deodorants containing phenol, creosote, or carbolic acid are harmful to animals and should not be used (Walker, 1942). In dry situations, baking soda will absorb odors.

Animal cages, cage racks, and accessory equipment such as feeders and water bottles should be washed as often as necessary to keep them clean. In addition, cages should always be disinfected before new animals are placed in them. It is good practice to have clean extra cages available to permit a systematic schedule for washing cages. This is particularly true when caring for large numbers of vampire bats. Thorough washing and rinsing with soapy water, detergents, and disinfectants should be done with a water temperature of 83°C or higher to assure destruction of most pathogenic organisms. Pressurized steam is an excellent method by which to sterilize cages. When using steam, care must be taken that glass and plastic materials will not be damaged by the high temperature.

A standard disinfecting and cleaning solution used in many zoological parks is made up as follows (Walker, 1942:313): "Stock solution—5 gallons of 5 percent solution of sodium hypochlorite and 18 ounces of caustic soda (lye). Dissolve the lye in 1 to 2 gallons of water in enamelware or earthernware container, then pour lye solution slowly into hypochlorite to avoid violent reaction. Stir while pouring. For use add 1 pint of stock solution to 2 gallons of water. . . . This mixture is good for disinfecting cement floors, walls, and dishes, but is injurious to paint." Orr (1958) washed his cages, as well as food and water receptacles, with a detergent and chlorine solution. Dickson and Green (1970) disinfected their soiled vampire bat cages and trays by soaking them in a 1.5 per cent solution of sodium hypochlorite for 24 hours, then scrubbed them in a one per cent Tego solution (see Appendix 18 for source).

For investigators studying rabies in bats, Kaplan (1973:15-16) recommended the following laboratory disinfecting procedures, "Quaternary ammonium disinfectants in 1:500 dilution, 45-70% alcohol [ethanol], 1% soap solution, and 5-7% iodine solutions kill the rabies virus within one minute. . . . For pipette receptacles at 1:1000 dilution of a quaternary ammonium compound, any iodine

disinfectant with a residual available iodine of at least 1:10,000, or 1% concentration of soapy water or detergent can be used. The solution should be autoclaved and discarded after each use. Hot soapy water or detergent can be used for swabbing floors and tables.

"Glassware, plasticware and instruments . . . should be discarded into plastic or glass receptacles containing one of the disinfectants mentioned above. They should be autoclaved.

"Carcasses and animal tissue . . . are best disposed of in plastic bags and incinerated."

Diet

Of all bats, the Phyllostomatidae probably have the most varied food preferences. Their natural feeding habits are discussed by Gardner (this volume), and his chapter on food habits will be indispensable to anyone who must prepare a diet for any phyllostomatid not yet successfully kept in captivity. Except for a few species, the literature is meager about the diets used by laboratories or zoological parks when keeping New World leaf-nosed bats in captivity.

For this discussion I have grouped the phyllostomatids as insectivorous, nectarivorous, frugivorous, omnivorous, carnivorous, and sanguivorous. No bat in captivity can eat exactly as it would under natural conditions and specific natural food items may be impossible to supply, making substitutions essential. A daily intake of protein appears necessary, but it is impossible to state what the required amounts should be in formulating a balanced diet. Hopefully, however, with vitamins, minerals, and other food additives, the nutritional requirements of a captive bat may be resolved. Various vitamin preparations are available and many investigators have their own preferences. One, Stuart Formula Liquid, seems almost to be a panacea for diet deficiencies, not only for bats but for other captive small mammals (see Appendix 18 for sources of products mentioned in this chapter).

Insectivores

In discussing the feeding habits of the Phyllostomatidae in another chapter, Gardner noted that the family's only true insectivore may be *Macrophyllum macrophyllum*. He cited examples of insect remains having been found in the stomachs or fecal remains of all subfamilies, suggesting that, regardless of the basic food preferences of each group, insects are probably an important food component of the diet. However, in the case of the Desmodontinae, insects probably were ingested accidentally when preparing a bite site on some animal selected as prey, or during grooming activity. Racey (1972:297-299), in his review of the care and management of bats, listed 33 genera and 54 species of insectivorous bats that have been kept in captivity, but the only phyllostomatid mentioned was *Macrotus*. *Micronycteris megalotis* was kept by Ruschi (1953*a*), who indicated that the bats lived and reproduced, but he did not provide further information. With the exception of *Macrotus* and *Micronycteris*, species of which also eat fruit, it is not surprising that the literature is wanting on the care of

insectivorous phyllostomatid bats. I believe, therefore, that it will be of value to describe diets used successfully to maintain insectivorous bats.

Insect diets.—Vespertilionid and molossid bats have been fed a variety of insects such as greenbottle flies (both adults and maggots), house flies, instars of grasshoppers, locusts, and crickets in addition to bees, June beetles, termites, waxworms, and waxmoths (Gates, 1936:270; Ramage, 1947:61). Most captive insectivorous bats thrive on a diet of mealworms (*Tenebrio molitor*); although the larvae are preferred, the pupae also are eaten.

Pye (1967) cautioned that dietary deficiencies may occur if bats are fed mealworms that have had a purely farinaceous diet. This deficiency may be overcome by the addition of a good quality commercial animal feed to the mealworm's diet. Also, mealworms may be dusted with vitamin and mineral mixes (Rasweiler, 1975) or coated with vitamin drops such as those used for children (Gardner, personal communication). Concerning a diet of mealworms, Racey (1972) and Ladische *et al.* (1967) advised that there may be some toxic quinones in some mealworm imagoes.

Gates (1938*b*) added pieces of honey bees to the diets of *Eptesicus*, *Myotis*, *Lasiurus*, *Plecotus*, and *Tadarida*. The bees seemed to improve the consistency of the feces and added to the palatability of the food. He tried other insects, such as grasshoppers and June beetles, but the bats preferred bees. Ramage (1947: 61) had no success in persuading various species of *Myotis* and *Eptesicus* to eat the foods suggested by Gates (1936) until she provided the larvae, pupae, and adults of greenbottle flies, "which can be easily reared in enormous quantities." A *Myotis californicus* she kept refused to eat flies but was raised successfully on termites. Ramage (1947:61) commented, however: "Termites have the dual disadvantage that they cannot be cultured rapidly enough to feed the bats and must be chloroformed or killed to keep them from crawling away before the bats have a chance to eat them."

Racey (1972:302), in his discussion on insects as food for insectivorous bats, mentioned that the larger bat species also will take early instars of many Orthoptera, "the most commonly cultured of which are locusts and cockroaches."

Orr (1954:168) mostly fed mealworms to *Antrozous pallidus* during the early phases of his study, but later he used a prepared diet recommended to him by Ernest P. Walker. However, he offered (p. 234) a listing of other kinds of animal foods such as a variety of flies, moths, and even snails. Elsewhere in his study, Orr (*op. cit.*, 232-233) cited, "records of captive pallid bats which were observed to eat western skinks (*Eumeces skiltonianus*), a Sonoran desert gecko (*Coleonyx variegatus*), and were suspected of eating the head and neck of a Mexican free-tailed bat (*Tadarida mexicana*). It seems likely that starvation was responsible for such deviation from an insectivorous diet, although . . . it is possible that small night lizards may be preyed upon locally by pallid bats."

Artificial diets.—I have used insect traps to catch insects for bat food. At times, however, insects may be either scarce or not available. Consequently, investigators have had to devise substitute diets. These are mashes or mixtures comprised of a number of items that are readily taken by the bats and usually in-

clude such things as banana, cottage cheese, hard-boiled egg, and vitamins. Such mixtures are commonly called "glop" by bat biologists. Gates (1936, 1938*b*) found that various species of *Myotis*, *Pipistrellus*, *Eptesicus*, and *Plecotus* do well in captivity on artificial diets that may be completely different from their normal diets. He (1938*b*:157) noted: "Under captive conditions they have been known to eat practically everything, unless it is too highly seasoned. This includes all cereals, breads, crackers, cakes, meats, eggs, vegetables of all kinds, both fresh and cooked, lettuce, celery, and all of the not too acid fruits, apples, pears, peaches, prunes, pineapples, and figs. All milk products, both fresh and sour milk, buttermilk, cheese, and even butter are acceptable. In fact, the author has hardly found any food which they will not eat. They of course have their preferences, apparently preferring the milder cheeses to anything else. However, bread crumbs moistened with buttermilk are also greatly enjoyed." Gates (1936: 270) first suggested that chitin was essential for the proper formation of fecal pellets and the prevention of intestinal obstruction in insect-eating bats. The ease of obtaining bananas and cottage cheese tempted Racey (1970) and others to feed a mash lacking insects. The bats did poorly, however, and their pelage deteriorated. Empirically, it was discovered that mealworms or other insects added to the mixture corrected the condition.

There are a number of recipes for glop. Walker (1966:138) developed a food mixture relished by many small mammals at the National Zoological Park (Appendix 9). Davis and Luckens (1966) used banana, cream cheese, canned dog food, and multivitamins to feed *Eptesicus* (Appendix 10). Mohos (1961) used the Walker (1966) formula to feed *Myotis*, *Pipistrellus*, and *Eptesicus*. However (p. 371), "occasionally equal parts of beef and beef liver were substituted for the cottage cheese, since it was found that, after an initial adaptation period, the bats fare equally well on this diet." J. Frederick Bell (personal communication) fed *Myotis lucifugus* homogenized whole baby mice, which were readily available in his laboratory. Krutzsch and Sulkin (1958:262-264) tried a number of feeding techniques and food combinations to induce their captive *Tadarida brasiliensis* to feed. Live mealworm larvae were unsatisfactory, and a nutrient fluid containing amino acids, simple sugars, and vitamins caused the bats to develop dysentery with fatal results. They were finally successful in maintaining *Tadarida* on glop.

Food storage.—Diet preparation may be simplified in that the various food ingredients, including insects, can be mixed in an electric blender, preweighed in wax paper or plastic bags, and then stored frozen at 4°C until used (Mohos, 1961:371; Davis and Luckens, 1966:226; Barbour and Davis, 1969:246; Rasweiler, 1975). The size of the food packets should depend on the number of bats to be fed at any one time. Before feeding the bats, frozen food should be removed from the freezer and allowed to thaw. Once thawed, food will last about a week under ordinary refrigeration. It is important not to serve wet mashes and other liquid diets too early in the day because they may begin to spoil before all bats have fed. This can lead to diarrhea and malnutrition.

Nectarivores

Until recently the standard diet for such captive nectar-feeding bats as *Glossophaga* and *Anoura* has been sugar or honey in water, fruit juice, succulent fruits, and vitamins (Ruschi, 1953*c*, 1953*d*, 1953*e*; Goodwin and Greenhall, 1961; McNab, 1969). Rasweiler (1975) claimed that "laboratory diets for frugivorous or nectarivorous species based solely upon fruit pulp and/or fruit juices may be grossly inadequate from a nutritional standpoint." He believed that addition of insects and pollen could significantly increase the protein, fat, mineral, and vitamin levels in diets of fruit-eating bats, as well as supply essential amino acids that are inadequately represented in the fruit component of the diet. Rasweiler and de Bonilla (1972) and Rasweiler (1973) have formulated diets (Appendix 12) that have been successful for the long-term maintenance of large numbers of *Glossophaga soricina*, *Anoura geoffroyi*, *A. caudifer*, and *Carollia perspicillata*.

The New York Zoological Park prepares an artificial nectar (Appendix 11) dispensed from large watering bottles hidden among the plastic plants of the exhibit. In these exhibits, the nectar-feeding bats also have access to the solid diet (Appendix 15) offered to the frugivorous phyllostomatids (House and Doherty, 1975). The bats housed in this exhibit have included *Glossophaga soricina*, *Anoura geoffroyi*, *Phyllostomus discolor*, and *Carollia perspicillata*.

Donna J. Howell (personal communication) successfully raised nectarivorous bats on a different diet (Appendix 13). She also maintained *Phyllostomus discolor* and *Carollia perspicillata*, but treated them as fruit eaters. Howell wrote: "I've kept *Leptonycteris*, *Choeronycteris*, *Glossophaga*, *Anoura*, and *Hylonycteris* on the nectar diet for periods exceeding a year. All the diet ingredients seemed necessary to duplicate the very nutritious contents of 'bat-adapted' pollen and nectar from chiropterophilous plants. One must be careful to give the bats enough protein, yet not over protein-load or over sugar-load their kidneys. Concentrating ability of the glossophagines is very poor. Protein should stay about 9 to 11 per cent, sugar 14 to 20 per cent."

Frugivores

The diet of nectarivorous and frugivorous bats is influenced mostly by the seasonal abundance of flowers and fruits (Greenhall, 1956, 1957; Goodwin and Greenhall, 1961; Fleming *et al.*, 1972). The diets of captive frugivores will be determined by the availability of fruits. In temperate regions, tropical fruits, with the exception of bananas, may not always be available.

Captive fruit-eating bats generally prefer sweet fruits such as bananas, mangoes, peaches, plums, melons, grapes, and papayas (Pye, 1967; Racey, 1972). Although citrus fruits are not preferred, sweet oranges and grapefruit occasionally may be accepted (Greenhall, 1966). Pye (1967) mentioned that apples can be substituted if exotic fruits are in short supply. The banana-based diet formulated by Rasweiler (1975) and Rasweiler and de Bonilla (1972) is given as Appendix 14.

When offering food, it is advisable to use small pieces, about 1-centimeter cubes, well mixed. This will prevent dominant individuals from selecting all the choice fruits or obtaining more food than their cage mates. Small pieces can be easily managed by bats while eating or flying. The smaller fruit-eating bats can handle whole fruits only when they are overripe or soft enough that a small hole can be bitten in the skin through which the fruit pulp and juice can be extracted.

Some biologists have fed phyllostomatids some unusual dietary items. For example, Ruschi (1953*f*) fed *Artibeus lituratus* blood as well as fruit and insects, because he believed that this species feeds upon blood in the wild.

Goodwin and Greenhall (1961) stated that *Phyllostomus discolor* will not eat flesh in captivity and prefers fruit such as bananas, mangoes, and papayas. McNab (1969) reported, however, that captive *P. discolor* require a small, but regular, intake of meat. Uwe Schmidt (personal communication) mentioned having successfully reared this species on sliced bananas, mealworms, and neonatal laboratory mice.

McNab (1969) reported that he kept a number of frugivorous phyllostomatids healthy for extended periods of time, but, unfortunately, provided no information on diets other than the fact that *Rhinophylla pumilio*, *Uroderma bilobatum*, *Artibeus cinereus*, and *A. concolor* were fed fruit. His *Phyllostomus elongatus* and *Vampyressa nymphaea* would not eat.

Polyphagous Phyllostomatids

A good example of an omnivorous phyllostomatid is *Phyllostomus hastatus*, which readily adjusts to captivity. Dunn (1933) fed *P. hastatus* mice, bats, birds, defibrinated blood, fruit, and raw meat, including liver. Ruschi (1953*b*) and McNab (1969) provided similar fare, the former adding cockroaches when available. Goodwin and Greenhall (1961) found that this species, in addition to accepting a wide variety of fruit, thrived on mice and young birds. It did not hesitate to kill and eat other bats placed in its cage although it appeared to be uneasy in the presence of *Desmodus*. The diet used by the New York Zoological Park for their colony of *P. hastatus* is given in Appendix 16. Donna J. Howell (personal communication) fed both *Phyllostomus hastatus* and *P. discolor* a special diet for frugivorous bats (Appendix 17) and commented that these bats also got a dish of mealworms at each feeding.

Carnivores

The best known carnivorous phyllostomatid is *Vampyrum spectrum*. It has been raised successfully in captivity on raw meat as well as dead whole chicks and pigeons (Ditmars, 1935, 1936; Goodwin and Greenhall, 1961; Crandall, 1964; Bradbury, 1970). Greenhall (1968) described the care of *Vampyrum*, which successfully raised young during the five years bats were maintained in captivity. They were fed pigeons, chicks, wild birds, and dead laboratory rats and mice as well as raw meat cut into 2-centimeter chunks. Although these *Vampyrum* never fought over food, there was always the risk of injury to their wings when they stalked live prey because the cage was too small. Therefore, all

food was killed and usually presented to the bats by forceps or placed on the cage floor. Food was thoroughly masticated by the bats; feathers and rodent tails usually were discarded.

Other carnivorous phyllostomatids kept in captivity include *Trachops cirrhosus* and *Phylloderma stenops*, which ate lizards (Pye, 1967), *Chrotopterus auritus*, which was kept on a diet of white mice by Villa-R. and Villa-C. (1969), and meat and bats by McNab (1969).

Vampire Bats

The three vampire bats, *Desmodus rotundus*, *Diaemus youngii*, and *Diphylla ecaudata* have been maintained in captivity with varying degrees of success. *Desmodus* adapts easily to captive conditions, whereas *Diphylla* is most difficult to maintain. *Diaemus* does fairly well once its basic requirements are recognized and met. Presently there are breeding colonies of *Desmodus* in many laboratories and zoological parks.

Ditmars and Greenhall (1935) were the first to describe keeping vampire bats in captivity. Trapido (1946) demonstrated that *Desmodus* easily adapted to laboratory conditions and reported a longevity record of 12 years. Wimsatt and Guerriere (1961) detailed the care of *Desmodus* in temperate zone laboratories, whereas Greenhall (1965*b*) described its maintenance in the tropics.

Wild *Desmodus* may consume amounts of blood equalling or exceeding their body weight (Wimsatt, 1969). The average weight of *Desmodus* is about 30 grams, and captive bats daily may drink up to 50 milliliters of blood, although 15 to 20 is usually sufficient (Pye, 1967). Wimsatt and Guerriere (1962) cited the unusual capacity of one captive 28-gram nonpregnant female they maintained in isolation for 17 days, which consumed blood in excess of her body weight on 13 days. On two days the amounts ingested were 47 and 52 milliliters, respectively.

Dickson and Green (1970), in order to reduce the time and labor required in the maintenance of vampires, utilized trisodium citrate (1 milliliter 3.8 per cent per 10 milliliters of blood) to prevent blood coagulation and dispensed the blood meal in plastic hoppers. The use of citrated blood instead of defibrinated blood reduced the preparation time and dispensing meals in plastic hoppers prevented splattering and spillage thereby reducing the time for cage cleaning. According to Dickson and Green (1970), defibrination results in the loss of blood volume and the removal of factors essential for the vampire's welfare. Blood can be stored frozen at $-20°C$ for up to six weeks without becoming unpalatable to vampires. Dickson and Green (1970) presented the daily ration warmed to 37°C at 1630 hours. Each food container was filled with 100 milliliters of blood—sufficient for five bats. These hoppers or glass-tubed drinking bottles prevented the wastage and contamination of the blood by urine and feces that usually occurs when vampires are fed from open dishes. Radiological examination revealed no evidence of bone decalcification following 15 months of citrate in the diet.

Frozen blood, whether defibrinated or citrated, has a tendency to spoil rapidly after thawing (Wimsatt and Guerriere, 1961; Greenhall, 1965*b*). Therefore, the blood meal should be offered when the bats normally commence feeding.

In the field, where fresh blood is usually difficult to obtain, an ingenious emergency supply was devised by Wimsatt and Guerriere (1961). This "instant blood" is shell-frozen and lyophilized defibrinated blood and is reconstituted with water, as needed.

Diaemus has been kept successfully in the laboratory on citrated bovine blood —the same diet fed to *Desmodus* (Dickson and Green, 1970). A weekly supplement of chicken blood was also provided by permitting the vampires to feed on the toes of a live chicken placed on the top of their cage. Nonetheless, Goodwin and Greenhall (1961) reported that *Diaemus* refused to drink defibrinated cattle blood even when mixed with chicken blood. Their bats, however, would accept chicken blood. At a later date, Greenhall (1970) reported observing *Diaemus* feeding on cattle. I believe that *Diaemus* should be fed citrated whole blood as individuals apparently refuse to drink defibrinated blood.

Diphylla has not been successfully kept in captivity for any length of time. Ruschi (1951) stated that he maintained *Diphylla* and *Desmodus* on both citrated and defibrinated blood, and that the latter was preferred. However, Villa-R. (1967) reported that *Diphylla* would not accept cattle blood, and although defibrinated chicken blood was consumed, the bats died within 48 hours. Perhaps captive *Diphylla* would accept citrated rather than defibrinated blood.

I recommend that liquid multivitamins be added to all blood meals. House and Doherty (1975) used 2.4 cubic centimeters of "Pet Drops" per pint of blood (Appendix 18).

An unusual observation about vampire bat diet was reported by Kumm (1932), who noted that *Desmodus* fed readily in captivity on bananas and live animals. I can find no confirmation that vampires feed on fruit.

Vampire fasting.—Schmidt *et al.* (1971) observed that wild *Desmodus* may not forage every night. If true, one must assume that such fasts are not deleterious. Wimsatt and Guerriere (1961) routinely skipped feeding their *Desmodus* on Sundays. On the few occasions that their bats were neglected accidentally for as long as three days, the effect was marked emaciation but not death. Greenhall (1965*b*:443) found that *Desmodus* could go without food for at least 62 and a half hours without apparent ill effects.

Vampire cannibalism.—The only reference to cannibalism among *Desmodus* in captivity was described by Wimsatt (1959). Wimsatt's colony consisted of four cages, each containing 15 to 20 bats. In one cage the daily ration of blood was always consumed, whereas in the other three there was always some blood left over. After several weeks, the bats in the first cage developed hairless patches on the shoulders, interscapular region, and back of the head. Associated lacerations were obviously caused by bites. This did not occur with the occupants of the other three cages, suggesting that this situation reflected unusual behavior. This abnormal behavior ceased and the injured animals subsequently recovered when blood was supplied in adequate amounts. The feeding on cage mates was

interpreted to be an attempt to secure blood in any way possible whenever the amount of blood available was deficient. Greenhall (1965*b*:442) observed that cannibalism might occur among newly captured vampires, but could easily be prevented by supplying the bats with a greater quantity of blood than could be consumed in one night.

Preparation of defibrinated and citrated blood.—A major obstacle to keeping a vampire bat colony in the laboratory is the uncertainty of a continuous fresh supply of blood. Defibrinated cattle blood has been used successfully for many years, but citrated blood may be preferable inasmuch as nothing is removed.

Blood for defibrinating should first be collected in a clean vessel as it flows from the slaughtered animal. The blood must then be whipped or agitated with either wooden applicators, cocoa beaters, swizzle sticks, large wire beaters, whisks, or roughened glass beads. After several minutes of agitation, the fibrin will adhere to the beating instrument or glass beads and then may be discarded. The remaining blood may then be poured into another clean vessel for storage. Defibrinated blood will remain as a liquid and will keep under refrigeration for a few weeks. The color, usually bright red, might slowly turn purplish. The blood will be accepted by the bats if not spoiled. Greenhall (1965*b*) froze defibrinated blood in ice cube trays and other containers. Frozen defibrinated blood may be maintained safely for several weeks. Inasmuch as it may spoil rapidly, only single rations of blood should be thawed each day, and this should be used as quickly as possible. I know of some laboratories and zoos that have used outdated human blood and plasma from blood banks. The consensus is that vampires apparently do not do well on either fare.

Dickson and Green (1970:40) described their method of citrating blood as follows: "Bovine blood is collected from a nearby slaughterhouse in 5 liter containers, each containing 500 ml of 3.8 per cent trisodium citrate to prevent coagulation. This blood is strained through muslin into 500 ml polythene bottles; it can be stored frozen at $-20°C$ for up to 6 weeks without becoming unpalatable to the bats."

Drinking Water

In their reviews of the care and management of bats, Pye (1967:498) and Racey (1972:303) stressed that all captive bats should have a plentiful supply of drinking water available. Most information about water requirements pertains to vespertilionid and molossid bats. Perhaps only a few phyllostomatids, such as *Desmodus*, are able to live for extended periods without drinking water. Most bats will learn to use drinking tubes, nozzles of inverted bottles (Racey, 1972: 303), or plastic hoppers of the types used for caged birds. Pye (1967), however, asserted that bats do not readily use drinking tubes and that water is best supplied in shallow dishes. These water dishes should be cleaned daily. According to Pye (1967:498), there is a danger that sick animals may drown in water dishes and the depth of the water, for smaller bats, should not exceed 3 to 5 millimeters. Some bats are reluctant to crawl on the floor so that food and water dishes should be placed on a shelf, fastened to the side, or suspended from the top of the cage.

Racey (1972) observed that vespertilionids will lap water from saturated cotton and this is a useful way of providing water during transport. Rasweiler (1975) daily provided water for his captive *Phyllostomus discolor*, *P. hastatus*, *Artibeus lituratus*, and *Sturnira lilium*.

There are divergent opinions as to whether captive *Desmodus rotundus* require water to drink. King and Saphir (1937) and Trapido (1946) provided water *ad libitum* to these vampires. Wimsatt and Guerriere (1961) expressed surprise that their *Desmodus* drank little if any water; bowls of fresh water were kept in the cages at all times, but were not used even when the bats missed a day's feeding. They finally discontinued the practice and, after nearly two years without water, the bats showed no ill effects. Greenhall (1965*b*) observed that his vampire colony required a constant supply of water for the bats' well-being. In addition to water supplied during the day, another 150 milliliters was given with the daily meal. During a two-month check period (May and June), 113 milliliters was the greatest amount of water consumed in one night, whereas 10 milliliters was the least. Water evaporation was not a factor owing to the constant high humidity. At high elevations in México, Greenhall *et al.* (1971) noted that the daily blood intake of *Desmodus* kept in glass jars increased when a supply of drinking water was added. However, when large numbers of vampires (about 200) were kept at one time, water was not provided in order to reduce the maintenance required to clean up to 100 extra water hoppers. Over a period of months the bats suffered no ill effects as a result of withholding water. Water was always provided for the small group of vampires in the flight cage. Uwe Schmidt (personal communication) provided his *Desmodus* with water *ad libitum* day and night, and blood only during the night. He wrote: "I don't know whether water is essential for keeping vampires, but my feeling is they need it for their well-being, especially if they have eaten spoiled blood." While maintaining a colony of *Desmodus* in a flight cage, Rexford D. Lord (personal communication) observed: "The other day I saw a vampire come down and drink water even before drinking blood which was also available. He drank about 5 milliliters of water, then flew up into the roost box." Lord described a food preference test where water was offered to 19 bats. Each drank an average of 23.4 milliliters of blood and 2.5 milliliters of water nightly, over a period of nine nights. On one night, no water was consumed but during another night the bats drank a total of 132 milliliters. Lord conducted another test where vampires were kept individually in oil can cages placed in an outdoor enclosure. Water consumption varied with the ambient temperature. On extremely hot days, the bats consumed 20 to 30 milliliters of water, drinking even during the day. On cool days the bats did not drink. Lord concluded: "I think water is necessary in hot climates or when there is no control of cage temperature."

General Care of Captive Bats

Acclimation

There is little information about the acclimation of bats to captive conditions. Rasweiler (1973) initiated acclimation of his phyllostomatids immediately

following capture. In the field, food is placed in the transport containers. Upon arrival at his laboratory, all bats are hand-fed to provide some nourishment. This quick introduction to the new diet probably assists the bats to cope with the trauma associated with capture, transit, and the initial period of adjustment to captivity. Recalcitrant, weakened, or torpid *Glossophaga soricina*, for example, usually can be induced to consume some of their new diet, if at first a small amount is placed over the bat's nostrils (Rasweiler, 1975). A second method of feeding bats that are reluctant to accept hand-offered food is to force carefully an eyedropper containing the liquid diet into the bat's mouth (Rasweiler and Ishiyama, 1973:57). Upon tasting a small sample of food, many animals will readily consume more. The bats are then fed from dishes. The same regimen was applied to *Carollia perspicillata*, *Phyllostomus dicolor*, *Artibeus lituratus*, and *Sturnira lilium*. Rasweiler and Ishiyama (1973:58) stated: "The hand-feedings were given in the hope that they would facilitate the transition of the animals to a laboratory existence."

Training Bats to Eat Mealworms

In the wild, most insect-eating bats catch their prey in flight, whereas a few may glean their prey from foliage or other substrates. In captivity, where food is placed in containers, many insectivorous bats require training before they will feed themselves. Racey (1972), who has had much experience with captive insectivorous bats, emphasized that this training is the most crucial and time-consuming stage in the acclimation of these bats to captivity. This is also true of weanling bats born in captivity. Novick (1963:51) stated that captive *Macrotus* must be hand-fed mealworms before they adapt to taking their own food from a dish. Although a number of other phyllostomatid bats feed on insects in the wild, there is no information as to how these bats were trained to feed on insects in the laboratory.

Lacking this information on insect-eating phyllostomatids, it may be valuable to describe how some investigators have trained vespertilionid and molossid bats to feed. The success of training bats to do what the investigator wants them to do depends in large measure on the patience and skill of the trainer, but also on the inclination of the bat to learn. Some bats require less training to eat mealworms than others. There are several methods, ranging from holding a bat in a gloved hand and offering food to simply allowing bats to learn to feed themselves from a pile of mealworms in a dish.

Constantine (1952:397) placed mealworms on the cage floor hoping that specimens of *Tadarida brasiliensis* would recognize their future diet after they ate their first few hand-offered worms. Racey (1970:178) held the bat in his hand, decapitated the mealworm, and then applied the viscera to the bat's lips. The bat's jaws closed and the bat usually would chew the insect. If the bat did not chew in half a minute, then a drop of water was placed in the corner of the bat's mouth. If there was still no response, the mealworm was squeezed so that its contents entered the bat's mouth. After the first mealworm was swallowed, the bat's nose was brought in contact with the insects moving in a dish or on the cage

floor. As the bat started snapping and eating, another worm was immediately given to the bat. If the bat still refused to eat, it was again held by hand and the above steps repeated. Thereafter, mealworms were left in shallow dishes to be eaten.

Orr (1958:342) trained *Antrozous*, *Myotis*, *Tadarida*, *Eptesicus*, *Plecotus*, *Pizonyx*, and *Lasiurus* (listed from the most rapid to the slowest learners) by first placing the bat on a table and covered all but the head with his hand. Pieces of mealworm were then forced into the mouth with forceps. Once the bat tasted a worm, it began to eat. Mohos (1961) offered *Myotis*, *Pipistrellus*, and *Eptesicus* food by spatula, and hand-feeding was carried out in the evening. Nellis (1969) found that placing *Myotis*, *Eptesicus*, *Lasiurus*, and *Noctilio*, in a container of squirming mealworms was sufficient to cause the bats to snap and then feed. This latter procedure was followed by Racey (1970) with *Nyctalus*, *Eptesicus*, *Plecotus*, *Myotis*, and *Pipistrellus*, after feeding had been initiated by hand. Tesh and Arata (1967) discovered that greater efficiency in feeding *Tadarida* could be achieved by placing the head of a bat into the open end of a modified 50-milliliter plastic hypodermic syringe. Mealworms were then presented to the bat through a hole cut in the needle end of the syringe. Several such syringes could be used simultaneously and 20 to 24 bats could be fed in an hour.

Behavior of Captive Bats

It is good animal husbandry for the handler to know the temperament of the animals in his care. Individual animals respond differently to different people. In addition it should be understood that group behavior of a species in captivity may differ from the behavior of an individual of the same species.

Although many phyllostomatid bats are gregarious, different species should not be kept together in a relatively small cage. If kept together, care should be taken in the choice of cage mates (Pye, 1967). This caution is important for those in charge of naturalistic zoo exhibits where a variety of animals are often caged together. For example, *Phyllostomus hastatus*, *Vampyrum spectrum*, and *Desmodus rotundus* may find their cage mates more attractive than the regular food offered.

Phyllostomus hastatus may be bold and aggressive in the wild (Goodwin and Greenhall, 1961). Yet, in captivity, these bats may become tractable and easily handled, but are capable of inflicting deep and painful bites (Beecher, 1971). *Phyllostomus discolor* is readily tamed and a delightful laboratory animal according to Uwe Schmidt (personal communication). *Vampyrum spectrum* also becomes tame and gentle in captivity (Greenhall, 1968). *Glossophaga soricina* is a nervous bat, and Rasweiler (1973) found, in order to keep noise and disturbance minimal in his laboratory, that he had to take over the care of the bats. Rasweiler (1973) reported *Carollia perspicillata* as easily handled and maintained. Conversely, Uwe Schmidt (personal communication) noted that *C. perspicillata* is shy, panicky, and sensitive to shock, and thus a difficult captive. His specimens regularly died following the stress of being photographed. He also said that *Artibeus lituratus* was easily maintained, but remained intractable, biting viciously when handled.

Biologists have had mixed success in taming vampire bats, particularly *Desmodus rotundus*. I found that vampires would become tame and made excellent laboratory and zoo animals. For a number of years, I kept a breeding colony of 20 individuals in my apartment. Wimsatt and Guerriere (1961:452) remarked: "When individually pampered, vampires tame readily and can be approached and handled without difficulty, but without this special attention they retain in large measure their naturally suspicious and aggressive nature. Any overt move to catch them results in violent attempts to escape and, being heavy-bodied, they sometimes damage themselves in the process, if there are many in a single cage, all behaving in this fashion, the result is pandemonium." Uwe Schmidt (personal communication) observed that individual *Desmodus* became extremely tame if handled daily. Dickson and Green (1970), however, were never successful in taming *Desmodus* or *Diaemus*, even though their animals were handled frequently.

Catching and Handling Bats

The usual way of catching bats in the laboratory is either to pick them up gently in a gloved hand or, if they can fly within their cage, to trap them in an aquarium, or insect, net of appropriate size. Bite-proof gloves should be worn when handling bats to avoid being bitten by a bat that might be rabid or capable of inflicting a deep and painful bite. Long-handled forceps may be used to hold bats. While some biologists prefer to handle bats without gloves, I believe this is a dangerous practice. Should a person be bitten on the hand a normal reflex is to withdraw the hand rapidly, resulting possibly in a severe laceration as well as throwing the bat and possibly injuring it. Gloves should be worn that are sufficiently thick to prevent penetrating bites and still be flexible enough to permit delicate handling.

Some procedures, such as the examination of testes or the taking of vaginal smears do, however, require manipulation of bats with the bare hands. Racey (1970:175) believed that the best method to handle bats with bare hands was to draw the bat's forearms together over the dorsum, using the thumb and middle finger, and at the same time to place the crooked index finger in the dorsal midline. For closer inspection, it is often necessary to extend the wing membranes. The thumb is pressed close to the ventral surface of the thorax and slipped upwards underneath the lower jaw, which will be lowered in an attempt to bite. The mouth is held shut between thumb and forefinger, and the dorsum supported by the palm of the same hand. A forearm is then gripped with the thumb and forefinger of the spare hand and the wing extended. The grip of the thumb and the forefinger holding the jaws shut is then shifted quickly to the other forearm in order to extend the wing, all in one continuous movement.

Rasweiler (1975) removed active bats from cages by using an aquarium net with a deep pocket. The chances of injuring a bat are reduced when one is maneuvering the animal against the soft net pocket. With larger species, a hand cupped firmly around the bat, and a thumb slipped upwards underneath the lower jaw will prevent a bite. With smaller bats, there is more danger of inflicting injury to the wings, and it is best to cup the hand lightly over the bat. Then the bat

can usually be encouraged to crawl upwards and present its head between the thumb and forefinger where it can be restrained. If the animal must be positioned for access to the ventral surface, a folded wing can be grasped with one hand and momentarily used to support the animal while the forefinger and thumb of the opposite hand are slid from head towards tail—down the bat's sides along the ventral base of the wings. The animal is then restrained with light pressure and supported from behind by the remainder of the hand. Rasweiler (1975) cautioned that haphazard grabs directed at either the entire bat or the nearest protruding appendage may inflict injury and certainly do not have a taming effect. Despite the best efforts of the handler, bats often maneuver into awkward positions. In such cases, it is much better to release a bat completely and recapture it than to risk harm by further manipulation.

When a bat bites a glove and holds on tenaciously, release usually may be induced by blowing into the bat's face. This is preferable to pulling or shaking the bat, as it reduces the chances of damaging the animal's teeth.

Uwe Schmidt (personal communication) handles *Desmodus* as follows: "The bat is grasped completely around the body with the four fingers underneath the belly and the thumb over the head. Nontame vampires are caught with a small hand net and grasped in the same way, except thin leather gloves are worn. Other bats that bite are similarly grasped but with thicker gloves."

Some biologists prefer to handle bats using forceps, the ends of which are padded with rubber tubing or foam rubber to give a good, secure grip and prevent injury. Bats may be held by the humerus or by one leg, which will give adequate control for a short period of time. The animal then may be grasped firmly by hand before the forceps are loosened.

Reproduction

The known reproductive patterns of the Phyllostomatidae are summarized by Wilson in his chapter (this volume) on reproductive biology. Although a number of bats have bred and raised young in captivity, there is little published information for phyllostomatids. Many captive colonies are initiated with wild-caught individuals and, unfortunately, females in advanced pregnancy either abort or die shortly after being placed in captivity.

Novick (1960) reported on the long-term, successful breeding of *Artibeus jamaicensis* maintained on a diet of bananas and melons augmented with a vitamin supplement. Warmth, seclusion, adequate diet, and freedom from handling appeared necessary for this successful maintenance. Rasweiler and Ishiyama (1973) were not so successful with *A. jamaicensis*, and pointed out that it was impossible to compare the relative value of Novick's methods with theirs because precise survival data and number of reproductive failures were not provided. Rasweiler and de Bonilla (1972) found that *Glossophaga soricina*, *Anoura caudifer*, and *Carollia perspicillata* can be kept in captivity for prolonged periods with low mortality rates. Rasweiler and Ishiyama (1973) noted that *Artibeus lituratus*, *Sturnira lilium*, and *Phyllostomus discolor* also do well in the laboratory over long periods. *Phyllostomus discolor* was an exceptionally adapt-

able captive, tamed easily, and raised young. Most of these same phyllostomatids have bred successfully in the New York Zoological Park colony (House and Doherty, 1975).

Desmodus rotundus can be reared in the laboratory provided reasonable postpartum care is provided. Young animals born in captivity are frequently bitten and killed by older bats. This seldom happens to young attached to their mothers most of the time, but mainly to those that are more mobile, although still unweaned. Perhaps the indiscriminate probing for nursing sites with the wrong adults may provoke the attacks (Wimsatt and Guerriere, 1961). Pregnant or nursing females should be isolated until their young have been weaned, after which they may be returned safely to the colony. Greenhall (1965*b*) stated that although a number of young were born in his Trinidad colony, only a few survived. This was probably due to overcrowding. Females recognized their young, but evidently had great difficulty in protecting them, and youngsters were fatally bitten at the back of the head by other adults. These attacks occurred about the time the young were being weaned. Dickson and Green (1970), noted that *Desmodus* born six months to a year after the mother's capture survived until weaning age and then died, or, in some instances, were apparently killed by bites about the head and neck. They concurred with Wimsatt and Guerriere (1961) in suggesting that the cause was due to overcrowding or competition for food. Subsequently, all pregnant femaels were removed and placed in boxes not containing more than two adult females and under these conditions three bats were reared past weaning age.

The main objection to using phyllostomatids as laboratory animals is their low reproductive rate. This may not be such a handicap when the advantages of easy handling, relatively small size of the subjects, and modest cost of maintenance of large numbers are considered.

Raising Young Bats

There is no information available on raising young phyllostomatids. Gates (1938*a*) successfully raised young *Lasiurus borealis* to adulthood. Skimmed milk (one to two per cent fat) was offered in a spoon three to four times a day and the baby bats readily accepted this diet. After a week, part of the yolk of a hardboiled egg was dissolved in the milk and this agreed with the bats. In due course, the bats accepted egg, bread, cheese, insects, meat, banana, raisin, and a variety of vegetables. Racey (1970) tried unsuccessfully to raise serotines and noctules using Ostermilk (Appendix 18). However, he reared one noctule on cow's milk diluted with a solution of glucose.

Taylor *et al.* (1974) have successfully hand-raised week-old *Eptesicus* and *Antrozous* by means of a stomach catheter. This technique facilitates the control of quantity and quality of nutrition and permits the isolation of the infant from the parent. The diet consists of distilled water to which has been added three parts of Borden's "Esbilac" and one part evaporated milk. The bats are fed at regular intervals, about six to eight times a day until 16 days of age, then four times a day at which time the diet is gradually shifted to a mash or glop.

Health of Captive Bats

Anyone who keeps wild animals in captivity has an obligation to maintain them in the best possible physical condition. Practically nothing is known about the cage ailments and diet deficiencies of bats. The following discussions will be of value in responding to some health problems that may arise.

Ectoparasites

The most obvious external parasites found on captive bats are mites, fleas, ticks, bed bugs, and streblid and nycteribiid flies.

Little is known about the role of ectoparasites or damage to hosts. Certain mites parasitize the dermal tissues of bats forming cystlike structures (Ubelaker, 1970). Macronyssid mites (*Radfordiella*) have been found in the oral mucosa of *Leptonycteris nivalis* causing osteolysis of the hard palate and odontolysis of the teeth (Phillips *et al.*, 1969).

Some biologists have observed that vampire bats, after a short time in captivity, appear to lose their ectoparasites (Wimsatt and Guerriere, 1961; Greenhall, 1965*b*; Dickson and Green, 1970). Rasweiler (1973), however, noted that his captive *Glossophaga soricina* did not lose their streblids. He suggested that survival of these flies indicated that a close approximation to the bats' natural environment was achieved in his laboratory.

Other investigators have preferred to eliminate any possibility of arthropod-borne disease transmission by removing ectoparasites with forceps, tweezers, or chemical washes. To control mites, Orr (1958) bathed bats in warm water containing tincture of green soap. A widely used method is the routine dusting of bats with pyrethrum powder (Orr, 1958; Mohos, 1961; Marshall and Liatt, 1968; Barbour and Davis, 1969; Racey, 1972). DDT is toxic to bats and should not be used to rid them of ectoparasites (Greenhall and Stell, 1960; Luckens and Davis, 1964; Racey, 1972). Uwe Schmidt (personal communication) noted that "it is better to remove ectoparasites as they can multiply in small cages. Once I found 60 ticks on one *Pipistrellus*. To remove ectoparasites, any insect powder will do if it is safe for small pets, chickens, etc."

Endoparasites

Of all the invertebrates associated with bats, only the protozoa are of public health importance and may be of concern to captive phyllostomatids. Ubelaker (1970) mentioned that *Trypanosoma cruzi*, the agent of Chagas disease in South America, taken from a human and from bugs (*Rodnius prolixus*), was ineffective to captive *Phyllostomus*, *Glossophaga*, *Carollia*, and *Artibeus*.

Quarantine

It is strongly advised that bats newly arrived from the wild should be placed in quarters isolated from the main collection until the health status of the newcomers has been evaluated. Local, state, and federal animal regulations pertaining to captive animals must be observed. This information may be obtained from the appropriate authorities.

Diet Deficiencies

During my zoological park experience, I observed that many unhealthy conditions of captive animals could be attributed directly to a faulty diet. Pye (1967) noted that many bats, after a time in captivity on an unsupplemented diet, were prone to listlessness and weakening jaws and limbs, which might be confused by the inexperienced biologist or caretaker with symptoms of a viral infection, such as paralytic rabies. On the other hand, I know of a laboratory containing vampire bats in which the symptoms of paralytic rabies were confused with those of diet deficiency. Nevertheless, I recommend that all bat diets be supplemented with a vitamin preparation. I also suggest that a weight record be kept and that bats be weighed at least once a week as a means of evaluating their condition.

Calcium deficiencies and rickets afflict many captive animals, and bats are no exception. Several cases of rickets have been diagnosed in young vespertilionid bats by Racey (1972), who corrected this condition by the addition of calcium to the bran diet for his mealworms.

The symptoms of a calcium-phosphorous imbalance, parathyroid disturbance, or vitamin D deficiency may resemble those of paralytic rabies (Constantine, 1970). Buckland-Wright and Pye (1973) described the fatal symptoms in some pteropodids, which followed the common pattern of a calcium-phosphorous imbalance as, "hyperexcitability during handling or other disturbance giving a tetanic condition with the wings partly unfolded, leading to death within minutes of an apparently healthy animal." There is no information concerning these conditions among the phyllostomatids but it is possible that they have occurred and have gone unrecognized among captives.

Diarrhea

Diarrhea may be a symptom of conditions ranging from diet deficiencies to baccillary infection, food poisoning, or unsanitary cages. Diarrhea may develop if the consistency of a food mixture is too thin. Chronic diarrhea and underfeeding may result from providing food so early in the day that wet mashes and other diets have begun to spoil before all bats have fed (Rasweiler, 1975). Gates (1936) was the first to discover (and other biologists have agreed) that chitin of insects is essential for the proper formation of fecal pellets in truly insectivorous bats. Racey (1970:179, 1972:302) found that his vespertilionid bats did not do well on an insect-free diet.

Loss of Hair

Too much cottage cheese in the diet may result in some hair loss (Racey, 1970, 1972). Orr (1958) attributed loss of hair to the high protein content of food he fed his insectivorous bats. *Antrozous pallidus* and *Tadarida brasiliensis* in his laboratory suffered loss of hair for over a year. They recovered normal pelage in a few months, however, following the use of the Stuart Formula Liquid—one drop per day per bat, administered by a small pipette inserted into the bat's mouth. Pye (1967:494) stated: "There is some evidence that preparations containing an excess of vitamin A can cause reversible depilation in both Mega-

chiroptera and Microchiroptera. This condition is unsightly, but there do not seem to be any other adverse effects. After some time in captivity on unsupplemented diets, many bats are prone to weakening of the jaws and limbs, and general listlessness. Stuart Formula Liquid effects a complete cure in some cases." Others have noted that bats fed on artificial diets sometimes lose their hair and that multiple vitamins added to the diet corrected the condition (Mohos, 1961; Davis and Luckens, 1966; Barbour and Davis, 1969).

Rasweiler (1975) mentioned correspondence from J. Frederick Bell, who found that food containers must be kept clean to prevent the loss of hair on bats' bellies. Rasweiler (1975) also observed that individuals of *Artibeus lituratus*, unable to fly in small cages, were forced to crawl and rub against the cage wire, which resulted in the loss of ventral hair. Uwe Schmidt (personal communication) discovered that large numbers of ticks on a bat will cause lose of hair through constant scratching by the bat in an attempt to remove the parasites. Temporary relief may be provided by washing the affected area of the bat with soap and lukewarm water.

Sore Limbs

Swelling of the wrist joints was observed by Orr (1958), who thought that the high protein content of food, after a year or two, may have caused this condition. Some bats will develop sores on the bottom of their feet from resting on a horizontal surface such as the bottom of a box or bottle. To correct this condition Barbour and Davis (1969:246) suggested fixing a screen to permit the bats to hang head downward. Racey (1970) believed that swelling of joints in noctules might be associated with the lack of exercise. Some pteropodids and possibly other large bats such as *Vampyrum*, which normally hang pendant and free, may suffer from sore feet if not supplied with proper roosting surfaces such as tree branches. Excessively curved claws may result from continued hanging on wire (Pye, 1967).

An excessively dry atmosphere in a laboratory may result in dry and brittle wing membranes. Raising the relative humidity and the application of a moistening skin lotion or baby oil may remedy the ailment.

Food Poisoning

Uwe Schmidt (personal communication) described some deaths in his *Desmodus* colony that he attributed to food poisoning. The condition may appear suddenly, even after bats have been in captivity for several years. Schmidt observed that "bats hung with stretched legs from the cage top and regorged blood (stomach was always completely filled) while urinating bloody urine." The cause, Schmidt believed, was ingested spoiled blood. Spoiled blood does not appear to be distasteful to vampires. Some bats died; others recovered. The animals that survived drank great amounts of water. The dead bats tested negative for rabies.

Exercise and Obesity

There are various opinions on the exercise requirements of captive bats. Orr (1958) found that *Antrozous*, like many captive animals, tends to overeat once accustomed to captivity. If more than one bat is in a cage, it is unwise to limit the amount of food offered because aggressive bats may consume more than their share. Overeating will lead to obesity and one solution is regular exercise. This may be accomplished by permitting the bats to fly in a room. Mohos (1961) provided a large room, 5 by 9 meters, for bats to fly unhindered on the assumption that exercise would keep them in good condition. The exercise flight was satisfactory for small numbers of bats. The practice was later discontinued due to accidents and high mortality when hundreds of bats were exercised at once. However, when the exercise was stopped, single and multiple pyogenic infections developed in many of the animals. Racey (1970) believed that flying is not a practical exercise for large-scale bat husbandry, but did mention conditions he thought to be caused by the lack of exercise. His serotines often developed sore wrist joints and occasionally fatal wrist joint infections of *Pseudomonas aeruginosa*. The wrist joints of his noctulus also became stiff and infected.

Wimsatt and Guerriere (1961) observed that, although exercise for vampire bats might be desirable for physiological reasons, their bats appeared healthy and vigorous without exercise. *Glossophaga* and *Carollia* are able to exercise within small cages because they can hover. Aldo M. Voûte (personal communication) reported that the best way he found to keep captive bats in good condition was to place their cage in a large room and allow them to leave the cage and fly about in search of food as they wished. Food was located at a specific spot on a shelf; the bats learned to find the food and always returned to their cage to roost.

Miscellaneous Laboratory Techniques

Anesthesia and Euthanasia

The use of anesthetics and euthanasics in laboratory animals is often necessary for humane and technical reasons. Muscle relaxants or paralytics are not anesthetics and should not be used alone for surgical restraint. They may be used for surgery in conjunction with drugs known to produce adequate analgesia.

Ether is an anesthetic used by many biologists. Mohos (1961) administered ether from a regular dripping bottle onto a small, gauze-lined, wire-mesh basket covering the bat's nose and mouth. Precautions must be taken to avoid heavily soaking the gauze inasmuch as the bat may swallow the ether and die. The depth of anesthesia can be regulated and recovery is usually fast and uneventful. Excessive ether may be used for euthanasia because bats have a narrow tolerance range for this anesthetic.

Mohos (1961) found that nembutal, although easier to apply than ether, gave less satisfactory results. Pye (1967) preferred pentobarbitone sodium (nembutal) instead of ether and used one volume of commercial solution to nine volumes of 10 per cent ethyl alcohol injected intraperitoneally to induce surgical anesthesia,

at 30 to 50 milligrams per kilogram of body weight. There is considerable individual variation in response and the bat should be fully aroused before injection, and a constant body temperature of 37° to 40°C must be maintained afterwards to ensure successful anesthesia and recovery. Overdosage with nembutal may be used to kill bats humanely (Pye, 1967).

To anesthetize safely vampire bats, Dickson and Green (1970:43) introduced a mixture of oxygen (2 liters per minute), nitrous oxide (1 liter per minute), and fluothane (halothane, 2.5 units Fluotec scale) into the cages. The bats were anesthetized in four to five minutes and recovered completely in three to four minutes. No bats died as a result of this method. Racey (1972) preferred the halothane/oxygen method of anesthesia for vespertilionid bats.

Marking Bats

Various methods are employed to mark bats for individual recognition. Numbered metal bands attached to forearms have been widely used. Another method utilizing differently colored plastic bands, such as used for cage birds, is satisfactory for a small number of bats. Some phyllostomatids, such as *Glossophaga soricina*, have a peculiar structure of the antebrachial membrane that makes attachment of bands to the forearm difficult. Neonates, the forearms of which are too small to take bands, may be numbered on the wing membrane with a tatooing forceps (Racey, 1970). This method is useful only for short-term marking, because the small holes outlining the numbers heal over and become obliterated in a few days. However, the holes can be reopened with a suitable needle without danger of infection. When scar tissue forms, it is often unpigmented and the number can be recognized for several weeks.

Rasweiler (1975) marked bats by means of spots bleached onto their fur. "The bleaching solution consists of six per cent H_2O_2, Lady Clairol Protinator and Lady Clairol Cremogenized Hair Lightener [Appendix 18] in the proportions of 10:2:5 respectively. The H_2O_2 and protinator are mixed vigorously for about five seconds in a small vial. The lightener is then added, and the mixture agitated for another 20 seconds. The working solution retains its activity for at least an hour after preparation. Immediately after the application of small amounts of the bleaching solution with a brush, the bats may be released back into their cages." Up to 30 different numbers are possible by varying the combination and position of the spots on the back and head of a bat. Several hundred *Glossophaga* and *Carollia* have been so marked, with only a few minor cases of hair loss in adults and skin damage in juvenile *Carollia*.

Cesarian Section

Adams and Baer (1966) described cesarian sections used on *Tadarida brasiliensis*. Ether was used. The hair of the abdomen was clipped and the area dampened with one per cent bensalkonium chloride. A midline incision was made through the skin and abdominal musculature with a scalpel, and the right horn of the uterus withdrawn. The uterine wall was carefully incised and the infant bat quickly withdrawn; fluids immediately were sucked out of its mouth

with a pipette or wiped out with a cotton swab. The umbilical cord was clamped with a hemostat, ligatures tied on either side of the hemostat, and the cord cut. It was necessary to perform the entire procedure rapidly because any delay meant increased mortality in the young. All young, after drying, were placed in an incubator (37°C) on a slightly moistened towel. No mention was made of whether any females survived the operation.

Extraction of Bat Milk

To determine some of the chemical and physical properties of bat milk, Huibregtse (1966:551) related a technique for removing milk from lactating *Leptonycteris sanborni* and *Tadarida brasiliensis* as follows: "The animals were lightly anesthetized with sodium pentobarbital (60 mg 20 ml). . . . A dose of 0.03 to 0.10 ml of the anesthetic was found to be satisfactory. This was administered prior to an injection of oxytocic hormone (Pitochin, Parke-Davis) of less than 0.1 ml. The mammae were bathed with warm water, and the milk expressed manually with thumb and index finger. The extruded droplets were collected in a small pipette on a rubber tube (a hemocytometer pipette served well)." A small drop of 10 per cent formalin was added to preserve refrigerated samples.

Bleeding Bats

Basic extraction techniques have been devised to obtain blood from bats, and two are generally used—one from the heart, the other from the eye. Cardiac puncture is the technique most widely used. Disposable needles and syringes are recommended. The appropriate needle size depends on the size of the bat. For bats of average size, Sudia *et al.* (1970) recommended a 25-guage, 3/8 to 5/8-inch needle. A 2-milliliter syringe is satisfactory. A suitable supply of needles are heparinized by drawing a one per cent solution of heparin through them and then allowing the needles to air-dry. The puncture site should be cleaned and disinfected before inserting the needle into the heart.

Some investigators prefer to take blood from the orbital sinus. Sudia *et al.* (1970) have described this method. The anesthetized bat is held firmly in the left hand, the thumb exerting sufficient pressure just behind the eye to cause it to bulge slightly. A microsampling pipette (hematocrit) of either a 50 or 100 microliters is inserted into the posterior orbit of the eye (carefully pushing the eyeball to one side to avoid damaging it) and gently rotated so that the capillaries are ruptured against the bone and thus initiate the flow of blood. Once the flow is started it is necessary to draw the tube back slightly and incline it downward. Usually the blood flows freely into the tube, at times so profusely that two tubes can be filled easily; sometimes, however, it is necessary to repeat the rotation a few times. The pipette is then discharged into a tube containing a measured volume of diluent. The hematocrit tube or microliter tube may be heparinized. A 50-microliter pipette will take up to 0.1 ml. of blood and a 100-microliter pipette will take up to 0.2 ml. blood (the amount usually taken from each bat). Larger amounts of blood may be obtained by holding the bat between the thumb and first and second fingers to apply pressure to the thoracic area. Apparently,

this raises the blood pressure and increases the yield of blood from the orbital sinus. Bats bled in this manner do not appear to be harmed seriously and such bleeding may be continued daily for up to 10 to 15 days if necessary.

Urine Collection

Bladder catheterization has been the technique used to obtain urine samples from small animals. The usual techniques require either continuous anesthesia, restraint, or extensive surgery. Kanthor (1965) devised a method of repeated and accurate urine collection from unrestrained *Myotis lucifugus* (body weight about 7 grams). He wrote (p. 326): "We developed a catheter which could be passed through their extremely well-developed urethral spincter with a minimum of subsequent irritation. Moreover, it prevented leakage and retention of urine in the bladder, while ensuring free passage to permit collection of serial samples over extended periods. Females were animals of choice as the use of these catheters in males involved extensive surgery." The bats were anesthetized with ether. More than 50 bats tolerated the procedure and none tried to remove the catheter. The catheters permitted freedom of movement under all conditions and remained functional for up to three days.

Saliva Collection

Dickson and Green (1970:41-43) required the collection of saliva from *Desmodus* and *Diaemus*. These biologists developed an ingenious plastic box for the safe restraint of these bats. The vampires first are anesthetized as described under "Anesthesia." They then are placed in the salivation units so that pilocarpine can be administered to the buccal mucosa and the saliva collected as described in detail by the investigators.

Operant Conditioning for Experiments

Bats, unlike most mammals, cannot operate the conventional gadgetry normally used in experimental situations with either of their specialized limbs. Beecher (1971) demonstrated that *Phyllostomus hastatus* could operate a conventional pigeon key by either nosing or licking it. Schmidt and Greenhall (1972) found that *Desmodus rotundus* would respond quickly to training. Their bats were conditioned to feed at an observation table from 1100 to 1300 hours. After a dish of blood was placed on the table, the cage was opened and a conditioning noise was made by scraping two forceps together. Conditioning could take up to a week, but, when bats were trained, they usually flew to the experimental table within five minutes after the noise in anticipation of a meal. After the bats were trained, a variety of small animals were introduced into the cage so that the investigators could observe and photograph the vampires as they stalked, attacked and fed on their prey. Thus, Schmidt and Greenhall had to wait approximately five minutes before they were able to observe the feeding behavior that otherwise might have required several hours.

Bat Brain Removal

Bats that have bitten people should be killed and sent to a diagnostic laboratory for examination. For the purposes of accurate taxonomic identification, the head probably is the most important part of the animal to the mammalogist, whereas brain and other body tissues are of paramount importance to the epidemiologist. The conventional laboratory techniques used for brain tissue removal for rabies diagnosis frequently mutilates the skin and skull, not only making accurate identification difficult but often completely ruining the specimen for museum purposes. To solve this problem, Greenhall (1965*a*) devised methods for tissue removal, with little or no head and body damage, that proved satisfactory to both mammalogist and epidemiologist. In the case of extremely small bats, or those with specialized attachments between the ears or unusual glandular structures on the head, it is unnecessary to open the brain case because sufficient brain tissue may be hypodermically withdrawn through a needle inserted into the foramen magnum without damage to the skull.

Human Health Problems

The World Health Organization (1973) reported that increasing numbers and kinds of animals are now used in biomedical studies. Zoologists should be aware that bats may carry diseases and, therefore, may be a hazard to human and animal health. Jones in his chapter on economics and conservation (this volume) has discussed the diseases occurring in wild phyllostomatids that may be transmitted to humans and livestock. A comprehensive review of zoonoses and bats was presented by Constantine (1970). There is always the risk that biologists and technicians working with captive bats may contract an infection from the parasites, urine, feces, skin, blood, and other tissues from their own laboratory animals. Yunker (1964) has reviewed some of the common arthropod associates of laboratory animals that are hazardous to man. The public health importance of Neotropical bats has been discussed in detail by Greenhall (1964), Acha (1967), Chalmers and Scott (1969), and Tamsitt and Valdivieso (1970).

Because little is known about the health of captive bats, any information on the causes of death in the laboratory is of value and autopsies should be performed when possible.

Personnel Precautions

All persons handling captive bats or in contact with them should be aware of the possible health risks in their routine work. Simple hygiene precautions should be observed, such as washing the hands after handling animals or immediately on leaving the animal facilities. In my laboratories, I have used wall-mounted dispensers containing either tincture of green soap, rubbing alcohol, or other general antiseptics. Laboratory coats should be worn to protect clothing. Handling bats with bare hands should be avoided if possible and leather gloves should be worn as a protection against bites. Rubber or disposable plastic gloves should be used while performing operations and autopsies. All cuts and abrasions

should be cleansed immediately and a good first aid kit should be easily accessible. Particular care should be given to eye protection and glasses or goggles should be worn when conducting postmortem dissection on suspected rabies cases. Disposable paper face masks serve as some protection against the inhalation of dust and spores and are recommended for persons suffering from allergies and respiratory ailments. Whether these masks are effective against infectious aerosols is not known. Strict adherence to all laboratory safety rules should be compulsory for staff as well as visitors.

Clinical Symptoms of Infections

Many people working with captive animals are not aware of the clinical signals that may be indicative of an infection acquired through exposure to miscellaneous animal material. If the symptoms fail to be resolved quickly, medical advice should be obtained. Irvin *et al.* (1972) listed the following symptoms: 1) allergies such as asthmalike symptoms of running, itching, and burning eyes, and skin hypersensitivity and irritation; 2) skin infections; 3) respiratory symptoms, especially a persistent cough, sore throat, or running nose; 4) influenza-type symptoms; 5) local inflamation and infection, expecially on the hand or exposed parts of the body; 6) swelling of lymph nodes; 7) generalized symptoms such as fever, headache, vertigo, diarrhea, nausea, vomiting, and malaise.

Rabies

Rabies is perhaps the greatest threat to the chiroptologist because any bat may contract rabies. A number of phyllostomatids (notably *Phyllostomus*, *Glossophaga*, *Carollia*, *Artibeus*, *Desmodus*, *Diaemus*, and *Diphylla*) have been found to be positive for rabies and these bats should be considered as potentially dangerous laboratory animals (Acha, 1967).

Dickson and Green (1970) emphasized that vampires from areas that are endemic for rabies should be kept only in laboratories especially equipped for the protection of the staff. The precautions observed in their laboratory are as follows (pp. 37-38): "The bats are housed in a quarantine room, which may be entered only by persons immunised against rabies; gowns, masks and gloves must be worn at all times; all waste materials are sealed in sacks before removal from the animal room, and autoclaved prior to disposal; the brains of all bats which die are removed and examined for rabies virus."

Rabies in a laboratory colony of vampire bats.—The unexpected appearance of rabies in a laboratory colony of vampire bats demonstrates the importance of quarantine measures and the practical value of using cages in which the bats are visible at all times. "The following incident is of interest because it was contrary to the usual pattern of behavior of vampires in captivity (Horst and Langworthy, (1972:903).

"In January 1970, 30 vampire bats (*Desmodus rotundus murinus*) were collected from . . . Mexico. The acclimation of these bats to laboratory conditions followed the pattern described by Wimsatt and Guerriere (1961) and 20 bats survived this adjustment.

"On 29 January 1971, 30 additional vampire bats were obtained in . . . Mexico and added to the 15 remaining animals in the laboratory colony. After a week of adjustment during which five of the new animals succumbed, the colony was stable and no unusual events occurred until the first week of April, two months later. Up to this time the bats, when disturbed, normally would bunch together, hiding in the darkest corner of the cage. However, beginning about 1 April 1971, there was intense fighting at the slightest disruptive stimulus, such as switching on the lights, moving the cage, or sudden loud noises. These fights were so intense that the entangled pairs would fall . . . onto the floor, still screaming and viciously biting each other." Mortality occurred at a rate of about one bat per day for about two weeks. Those bats checked by the fluorescent antibody method were positive for rabies.

Horst and Langworthy (1972:904) correctly recommended that "individuals who maintain these animals in captive colonies are well advised to take proper quarantine precautions with recently captured vampires, lest they suffer a similar loss of valuable animals." Although Wimsatt and Guerriere (1961) described their routine care and maintenance of vampires, I could not find one mention of the pattern of acclimation of bats referred to by Horst and Langworthy (1972:903).

Nonbite rabies in laboratory animals and technicians.—Winkler *et al.* (1972, 1973) reported an unusual outbreak of nonbite transmitted rabies in a laboratory colony of wild carnivores and a fatal case of nonbite rabies in a laboratory worker possibly caused by a strain of bat rabies virus. Sixty-four animals died, including 39 that had no known exposure history. The human victim had been vaccinated against rabies 13 years earlier, but had not developed demonstrable serum antibodies. Investigation confirmed that direct contact transmission did not occur and suggested that airborne bat virus may have been responsible. The human case emphasizes the necessity for biologists and technicians working with potentially rabid animals to be immunized, followed by verification of demonstrable serum antibodies.

Preexposure immunization.—The best protection against rabies an individual can have is preexposure vaccination, as recommended by the United States Public Health Service (1974:16) and the World Health Organization (WHO) Expert Committee on Rabies (1973:30): Preexposure immunization consists of three injections of duck embryo vaccine (DEV) spaced over a period of several weeks, followed by a booster injection of vaccine one month later, and lastly by the confirmation of antibodies (that is, immunization) in the serum of the vaccinated individual. If negative, booster doses should be repeated until antibodies become demonstrable. Further booster injections should be given at intervals of one to three years as long as the person remains exposed. Some people have been reluctant to accept the preexposure immunication because of the misconception that the regimen required a large number of daily injections.

First aid treatment for bite wounds.—According to the WHO Expert Committee on Rabies (1973:28) and Kaplan (1973:15-16), the most important first aid treatment for all bite wounds and scratches in preventing possible rabies infec-

tion is the gentle washing and flushing of the wounds with soap and water, detergent, or water alone. Next apply either 40 to 70 per cent alcohol, or a 5 to 7 per cent tincture or aqueous solution of iodine, or 0.1 per cent quaternary ammonium compounds, which can kill rabies virus on contact within one minute. Alcoholic beverages of 86 proof or greater can be used in emergencies. When soap has been used to clean wounds, all traces of it should be removed before the application of quaternary ammonium compounds because soap neutralizes their activity. The WHO Expert Committee on Rabies (1973:28) stated: "Although judicious use of concentrated nitric acid in puncture wounds has its advocates, there is no evidence that this product is more effective than quaternary ammonium compounds or 20% liquid soap solution."

Postexposure treatment.—The United States Public Health Service (1974:1) has recommended the following postexposure treatment against rabies. "If an immunized person is bitten by a rabid animal [bat], the rabies virus stimulates rapid production of antibodies because the individual has already been sensitized by his preexposure vaccination. Therefore, an immunized person needs only 1 to 6 doses of DEV [Duck Embryo Vaccine] even after being bitten by a known rabid animal, instead of the regimen of antiserum and up to 23 doses of DEV recommended for an unimmunized person in the same situation. But, most importantly, a person who has received pre-exposure vaccination and receives 6 doses of vaccine after exposure is considered significantly better protected than someone who receives only the full post-exposure regimen of antiserum and vaccine."

The physician attending a bite exposure must decide whether antirabies treatment is indicated and, if so, must administer the most effective treatment available to him. If serum is indicated, the physician must first test for allergies and check the patient's history for allergenic reaction. At present the duck embryo vaccine (DEV—Eli Lilly & Co., Indianapolis, Indiana) is the most widely used in the United States. Newer and safer vaccines such as the Wistar Vaccine, are being investigated. Physicians are strongly urged to check for the most recent recommendations at either of the following two World Health Organization Rabies Reference Centers located in the United States:

United States Public Health Service
Center for Disease Control
Bureau of Epidemiology, Viral Zoonoses Section
Atlanta, Georgia 30333
Telephone (404) 633-3311, Extensions 3415 or 3683
After 5 p.m. (404) 633-2176
or
The Wistar Institute
Rabies Division
36th Street at Spruce
Philadelphia, Pennsylvania 19104
Telephone (215) EV 7-6700.

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APPENDICIES

1. *Cage and Roosting Box for Nectarivorous Bats*

The following cages are comparable in design, but the dimensions described by Rasweiler and de Bonilla (1972:660) are more desirable than those described by Rasweiler (1973:392). The Rasweiler and de Bonilla cage measured 80 centimeters high, 92 centimeters deep, and 138 centimeters wide. The right end is completely enclosed by plywood to form a darkened roosting box with an exit hole, 25 centimeters wide by 15 centimeters high, leading to a wire-enclosed feeding area. This roosting box measures 80 centimeters high, 92 centimeters deep, and 51 centimeters wide. Aside from the cage floor and the front and back of the roosting box, all cage surfaces are lined by 1/4-inch galvanized hardware cloth. Access to both the roosting box and the feeding area is gained by means of double doors. The cage floor consists of two metal pans that are covered with paper or dried clay chips. Rasweiler (1975) further modified the cage by attaching thin sheets of galvanized iron to the under surface of the roof, immediately above the food dishes, to discourage roosting in an attempt to minimize fouling of the food by feces. See Rasweiler and de Bonilla (1972:659) and Rasweiler (1973:392) for illustrations of these cages.

2. *Cage and Roosting Box for Frugivorous and Omnivorous Bats*

The *Artibeus lituratus* and most *Phyllostomus discolor* kept by Rasweiler and Ishiyama (1973:57) "were housed in wood and wire cages (cage dimensions: 90 cm high × 70 centimeters wide × 90 centimeters deep; removable roosting box: 20 centimeters high × 67 centimeters wide × 30 centimeters deep) that are a modification of the Wimsatt vampire cage" [see Appendix 3 and Wimsatt *et al.*, 1973:252]. All inner surfaces except the floor are wire-lined, and only the roosting box is surrounded by plywood in addition to the wire. *Sturnira lilium* and some *P. discolor* were kept in cages of the design described in the Appendix 1. See Rasweiler and Ishiyama (1973:58) for a diagram of this cage.

3. *Cage and Roosting Box for Sanguivorous Bats*

The materials used for the construction of this vampire bat cage (Wimsatt *et al.*, 1973:252) are stainless steel (18 gauge) and stainless wire mesh, with welded construction throughout. The front panel and the compartment insert are plexiglass and the detachable paper roll brackets are aluminum. Overall outside dimensions are 50.8 by 50.8 by 50.8 centimeters. Inside dimensions of the removeable roosting compartment are 48.3 by 20.3 by 15.2 centimeters; its door panel measures 15.2 by 12.7 centimeters. This compartment is lined with stainless mesh on all sides except the back, which contains the door. The compartment plexiglass insert, which is used to close the bottom of the roosting box, is accommodated on each side by a shallow metal trough in which it freely slides. Metal flanges position and support the removable roosting compartment within the cage interior. A similar flange along the bottom of each side wall of the main box prevents the fall of excreta on the edge of the floor paper. The sliding front panel of the cage is removable and contains a hinged plexiglass door that measures 20.3 by 25.4 centimeters. Ventilation is provided by a few holes high in the sides and in the plexiglass front panel. This cage will easily accommodate 15 to 20 vampires.

See Wimsatt *et al.* (1973:252-254) for diagrams of this cage. Photographs and diagrams of the vampire bat cages used by Wimsatt and Guerriere (1961:452-453) also may be useful.

4. *Cage for Vampire Bats*

Dickson and Green (1970:39-40) originally housed their bats in wire mesh cages 60 centimeters long, and 30 centimeters wide, with 15 to 20 bats per cage, but these cages proved to be unmanageable and extremely difficult to clean. They decided that a smaller, lighter, and easier-to-handle cage facilitating frequent changing and cleaning was needed.

Their new cage was described (p. 39) as follows: "Translucent polypropylene rat cages 35 × 26 × 17 centimeters (North Kent Plastic Cages Ltd., Home Gardens, Dartford, Kent) have been adapted for use. New stainless steel mesh tops were made by the manufacturer which dispensed with the pellet and water hoppers.

"A small hole was made in front of the box and a 'Terry' clip fixed above it to hold the food hopper . . . The polypropylene trays placed under the cages are lined with absorbent, disposable cardboard trays to collect faeces and any spilled blood . . . The cages and trays are supported in a tubular steel, double-sided rack, capable of holding 40 such cages, each cage containing 5 bats. Strips of black plastic are laid above the cages to keep out most of the daylight, to simulate the bats' natural environment. The bats do not attempt to chew at the plastic boxes or covering sheets."

Photographs of these cages are found in Dickson and Green (1970:38-39).

5. *Flight Cage for Vampire Bats*

Schmidt and Greenhall (1972:242-243) housed a "small colony of vampire bats (two males, three females) . . . in a flight cage (5 × 5½ × 3 meters) closed on one side by 1.3 centimeters mesh; the other three sides were solid wall. This flight enclosure contained a roosting cage hung in one corner and an observation area at the other end. The roosting cage (40 × 40 × 50 centimeters) was made of wire mesh and contained two small wire mesh partitions and a wooden sliding door. The walls and floor of the flight cage were covered with plastic sheeting, replaced as necessary to keep the enclosure clean.

"The observation feeding area consisted of a table (100 × 80 centimeters) with a wire mesh bottom and a removable tray underneath. Three sides of the table were enclosed by wood panels 50 cm high, while the fourth side was of glass. Our observations were made through this glass window. From 8 a.m. to 8 p.m. [0800 to 2000 hrs.] the observation table was illuminated by one 20 watt red fluorescent tube. At night the entire room was illuminated by three 40 watt white fluorescent tubes. The light changes were controlled automatically. Temperature was maintained between 25°C and 30°C, with the relative humidity maintained above 55%. A small exhaust fan circulated air in the room."

6. *Flight Cage for Vampire Bats*

The vampire bat flight cage devised by Rexford D. Lord (personal correspondence) measures one cubic meter. The walls and roof are made of plexiglass bound to an aluminum frame. The cage door may be pulled up by a cord attached to a counter-weight and is large enough to permit entry for cleaning. The door is made of glass, which is clearer than plastic and facilitates observation and photography. The cage floor is covered by thin plastic sheeting dispensed from a roll. Two roosting boxes, about 25 centimeters square, are located above and outside the cage. Each may be closed by a sliding panel and the roosting boxes can be removed with the bats inside. The hole left after removing a roosting box can be sealed with another sliding panel. Both roosting boxes have plexiglass fronts. Food is provided in blood tubes inserted through holes in the lower portion of the front of the cage. Additional holes in the top of the cage and each roosting box provide ventilation.

7. *Cardboard Bat Cage*

Constantine (1952:396) provided the following information: "Each bat was housed separately in a pint-sized ice cream carton with screen lid. This carton served as sleeping and eating quarters. During the sleeping period a cylinder of plastic window screen, the length of the carton and slightly smaller in circumference, was placed inside the carton in order that the bat would have vertical footholds for assuming a head-downward position. During the feeding period the cylinder was removed to encourage the bat to remain on the floor of the carton and thus be in immediate contact with the mealworms which were placed there at the beginning of that period."

8. *Cardboard Bat Cage*

Tesh and Arata (1967:106) wrote as follows: "Bats were housed individually in marked, half-gallon, cardboard [ice cream] containers. This type of container was selected because it could be autoclaved easily, was relatively inexpensive, and could be discarded after several days of bat excrement had accumulated. A hole (8 centimeters in diameter) was cut in the lid of each container, and a piece of metal house screen (approximately 10 centimeters in diameter) was then fitted and stapled to cover the hole . . . This allowed for air exchange and provided the bats a rough surface to which they could attach their feet and hang in their preferred head-downward position. The lids were autoclaved and re-used; only the bottoms of the containers were discarded.

"As a security measure, cardboard containers housing bats were kept within metal rabbit cages. The sides of these cages were covered with heavy brown paper to exclude light and keep the interior of the cage dark, thus approximating the bats' natural habitat."

9. *Food Mixture for Insectivorous Bats*

This food mixture was developed by Walker (1966:138) and probably was patterned after the original formula for glop. This, his most recent recipe, was relished by shrews, moles, some monkeys, and many insectivorous bats: one yolk of a hard-boiled egg; approximately equal amounts of cottage cheese, ripe banana, and meal worms; six drops of Jeculin (or Jeculin powder from a capsule) dissolved in a few drops of water; six drops of wheat germ oil; three grains Theragran.

"If the wheat germ oil is in 3-minim capsules, cut in half; also add the Theragran, which is a yellowish paste. Add a few drops of water to soften the gelatin of the wheat germ oil capsules and to dissolve the Theragran. Thin out in the other ingredients and grind together in a mortar with pestle until a paste is formed with the chitin of the worms scattered through it.

"Fresh avocado is relished by many small creatures and can be mixed with the formula or used separately as a supplement.

"One zoologist who fed this formula to noctule bats for a year noticed white spots developing on the wings. These disappeared when the following formula was added to the one given above:

30 gr. calcium phosphate	10 mg. manganese sulfate
30 gr. calcium lactate	50 mg. ferrosulfate
15 gr. yeast	30 mg. copper sulfate
100 gr. bonemeal vita-chalk	900 mg. natrium chloride (perhaps not essential)
10 mg. cobalt sulfate	trace elements

"Several different kinds of bats other than noctules have been fed this food mixture without the addition of the last formula for periods up to seven years without apparent dietary deficiencies. However, the American *Plecotus* does not survive on the mixture."

10. *Mash for Insectivorous Bats*

This formula is taken from Davis and Luckens (1966:225-226): one part ripe banana; one part dry curd cottage cheese or cream cheese; one part canned dog food; one part mixed insects (obtained from light traps) or mealworms; a few drops multivitamin preparation.

The ingredients (equal parts by weight) are run through a meat grinder and then mixed by hand. The final mixture must be of firm consistency; if too thin, the bats eat poorly and develop diarrhea. It may be stored in a freezer or will keep about one week in a refrigerator. Each bat was fed about three to five grams of food per day.

11. *Artificial Diet for Nectarivorous Phyllostomatid Bats (Bronx Zoo Diet)*

This formula is from House and Doherty (1975): one pound honey; three-fourths of a cup condensed milk; 12 teaspoons Mellin's Food; six teaspoons Super Hydramin; 1.8 cubic

centimeters multivitamin drops (Vi-Penta); six teaspoons Marine Protein Concentrate; three teaspoons beef extract. Add water to make one quart and blend. Then add two quarts of water and stir. Amount sufficient for approximately 50 bats.

12. *Artificial Diet for Nectarivorous Phyllostomatid Bats*

This formula was given by Rasweiler and de Bonilla (1972:661) and Rasweiler (1973: 394): 700 milliliters fruit base (peach nectar or guava nectar); 29.52 grams cereal (high protein); 4.92 grams wheat germ; 12.81 grams milk powder; 20.39 grams calcium caseinate; 68.00 grams sugar; 3.99 grams protein (Gevral); 1.68 grams mineral supplement; 0.69 grams vitamin mix; 9.00 milliliters corn oil mixture; 300 milliliters water.

To facilitate suspension in the liquid diet, the cereal and wheat germ are reduced to a fine powder by passage through a coffee mill prior to their mixture with the other dry components. The dry mixture can be stored at 4°C until use. The composition of the corn oil mixture (polyoxyethylene sorbitan mono-oleate as an emulsifier and isopentylacetate as a flavoring agent) can be stored at 4°C until use. The final diet consisting of peach nectar, the powdered premix, and the corn oil mixture is prepared freshly each day in an electric blender and served to the bats in shallow dishes. The amount offered by Rasweiler and de Bonilla was approximately 24 milliliters per bat per day.

13. *Artificial Diet for Nectarivorous Bats*

This formula was provided by Donna J. Howell (personal correspondence): 10 eggs; nine tablespoons Brewer's yeast; nine tablespoons instant protein (Alpine Marine); one tablespoon bone meal; 18 capsules amino acids (Wolin's); 18 cubic centimeters multivitamin drops (Poly-Vite Wolin's); 18 ounces (2¼ cups) condensed (*not* sweetened) milk; three pounds honey or strawberry jam; two small jars "high-meat diet" baby food (strained beef or chicken); three-fourths beef extract (Difco Culture Medium); 18 tablespoons Super Hydramin (Nion).

Mix the ingredients well in blender, add six quarts water, and mix again. Makes one and a half gallons. The mixture is frozen in pint containers and used as needed. Each jar must be shaken very thoroughly before it is poured into bat feeders. The beef extract provides salt.

14. *Banana-based Diet for Frugivorous Phyllostomatid Bats*

This diet was taken from Rasweiler (1976) and Rasweiler and Ishiyama (1973:59): 700 grams banana; 9.87 grams wheat germ (pulverized in a coffee mill); 12.90 grams whole milk powder; 24.00 grams calcium caseinate; 24.48 grams sugar; 4.04 grams protein (Gevral); 1.71 grams mineral supplement; 0.70 grams vitamin mix; 8.68 milliliters corn oil mixture.

The bananas are cut into slices 1-centimeter thick and gently mixed with the other ingredients. The slices are kept intact so that the bats can hold and carry away the pieces. An excess of food is provided. The daily amount offered each bat is approximately 32 grams for *Artibeus lituratus* and *Phyllosotmus discolor*, and about 20 grams for *Sturnira lilium*.

15. *Bronx Zoo Diet for Frugivorous Phyllostomatid Bats*

House and Doherty (1975) used this diet for their frugivores: 24 bananas; one apple; one-fourth pound grapes; 5 ounces Zu/Preem Primate Diet (canned); four ounces Zu/Preem Feline Diet (canned); six tablespoons Mellin's Food; six tablespoons Super Hydramin. The daily quantity fed was approximately 25 to 30 grams per bat *ad libitum*.

16. *Bronx Zoo Diet for* Phyllostomus hastatus

House (1968:141) used this formula to maintain *Phyllostomus hastatus*: 50 per cent bananas; 30 per cent grapes; 20 per cent chopped meat; vitamin supplement; one teaspoon Mellin's Food (per day). The daily amount offered each bat was approximately 35 grams *ad libitum*.

17. *Diet for Frugivorous and Omnivorous Phyllostomatid Bats*

Donna J. Howell (personal communication) recommended this formula for maintaining frugivorous and omnivorous phyllostomatids: 10 bananas (very ripe, chopped); three to four cups melon pieces (cantaloupe or honeydew); eight ounces cottage cheese; one pound hamburger or one can dog food; one-fourth tube beef extract; one-half Pervinal powder (available in pet stores); two eggs.

This should be tossed to mix, or else the first bat at the dish will eat all the choice pieces. However, it should not be mixed into a mush or paste because bats will get the mush on themselves in their enthusiasm and competition for the food. If bats are obviously pregnant, condensed milk and bone meal should be added. The formula has proved satisfactory for *Phyllostomus hastatus*, *P. discolor*, *Carollia*, *Artibeus*, and *Sturnira*.

18. *Products Mentioned in the Text**

Beef Extract—Difco Laboratories, Detroit, Michigan (Difco Culture Medium); Gevral-Protein—Lederle Laboratories, Pearl River, New York; Instant Protein—Alpine Marine Industries, New Bedford, Massachusetts 02742; Jeculin—Upjohn Company, Kalamazoo, Michigan 49001 (liver extract and iron); Lady Clairol Protinator—Clairol Incorporated, Stamford, Connecticut; Lady Clairol Cremenogenized Hair Lightener—Clairol Incorporated, Stamford, Connecticut; Marine Protein Concentrate—Alpine Marine Industries, New Bedford, Massachusetts 02742; Mellin's Food—Consolidated Royal Chemical Company, Chicago, Illinois 60610 (maltose-dextrin mixture with added thiamin ferric glycerophosphate and potassium bicarbonate); Ostermilk—Glaxo laboratories, Ltd., Greenford, Middlesex, England (reconstituted milk); Pet Drops—Upjohn Company, Kalamazoo, Michigan 49001 (multivitamins); Poly Vite Drops—Wolins Company, Farmingdale, New York (multivitamins); Stuart Formula Liquid—Stuart Company, Pasadena, California (multivitamins); Super Hydramin Powder—Nion Corporation, Los Angeles, California 90038; Tego Solution—Hough Hoseanson Ltd., Chapel Street, Manchester 19, England; Theragran—E. R. Squibb and Sons, New York, New York 10022 (multivitamins); Vi-Penta—Roche Laboratories, Nutley, New Jersey 07110; Zu/Preem Diets—Riviana Food, Inc., Hills Division, Topeka, Kansas 66601.

*Mention of trade names or products does not imply endorsement by the U.S. Government.

ECONOMICS AND CONSERVATION

CLYDE JONES

Historically, bats have been considered by man as objects of mystery, superstition, fear, and basically as indicators of some unknown or evil significance. The role of bats in the writings of early naturalists, as subjects of early artists, as objects of superstition and even worship, and as ingredients of concoctions for varied purposes was summarized in detail by G. M. Allen (1939), who prepared the first general summary on the biology of bats.

In modern times, there has been an increasing awareness of bats for several reasons, mostly because of the development of tools with which to obtain numerous species for study, as well as an increase in knowledge of some diseases of bats important to man. As a result of these and other factors, there has been a great surge of interest and activity in various studies of bats during the past two decades. A few of the major general works on bats within this period of time include the summaries provided by Brosset (1966), Barbour and Davis (1969), Leen and Novick (1969), Slaughter and Walton (1970), and Wimsatt (1970). As an additional indication of current interest in studies of bats, four international conferences have been held since 1968, and annual conferences have been held in the United States since 1970. Newsletters about bats have appeared during recent years in Australia, Europe, and the United States. A detailed review of the proliferation of literature on Chiroptera in the past few years was provided by Anderson and Van Gelder (1970). In spite of the aforementioned interests and activities, much remains unknown with regard to the biology of bats. It seems that certain groups, such as the Phyllostomatidae and some other tropical taxa, as well as special topics, such as the status of populations and the need for conservation, have been relatively neglected.

This report attempts to summarize and discuss some of the broad problems concerning the economic importance and conservation of the Phyllostomatidae, and to review briefly some of the specific needs for conservation of these bats.

PROCEDURES

It is not within the scope of this report to present a complete summary of literature containing information and notes on the aspects of the biology of phyllostomatids. References are provided that contain either additional information or examples pertinent to the purposes of this paper. Information was obtained from the literature, from newsletters and various reports on bats, and from correspondence with researchers who either worked on phyllostomatids or conducted field studies in areas where these bats occur. Data were taken also from the files of the bat-banding program of the National Fish and Wildlife Laboratory.

The scientific names used herein are in accordance with the nomenclature provided by Jones and Carter (this volume).

Economics

It seems impossible to attempt to determine meaningful economic values with regard to most bats; at least, no precise determinations will be made herein. However, it is relevant to review briefly the role of bats within ecosystems, especially with regard to relationships between phyllostomatid bats and certain things that seem important to man.

Relationships with Plants

Bats play a role in the natural dispersal of plants. Members of the family Phyllostomatidae are the principle agents of chiropterochory in the New World tropics. In general, most dissemination of plants by bats results from seeds that are dropped from the mouths of animals either in flight or in roosts. Relatively few plant seeds are passed through the digestive tracts of bats, although seeds of some plants, such as *Ficus*, probably are scattered in this manner.

Chiropterochory is highly developed in certain families of plants, especially the Moraceae, Palmae, Anacardiaceae, Sapotaceae, and Meliaceae. However, this condition also is present in many other families. For lists of chiropterochorous plants, characteristics of bat fruits, and discussions of the syndrome of dispersal of plants by bats, see the works by Van der Pijl (1957, 1968, 1969, and others). Some specific examples of synzooic relationships between plants and *Phyllostomus discolor*, *P. hastatus*, *Artibeus jamaicensis*, *A. lituratus*, and *Carollia perspicillata* are given by Van der Pijl (1957) and Greenhall (1956, 1965, 1966).

Phyllostomatids are the agents of chiropterophily in the Neotropical region. According to Van der Pijl (1969), bat flowers occur mostly in the genera *Musa*, *Parkia*, *Sonneratia*, *Agave*, and *Carnegiea*, but are present also in various stages of evolutionary development in some other taxa. Flowers pollinated by bats show some specialized traits; they have an abundance of nectar and pollen and tend to open at night. There is some evidence that pollen of chiropterophilous plants have more amino acids than do related species pollinated in other ways (Howell, 1970). Because flower bats rely on flowers for a supply of protein in the form of pollen, mutualistic adaptations are exhibited by some pollinating bats. For example, projections on the cuticular scales of hairs of some glossophagines seemingly are correlated with chiropterophily (Howell, 1971). Other morphological adaptations related to feeding and flight, as well as seasonal movements of bats that coincide with flowering of certain plants, are better known than the aforementioned example.

There is no doubt that phyllostomatid bats are important as agents of dispersal of seeds and pollen, at least in a limited range. Some botanists are of the opinion that, among mammals, bats are the most important dispersers of seeds (Van der Pijl, 1957). Recent analyses of trophic roles of bats demonstrate the richness of the Neotropical region with regard to frugivory and nectarivory of the chiropteran fauna (Wilson, 1973). There are similarities between the distributions of certain phyllostomatids and chiropterochorous and chiropterophilous plants; in fact, the ranges of some plants may result from the actions of bats on the re-

production of the plants. Numerous plants with typical bat flowers and bat fruits are economically important to man either as sources of food or for ornamental purposes.

Relationships with Insects

Phyllostomatid bats are associated ecologically with an array of insects. Although usually referred to as fruit bats or fruit-eating bats, members of this family consume considerable quantities of insects. For example, 33 of 143 stomachs from a total of 11 taxa of phyllostomatids examined by Arata *et al.* (1967) contained insect materials. Information provided by Wilson (1973) revealed the relative importance of insects in the diets of the genera of phyllostomatids. Wilson also indicated the need for additional information on the food habits of bats. Few data are available for evaluating the role of phyllostomatids with regard to the consumption of insects within an ecosystem. For some limited information on the impact of large colonies of insect-eating bats on insect populations, see the articles by Cockrum (1969, 1970). Although almost impossible to quantify on the basis of current knowledge, it is obvious that the predator-prey relationships between phyllostomatid bats and insects are important.

Relationships with Man

Phyllostomatid bats are considered occasionally as pests of fruit trees. The possibilities of these bats damaging fruit trees were implied in the discussion of the relationships between bats and plant dispersal and reproduction. There are, however, few reports of serious damage to fruit trees by bats in the New World tropics. Some data on disturbances to crop plants by phyllostomatids were presented by Greenhall (1956, 1966). All of the available data indicate that whatever harm phyllostomatids do to the fruit industry is of little or no consequence, except for some isolated instances where only limited damage is done. Phyllostomatids create some annoyances for man because of fruit consumption in gardens and homes and corresponding deposition of fruit pulp and other dropped materials.

Phyllostomatids also create a nuisance by roosting in man-made structures. Bats commonly occur in attics, walls, and between layers of thatch of buildings throughout the Neotropical area. People usually object to noises made by either vocalizations or movements of the animals, odors and stains from urine and fecal materials, and rejected food particles that frequently accumulate below roosting sites. In addition, ammonia gas may accumulate in guano deposits and cause unpleasantness to man. For an indication of the relationship between ammonia and *Macrotus californicus*, see the report by Mitchell (1963). Human food may become contaminated by droppings from bats that inhabit buildings or from insects and arthropods that live in guano deposits.

Guano deposited by bats has been used as fertilizer, especially in the early stages of the development of the fertilizer industry. Except for some figures for guano production and mining in northern México and the southwestern United States (Hutchinson, 1950), good data on modern production and use are not

TABLE 1.—*Occurrence of bacterial diseases in phyllostomatids.*

Bacteria	Disease	Host species	Country
Salmonella	Salmonellosis	*Glossophaga soricina*	Panamá
		Artibeus lituratus	Colombia
		Sturnira lilium	Colombia
Bartonella and *Grahamella*	Bartonellosis	*Carollia perspicillata*	Brazil
		Desmodus rotundus	Perú

available. Guano is still mined, especially in some areas in México, and some of the larger caves apparently yield worthwhile amounts. However, the importance of bat guano as fertilizer is not what it was previously because of the depletion of supplies and sources, as well as the development of other commercial fertilizers in recent years. The role of phyllostomatids as producers of guano in sufficient quantities for commercial exploitation is poorly known.

Members of the Phyllostomatidae also are considered pests because they harbor ectoparasites that cause some concern to humans. However, no further discussion is warranted herein because this topic is dealt with in detail by Webb and Loomis (this volume).

Phyllostomatids, like other bats, are often considered as pests by man in connection with diseases that may be carried by the animals and possibly transmitted to man. A list of the bacterial, mycotic, and protozoan diseases known to occur in wild phyllostomatids is presented in Tables 1 to 3. Known occurrences of viruses in these bats are summarized in Tables 4 and 5. Most of these data are from Constantine (1970), who also gave detailed discussions of each disease and virus, including information on how these diseases are manifested in humans. For additional information on pathogens in the Neotropical area, with special emphasis on Puerto Rico, see the paper by Tamsitt and Valdivieso (1970).

The reported occurrences of rabies virus infections in wild phyllostomatids are summarized in Table 5. Rabies in vampire bats is more common than in all other members of the family. According to Constantine (1970), reported deaths of humans from rabies transmitted by vampire bats are relatively insignificant causes of human mortality (Table 6). However, rabies transmitted by vampire bats to livestock is an important concern because this disease is a major cause of mortality in cattle in Latin America. Rabies in cattle has been reported in all Latin American countries except Chile and Uruguay. Estimates of annual cattle mortality vary considerably. For example, Constantine (1970) provided a summary of data on estimated cattle losses that totaled half a million head (47.6 million dollars) in 1966 and two million head (100 million dollars) in 1969. The magnitude of this problem is reflected in the rash of investigations in recent years concerned with the control of either rabies or vampire bats. "Vaccination has been the most effectively applied method of combatting the problem in livestock" (Constantine, 1970). Some methods for controlling vampire bats have resulted from studies of certain biological aspects of these animals in programs operated by the Food and Agriculture Organization of the United Nations and the

TABLE 2.—*Occurrence of mycotic diseases in phyllostomatids.*

Fungus	Disease	Host species	Country
Histoplasma	Histoplasmosis	*Leptonycteris sanborni*	United States
		Desmodus rotundus	México, Panamá, Colombia, Trinidad
		Phyllostomus discolor	El Salvador, Panamá
		Artibeus jamaicensis	El Salvador, Panamá
		Carollia perspicillata	Panamá, Colombia, Trinidad
		Glossophaga soricina	Panamá, Colombia, Trinidad
		Lonchophylla robusta	Panamá
		Lonchorhina aurita	Panamá
		Micronycteris megalotis	Panamá
		Tonatia bidens	Panamá
		Phyllostomus hastatus	Trinidad
		Anoura geoffroyi	Trinidad
Blastomyces	Blastomycosis	*Artibeus lituratus*	Colombia
Scopulariopsis	Scopulariopsosis	*Glossophaga soricina*	México
		Carollia perspicillata	México
		Artibeus lituratus	México
		Desmodus rotundus	México
Cryptococcus	Cryptococcosis	*Carollia perspicillata*	Colombia
		Desmodus rotundus	Colombia
		Leptonycteris sanborni	United States
Candida	Candidiasis	*Carollia perspicillata*	Colombia
		Desmodus rotundus	Colombia
		Leptonycteris sanborni	United States
Torulopsis	Torulopsosis	*Leptonycteris sanborni*	United States
Trichophyton, *Microsporum*, *Trichosporon*	Superficial mycoses	*Glossophaga soricina*	Colombia

Denver Wildlife Research Center of the United States Fish and Wildlife Service. The attempt to reduce rabies in cattle by the control of vampire bats is a complex and sometimes controversial issue. For additional information, consult the reports by Constantine (1970), Schmidt *et al.* (1970), Rosenthal (1972), Yosti *et al.* (1971), Mendez (1971), Greenhall (1971, 1972), Tamsitt and Valdivieso (1970), Thompson *et al.* (1972), and Turner (1975).

Bats are extremely useful to man as objects of research. Some indications of the increasing awareness of this importance are implicit in the introductory remarks with regard to the proliferation of literature on these mammals in recent years.

Bats are used in several aspects of medical research, especially vaccine development, epidemiological studies, mechanisms of disease resistance, aging, and thermoregulation. Transillumination of bat wings is a convenient way to make gross and microscopic observations of natural and experimental physiological phenomena, as well as for pathological studies and culturing of organisms in animal tissues.

TABLE 3.—*Occurrence of protozoan diseases in phyllostomatids.*

Protozoa	Disease	Host species	Country
Trypanosoma	Trypanosomiasis	*Carollia perspicillata*	Colombia
		Phyllostomus discolor	Colombia
		Phyllostomus hastatus	Colombia
		Desmodus rotundus	Colombia, México
		Glossophaga soricina	Colombia
		Artibeus lituratus	Colombia
Toxoplasma	Toxoplasmosis	*Artibeus lituratus*	Colombia

Bats are important in space biology for studies dealing with a wide array of tolerances of environmental extremes and stresses. They also are useful in numerous investigations of aerodynamics and related topics.

Studies in bat echolocation are useful for many purposes, as documented in some detail by Griffin (1958). Some interesting and sophisticated studies of ultrasonic orientation in bats have been conducted in recent years. For some ex-

TABLE 4.—*Occurrence of viruses in phyllostomatids.*

Virus	Host species	Country
	Group A Arboviruses	
Eastern equine encephalitis	*Artibeus jamaicensis*	Brazil
Venezuelan equine encephalitis	*Carollia perspicillata*	Colombia
	Artibeus lituratus	Panamá
Mucambo	*Carollia perspicillata*	Brazil
	Artibeus jamaicensis	Brazil
	Group B Arboviruses	
Saint Louis encephalitis	*Rhinophylla pumilio*	Brazil
Yellow fever	*Glossophaga soricina*	Brazil
	Miscellaneous Arboviruses	
Carapara	*Artibeus lituratus*	Brazil
Jurona	*Artibeus lituratus*	Brazil
	Artibeus jamaicensis	Brazil
	Carollia perspicillata	Brazil
Utinga	*Artibeus lituratus*	Brazil
Tacaribe	*Artibeus lituratus*	Trinidad
	Artibeus jamaicensis	Trinidad
Catu	*Artibeus fulginosus*	Brazil
	Artibeus lituratus	Brazil
	Artibeus jamaicensis	Brazil
Itaporanga	*Artibeus lituratus*	Brazil
	Artibeus jamaicensis	Brazil
	Phyllostomus hastatus	Brazil
	Vampyrops helleri	Brazil
Tacaiuma	*Artibeus jamaicensis*	Brazil

TABLE 5.—*Occurrence of rabies in phyllostomatids.*

Host species	Country
Macrotus californicus	United States, México
Phyllostomus discolor	British Honduras, Guatemala
Phyllostomus hastatus	Brazil
Glossophaga soricina	México
Leptonycteris nivalis	México
Carollia perspicillata	Trinidad, Colombia
Uroderma bilobatum	Panamá
Artibeus sp.	México
Artibeus jamaicensis	Panamá, Trinidad, Brazil
Artibeus lituratus	British Honduras, Guatemala, México, Trinidad, Brazil
Desmodus rotundus	British Honduras, Guatemala, México, Trinidad, Brazil
Diaemus youngii	Trinidad
Diphylla ecaudata	Brazil

amples, note the studies by Pollak *et al.* (1972), Simmons (1970), Simmons and Howell (1971), Howell and Pylka (1972), and Simmons *et al.* (1972). Bats may serve as important bioholographic models in the future (Greguss, 1968).

In addition to the aforementioned usefulness in research, bats are important research objects for other biologists. For example, there still is need for, and interest in, basic studies of ecology, life history, distribution, morphology, and the like. The taxonomy of bats is still an intriguing topic, and considerable interest has developed in studies of their behavior and population dynamics. This may become a more active research area in the future, especially with regard to studies of mechanisms permitting bats to survive in extremes of population congestion.

CONSERVATION

Needs for conservation of American bats in general were recognized by Manville (1962), Davis (1967), and Cockrum (1969, 1970), and presented in their pleas for conservation. Additional comments on needs for bat conservation were presented by Barbour and Davis (1969), Gould (1970), Greenhall (1973), and Findley (1973). Phyllostomatids, as well as some other bats, have been given

TABLE 6.—*Some reported incidences of rabies transmitted to humans by vampire bats.*

Deaths	Years	Country
89	1925-1937	Trinidad
31	1951-1961	México
17	1953-1961	Guyana
1	1960	Bolivia
8	1960	Brazil
5	1965	Argentina

TABLE 7.—*Information on phyllostomatids from surveys of researchers.*

Country	Dates	Genus	Status of population
United States	1965-1971	*Leptonycteris, Choeronycteris*	Declining
United States	1967-1971	*Leptonycteris*	Declining
United States	1962-1969	*Leptonycteris, Choeronycteris*	Declining
United States	1960-1970	*Macrotus*	Declining
United States	1965-1970	*Macrotus*	Declining
México	1961-1965	*Glossophaga*	Increasing
México	1961-1971	*Desmodus*	Increasing
México	1968-1971	*Desmodus*	Increasing
México	1969-1971	*Desmodus*	Increasing
Costa Rica	1957-1971	*Desmodus, Phyllostomus, Artibeus, Vampyrops, Sturnira, Uroderma, Glossophaga*	Increasing
Costa Rica	1966-1967	*Glossophaga, Carollia*	Increasing
Colombia	1963-1970	*Desmodus*	Decreasing
Colombia	1963-1970	*Artibeus, Carollia, Phyllostomus*	Stable
Colombia	1965-1970	*Glossophaga*	Increasing
Argentina	1969-1970	——	Stable
Trinidad	1953-1963	*Desmodus*	Increasing

some attention in the popular and conservation oriented works by Rood (1971), Curry-Lindahl (1972), and Novick and Dale (1973).

Awareness and concern for bat conservation has been expressed by numerous spelunkers and the National Speleological Society. For additional information and recommendations of this organization, see the paper by Mohr (1972).

Some concerns for bat populations in the New World have been expressed by bat researchers. For example, resolutions were developed during the Third Symposium on Bat Research, held in San Diego, California, on 24-25 November 1972 with some guidelines for bat conservation. These actions were based in part on a recent survey that revealed reduced populations of 22 species of bats in the United States, including three species of phyllostomatids (Jones, 1971).

In connection with the aforementioned survey, limited data were accumulated on the population status of phyllostomatids at several places in Latin America. Of more than 100 requests for information sent to bat researchers, only 16 of those returned included information on phyllostomatids. Pertinent information from these replies is summarized in Table 7. All reports on phyllostomatids in the United States indicate declining populations; reports for other areas mostly reveal increasing populations, except for one report of decreasing populations and two reports of stable populations. However, most respondents stated that populations of *Desmodus* were actually reduced or absent in local areas due to eradication or control measures. For a wealth of information on populations of vampire bats, see the work by Turner (1975).

All reports included lists of reasons for population changes. Increased populations of bats were associated with increased cultivation of fruit crops and the

rapidly developing livestock industry. Several reports included comments with regard to increased deforestation and general habitat disturbance in the areas studied, and predictions were made for adverse effects in the future on bat populations. In addition, several respondents expressed concern about the effects of vampire bat control methods on other species of bats. In earlier recognition of this problem, the participants in the I.U.C.N. Latin American Regional Conference on Conservation of Renewable Natural Resources, who met at San Carlos de Bariloche, Argentina, on 2 April 1968, passed a resolution recommending some guidelines with regard to control of vampire bats. Because of the importance of this matter, the entire resolution is reproduced in Appendix 1. As mentioned above, eradication and control were given most frequently as the reasons for reductions of bat populations in Latin America.

Reasons given for declining populations of phyllostomatids in the United States included destruction of roosts, disturbances to bats by researchers (especially bat banders and collectors), spelunkers, and vandals.

All respondents for the United States and many for Latin America listed pesticides as a major cause of reduction in bat populations. For information on what is known about the effects of pesticides on bats, see the works by Luckens and Davis (1965), Cockrum (1969, 1970), Reidinger (1972), Jefferies (1972), and Clark *et al.* (1975).

There is some evidence of interest by national governments in conservation and protection of bats. For example, several Latin American countries have legislation and corresponding regulations that require permits for the collection of bats. Although federal permits are not required in the United States, the Fish and Wildlife Service has an official policy that recognizes some of the needs for conservation of bats (Appendix 2).

Information from numerous sources on the need for conservation of bats —especially the two appendices of this report, Greenhall (1973), Mohr (1972), Jones (1971), and discussions held during the annual Symposia on Bat Research —provides a basis for the general recommendations summarized below. These suggestions all seem particularly important with respect to conservation of phyllostomatids.

1. Appropriate investigations on the biology of bats should be encouraged. Basic information, especially on general ecology and status of populations, is essential for the development of sound conservation measures.

2. Steps should be taken to establish and enhance cooperative relationships among health authorities, pest control and exterminating firms, and biologists. Every effort must be made to limit control and eradication activities to selective reduction of bats in local problem areas, with these activities based on sound biological data. Procedures must be established for salvaging materials for research purposes in cases where control or eradication activities are unavoidable.

3. Efforts must be increased to inform the general public, as well as scientists, with regard to the important significance of bats in ecosystems. It seems that a most important need is for publication of the facts that the majority of bats perform functions that are in many ways useful to man.

4. Attempts must be made to persuade private groups and government agencies to provide adequate protection to certain roosting sites of bats. Acceptable codes of ethics should be developed for visiting, and working in or near, roosting sites, such as caves, for the purposes of minimizing disturbances to the organisms found there.

5. An educated public should help encourage the development of national legislation and international agreements to protect bats from disturbance and destruction except as authorized by permits issued for scientific or public health purposes.

Conservation-management programs for bats must be developed and based on what is best for these important wildlife resources, with detailed knowledge of bat biology utilized as the basis for decisions on preparing appropriate regulations and corresponding enforcement procedures for a permit system.

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APPENDIX 1.—*Resolution no. 1 of the I.U.C.N. Latin American Regional Conference on Conservation of Renewable Natural Resources, San Carlos de Bariloche, Argentina, 2 April 1968.*

VAMPIROS

CONSIDERANDO que los murciélagos vampiros, *Desmodontidae*, constituyen un serio problema económico, veterinario y de salud pública en Latinoamérica, no solamente porque los vampiros pueden transmitir la rabia y otras enfermedades a los animales domésticos y al hombre, sino también porque solamente se alimentan de sangre de aves y mamíferos, incluyendo al hombre,

CONSIDERANDO además que la erradicación de los vampiros, sea esto deseable o no, es impracticable debido a su amplia dispersión, abundancia y a la inaccesibilidad de sus refugios,

Y CONSIDERANDO que muchas otras especies de murciélagos, conviviendo con los vampiros, pueden ser confundidos con ellos, y juegan un papel importante en la naturaleza, tal como la reducción de insectos que dañan la economia.

la Conferencia Latinoamericana Regional sobre la Conservación de Recursos Naturales Renovables, reunida en Bariloche el 2 de Abril de 1968,

RECOMIENDA a todos los gobiernos que les concierna, que la lucha contra los murciélagos vampiros en las áreas afectadas, se base en estudios biológicos, ecológicos e inmunológicos eficientes, dirigidos unicamente hacia una reducción selectiva de las poblaciones locales de los vampiros, y

URGE que las personas a cargo de las medidas de lucha sean apropiadamente adiestradas y que se preste especial atención a fin de evitar una destrucción masiva e indiscriminada, dinamitando y fumigando cuevas y demás guaridas que sirvan de refugio a gran número de murciélagos y otras especies animales y vegetales benéficas al hombre o de gran valor científico.

APPENDIX 2.—*Fish and Wildlife Service Policy on Bat Banding and Bat Conservation.*

In view of the obvious needs for conservation of bats in North America, the Bureau of Sport Fisheries and Wildlife has adopted a new policy with regard to this important matter. The three major points of the Bureau policy are as follows:

1. Because it has been demonstrated that bat banding and corresponding activities are a major cause of disturbance to bat colonies, a moratorium has been placed on the issuing of bat bands either to new bat banders or for new banding projects. The current supplies of bat bands will be issued to investigators for use in the completion of ongoing, pertinent projects that do not involve species of bats with greatly reduced populations.
2. A detailed evaluation will be made of the files of the bat-banding program. The purposes of this review are to determine the value and relevance of the biological data that have been accumulated in the files, and to study the feasibility of automated techniques for storage and retrieval of data if the program is to continue.
3. Appropriate steps will be taken to explore the possibility of developing an international treaty for the protection of North American bats. Every effort will be made to establish a conservation program based on what is best for bat populations, with detailed knowledge of bat biology utilized as the basis for decisions. Necessary actions will be implemented as soon as possible with regard to this part of the program.

BRAIN ANATOMY

V. RICK MCDANIEL

The chiropteran family Phyllostomatidae is exceptionally diversified with respect to feeding habits, at least six different modes of which are identifiable: insectivory, nectarivory, frugivory, carnivory, omnivory, and sanguivory. Adaptation to these various feeding habits has resulted in considerable anatomical diversity among members of this family (Miller, 1907; Hall and Kelson, 1959; Tepaske, 1964; Federschneider, 1967; Walton and Walton, 1968; Harrison and Horne, 1971; Forman, 1972). Although it is generally accepted that normal environmental stress does not result in modification of nervous tissues to the extent observed in teeth and cranial bones (Weidenreich, 1941; Bennett *et al.*, 1964; Atkins and Dillon, 1971; Neville and Chase, 1971), even a cursory examination of phyllostomatid brains reveals an exceptional array of cephalic diversity.

Even though the cerebral diversity encountered within the Phyllostomatidae has been commented on repeatedly, few systematic studies have been performed. Pirlot and Stephan (1970) computed progression indices of encephalization for a number of bats, including 12 species of phyllostomatids. Based on total brain size, they reported low encephalization values for insect feeders, and ascending values for nectar feeders, fruit eaters, and vampires. Subsequently, Stephan and Pirlot (1970) utilized progression indices based on relative volumes of various regions of the brain to correlate brain structures with feeding habits; but again, the Phyllostomatidae was poorly represented (for example, *Glossophaga* was the only nectar-feeding genus represented). Two recent qualitative studies exist that include phyllostomatid data (Mann, 1960; McDaniel, 1973). In addition, there are several more general studies that contain limited information on phyllostomatids (Schneider, 1957; Mann, 1963; Edinger, 1964; Findley, 1969). Considerable information on phyllostomatid brain anatomy is contained in the admirable compilations of Henson (1970) and Quay (1970). There are also several histological studies available that involve phyllostomatid species (see, for example, Palacios-Prü and Mendoza-Briceño, 1972). In light of the relative paucity of descriptive and comparative data, the intent of this report is to acquaint the reader with the nature of diversity present in phyllostomatid brain anatomy and, hopefully, to incite further work. Toward these ends, it has been necessary to rely heavily upon my own comparative data, which are unpublished (McDaniel, 1973). Species examined and the nature of study are presented in Table 1.

Insofar as possible, I have adhered to the nomenclature of the *Nomina Anatomica* (3rd edition). In some cases I have followed the terminology of other workers, and in a few cases I have had to utilize terms for which the actual homology has yet to be determined.

TABLE 1.—*Brains of phyllostomatid species studied.*

Species	Nature of study	
	External	Internal
Phyllostomatinae		
Lonchorhina aurita Tomes	X	
Macrophyllum macrophyllum (Schinz)	X	
Macrotus californicus Baird	X	X
Micronycteris hirsuta (Peters)	X	
Micronycteris megalotis (Gray)	X	X
Micronycteris minuta (Gervais)	X	
Micronycteris nicefori Sanborn	X	
Micronycteris schmidtorum Sanborn	X	
Mimon crenulatum (É. Geoffroy St.-Hilaire)	X	X
Phylloderma stenops Peters	X	
Phyllostomus discolor (Wagner)	X	
Phyllostomus elongatus (É. Geoffroy St.-Hilaire)	X	
Phyllostomus hastatus (Pallas)	X	X
Tonatia bidens (Spix)	X	X
Tonatia nicaraguae Goodwin	X	X
Trachops cirrhosus (Spix)	X	
Vampyrum spectrum (Linnaeus)	X	X
Glossophaginae		
Anoura geoffroyi Gray	X	X
Choeroniscus godmani (Thomas)	X	
Choeroniscus intermedius (Allen and Chapman)	X	
Choeronycteris mexicana Tschudi	X	X
Glossophaga alticola Davis	X	
Glossophaga commissarisi Gardner	X	
Glossophaga soricina (Pallas)	X	X
Hylonycteris underwoodi Thomas	X	X
Leptonycteris sanborni Hoffmeister	X	X
Lichonycteris obscura Thomas	X	X
Lonchophylla robusta Miller	X	X
Monophyllus redmani Leach	X	
Carolliinae		
Carollia perspicillata (Linnaeus)	X	X
Carollia subrufa (Hahn)	X	
Rhinophylla pumilio Peters	X	X
Stenoderminae		
Ametrida centurio Gray	X	
Artibeus aztecus Andersen	X	
Artibeus cinereus (Gervais)	X	
Artibeus hirsutus Andersen	X	
Artibeus inopinatus Davis and Carter	X	
Artibeus jamaicensis Leach	X	X
Artibeus lituratus (Olfers)	X	X
Artibeus phaeotis (Miller)	X	X
Artibeus toltecus (Saussure)	X	
Artibeus watsoni Thomas	X	
Centurio senex Gray	X	X
Chiroderma salvini Dobson	X	X
Chiroderma villosum Peters	X	

TABLE 1.—*Continued.*

Ectophylla macconnelli Thomas	X	
Enchisthenes hartii (Thomas)	X	
Stenoderma rufum Desmarest	X	
Sturnira lilium (É. Geoffroy St.-Hilaire)	X	
Sturnira ludovici Anthony	X	
Sturnira mordax (Goodwin)	X	
Uroderma bilobatum Peters	X	
Uroderma magnirostrum Davis	X	
Vampyressa nymphaea Thomas	X	X
Vampyressa pusilla (Wagner)	X	
Vampyrodes caraccioloi (Thomas)	X	
Vampyrops dorsalis Thomas	X	
Vampyrops helleri Peters	X	X
Vampyrops infuscus Peters	X	
Vampyrops vittatus (Peters)	X	
Phyllonycterinae		
Brachyphylla cavernarum Gray	X	X
Erophylla bombifrons (Miller)	X	X
Desmodontinae		
Desmodus rotundus (É. Geoffroy St.-Hilaire)	X	X
Diaemus youngii (Jentink)	X	X
Diphylla ecaudata Spix	X	

METHODS AND MATERIALS

Bats were mist-netted from natural populations or were collected by hand from roosting sites. Brains were prepared by removing the head immediately after the specimen was killed and chipping away the parietal region of the skull case to expose the brain. Fixation with 10 per cent formalin was allowed to proceed for several weeks. To facilitate handling, fixed brains were stored in 70 per cent ethanol. A few species are represented by specimens preserved originally in alcohol that were collected by other workers. Brains from the latter often showed varying degrees of internal deterioration, and in some cases their value was limited to external study only.

The skull and meninges were removed carefully from each brain. Then, the available series of brains from each species was examined to determine subjectively a "typical" specimen for each species. These brains were photographed from dorsal, ventral, and lateral views. Such photographs served as a convenient basis for comparison; however, final judgments were made from observations on the specimen.

Certain species were selected for detailed examination of internal anatomy. For these histological preparations, species were selected that were: 1) representative of each major type of external anatomy; 2) representative of each major taxonomic unit; and 3) of questionable phylogenetic position (such as *Brachyphylla*, which has been assigned by past workers to one of several different subfamilies). Brains for histological study were infiltrated with a gum arabic solution (Humason, 1967) and frozen sections were made in the cross-sectional plane at 18

microns. Every second section (third section on some large species) was collected and mounted in step fashion on microscope slides. Sections were stained with "Luxol" fast blue MBSN (Matheson Coleman and Bell) to demonstrate myelinated areas and counterstained with cresyl violet acetate (Matheson Coleman and Bell) to outline concentrations of cells in discrete nuclei. Staining was by a modification of techniques described by Drury and Wallington (1967). Specifics for preparation of sections was as follows: 1) sections were dehydrated in 95 per cent ethanol; 2) stained in Luxol fast blue (see McDaniel, 1973, appendix A) for four to eight hours, at 50 degrees Centigrade; 3) hydrated through an ethanol gradient to distilled water; 4) dipped into 0.05 per cent lithium carbonate at one to three degrees Centigrade for 15 to 20 seconds (solution must be freshly prepared daily); 5) differentiated in 70 per cent ethanol until there was a clear distinction between myelinated (blue) and nonmyelinated tissues (clear); 6) hydrated through an ethanol gradient to distilled water; 7) counterstained in cresyl violet acetate (see McDaniel, 1973 appendix A) for five to 10 minutes; 8) counterstain differentiated in 95 per cent ethanol to which a few drops of acetic acid had been added; 9) sections dehydrated in 100 per cent ethanol, cleared in xylene, and mounted in Permount. Steps 4 and 5 may be repeated if necessary. This staining procedure yields sections with deeply blue-stained myelinated areas (ranging from large tracts to individual axons) and purplish-red cell bodies embedded in a pale violet matrix.

External Morphology of the Brain

General Description

The cerebral hemispheres of phyllostomatid bats are relatively smooth and without convolutions (Fig. 1). A few depressions, which are usually shallow, are found in most species. In the past, these were conveniently regarded as true sulci, but more recently, they have been termed fossae or fissurelike depressions resulting from the presence of adjacent osseous and vascular features (Schneider, 1957; Henson, 1970). My comparative histological examination of a series of phyllostomatid brains (McDaniel, 1973) revealed that in some cases these depressions are not shallow, and apparently represent more than a conformity of brain to skull (for an extreme example, see the cingulate sulcus of *Phyllostomus hastatus*). There are no cortical maps published for chiropteran brains; therefore, there are no data concerning functional interpretation of the sulci or pseudosulci, and gyri or pseudogyri. In the absence of a functional interpretation, the following terminology is based on morphological similarity rather than on actual, or even assumed, homology with brains of higher mammals. Homology within the family Phyllostomatidae is assumed, and hopefully will be substantiated experimentally in the future.

Within the Phyllostomatidae, three sulci are consistently well developed: the interhemispheric sulcus, which separates the right and left cerebral hemispheres; the anterior rhinal fissure, which separates the olfactory bulbs from the main mass of the cerebrum; and the hippocampal sulcus, which is ventrally located. Of the remaining sulci, the most consistently present is one that divides the cere-

bral surface into anterior and posterior portions. This fissure is similar to, but not homologous with, the central sulcus (Sylvian sulcus) of higher mammals. In this paper it will be referred to as the pseudocentral sulcus. In some cases, another fissure is developed somewhat anterior to the pseudocentral sulcus.

The various lobes of the cerebral cortex are relatively unobtrusive and in most cases do not show a tendency to bulge in the manner typical of higher mammals. All phyllostomatids have well-developed olfactory bulbs on the rostral end of the cerebral hemispheres. In addition, caudad to the pseudocentral sulcus, a pseudotemporal lobe projects ventrally or somewhat posteriorly from the body of the cerebrum.

The diencephalon (Fig. 1) is exposed only along its ventral surface. A portion of the base of the thalamus is exposed anterior to the optic chiasma, and the hypothalamus is exposed posterior to the optic chiasma.

The cerebellum (Fig. 1) occurs as a dorsal foliated body posterior to the cerebral hemispheres. The cerebellar surface is relatively simple, and rarely has more than primitive sulci developed. The cerebellar body is composed of a medial vermiform body flanked by a pair of lateral lobes. As in other mammals, the cerebellum is attached to the brain stem by the inferior, medial, and superior peduncles.

The mesencephalon of phyllostomatid bats is rarely seen unless the hypophysis has been removed. The cerebral peduncles are never visible externally, and of the tectal structures, the enlarged inferior colliculi are generally the only structures visible (but even they are not always so). The pons is almost completely covered ventrally by the hypophysis and laterally by the trigeminal nerve.

The medulla oblongata (Fig. 1) occurs as a rather broad structure in phyllostomatids. Ventrally, the anterior trapezoid body, posterior olives, and medially located pyramidal decussation are visible. As in other vertebrates, the medulla grades posteriorly into the spinal cord.

Aspects of Variation in External Anatomy

Within the Phyllostomatidae, a surprising array of variation in features of external brain anatomy is encountered. Data concerning inter and intrasubfamilial variation are available for 65 species representing 38 genera and six subfamilies (McDaniel, 1973).

Subfamily Phyllostomatinae

Data are available for 10 of the 11 genera listed in this subfamily by Jones and Carter in the systematic account in this volume. Pronounced variation of several morphological features creates difficulty in characterizing a generalized brain for this subfamily.

The brain of *Mimon* (Fig. 2) is characterized by the presence of extremely short, deep cerebral hemispheres, pseudotemporal lobes that project ventrally in a rounded rather than angular fashion, and a slight indication of a pseudocentral sulcus. The caudal termination of the cerebral hemispheres is dorsally anterior to the inferior colliculi (which are contiguous to one another), resulting in dorsal exposure of precollicular tectum. *Mimon* is the only phyllostomatid bat in which

the tectum is broadly exposed anterior to the inferior colliculi. The cerebellum of *Mimon* is simple, having shallow foliations.

The brain of *Lonchorhina* (not figured) resembles that of *Mimon* in having a short, deep cerebrum and a simple cerebellum. In *Lonchorhina*, the pseudocentral sulci cut more deeply into the cerebral hemispheres than in *Mimon*, and the posterior margin of the cerebrum extends almost to the anterior margin of the inferior colliculi. The brains of five species of *Micronycteris* (Figs. 3-7) vary only slightly among species. The cerebrum of *Micronycteris* is relatively longer than that of *Mimon*. The cerebrum is shortest in *M. nicefori* (Fig. 3) and *M. minuta* (Fig. 4), longer in *M. schmidtorum* (Fig. 5) and *M. megalotis* (Fig. 6), and longest in *M. hirsuta* (Fig. 7). The cerebral pseudocentral sulci are well developed in all species except *M. nicefori*. There is shallow development of a sulcus anterior to the pseudocentral sulcus. The cerebellum is simple in all species. Consistently within the genus *Micronycteris*, but in no other phyllostomatine genus, the inferior colliculi are exposed dorsally and are not contiguous dorsally with one another. In *Micronycteris*, the inferior colliculi are separated by the anterior lobe of the vermiform body of the cerebellum.

The brain of *Macrotus* (Fig. 8) resembles that of *Micronycteris megalotis* in most details. However, the dorsally exposed inferior colliculi are contiguous. The degree of contiguity is reduced and approaches the condition found in *Micronycteris* because the anterior lobe of the cerebellar vermiform body projects anteriorly to cover the most posterior portion of the inferior colliculi.

In *Macrophyllum* (Fig. 9), the cerebral hemispheres are elongate relative to the condition in *Mimon*, and are exceptionally smooth, with only a shallow interhemispheric sulcus. The inferior colliculi are exposed dorsally and are contiguous with one another. The cerebellar tissue is exceptionally nondescript and lightly fissured.

The brains of *Trachops* (Fig. 10) and two species of *Tonatia* (Figs. 11-12) are similar in external anatomy. The brain of *Tonatia nicaraguae* (Fig. 11) is the smallest and least ornamented of the three. It is characterized by the presence of deep cerebral hemispheres that are relatively longer than those of *Macrophyllum*. The pseudocentral sulci of the cerebrum are well developed, and there is shallow development of the sulci anterior to the pseudocentral sulci. The inferior colliculi are exposed dorsally, and are contiguous middorsally. As in *Macrotus*, the anterior edge of the vermiform body of the cerebellum protrudes forward to cover the posterior portions of the inferior colliculi. The cerebellum is simple in appearance. The brain of *Tonatia bidens* (Fig. 12) is similar to that of *T. nicaraguae* except that the cerebral hemispheres are relatively longer and the pseudocentral sulci of the cerebrum are extremely deep. The brain of *Trachops* (Fig. 10) differs from that of *Tonatia bidens* by the presence of shallower pseudocentral sulci, but somewhat deeper sulci anterior to the pseudocentral sulci. The brain of *Trachops* has some secondary foliation at the lateral edge of the vermiform body of the cerebellum.

Brains of the genera *Phyllostomus* (Figs. 13-15) and *Phylloderma* (Fig. 16) reveal another subgroup within the Phyllostomatinae. The brains of both genera

are characterized by massive cerebral hemispheres that are elongate and anteriorly blunt. Sulcation of the cerebrum is pronounced, and the pseudocentral sulci and sulci anterior to them are well developed. The cerebral hemispheres are well provided with small secondary fissures radiating from the larger sulci. In *Phyllostomus elongatus* (Fig. 13), the inferior colliculi are exposed dorsally; but in *Phyllostomus hastatus* (Fig. 14), *P. discolor* (Fig. 15), and *Phylloderma* (Fig. 16), the inferior colliculi are completely covered by cerebral and cerebellar tissues. In all four species, the cerebellum has ornamentation in the form of secondary foliation at the lateral edges of the vermiform body, which is itself enlarged to form a pronounced medial crest to the cerebellum.

The brain of *Vampyrum spectrum* (Fig. 17) is extremely large, but is not as massive in appearance as that of *Phyllostomus* because of more pronounced elongation. The cerebral hemispheres are well convoluted and sulcated and have secondary fissures radiating from the major sulci. The cerebellum achieves its maximum ornamentation in *Vampyrum*. The vermiform body is raised to form an extraordinary medial ridge, and there is considerable secondary foliation at the lateral edges of the vermiform body.

Subfamily Glossophaginae

Brains of nine genera and 12 species were examined from the Glossophaginae. Brains from this subfamily have relatively smooth and shallow cerebral hemispheres, shallow development of the major sulci, and dorsally unexposed inferior colliculi. The cerebellum is simple and without secondary ornamentation.

The brains of *Choeroniscus godmani* (Fig. 18) and *C. intermedius* (not figured) are probably impossible to differentiate externally. The brain of *Choeroniscus* is characterized by the presence of a short cerebrum having a smooth surface and small olfactory bulbs. The pseudocentral sulcus is extremely shallow, and the pseudotemporal lobes are smoothly rounded on the ventral side. The cerebellum is simple and has no secondary lobation.

Hylonycteris (Fig. 19) and *Lichonycteris* (Fig. 20) have brains similar to that of *Choeroniscus*. The cerebrum is short and smooth, the olfactory bulbs are small, and the pseudocentral sulci are shallow. The pseudotemporal lobes of *Hylonycteris* are ventrally rounded as in *Choeroniscus*, but those of *Lichonycteris* are ventrally angular. The cerebellum is simple in both genera.

The brains of *Glossophaga alticola* (Fig. 21), *G. commissarisi* (Fig. 22), and *G. soricina* (not figured) are virtually indistinguishable externally. In *Glossophaga*, the cerebral hemispheres are short, smooth, and almost lacking sulci. The olfactory bulbs are small. The pseudotemporal lobes are somewhat angular and the cerebellar foliations are simple.

The brains of *Choeronycteris* (Fig. 23) and *Monophyllus* (not figured) are characterized by relatively elongated cerebral hemispheres that are vertically shallow. The pseudotemporal lobes are the shallowest within the Glossophaginae and the cerebellum has only primary foliations.

Leptonycteris (Fig. 1) has a brain much like that of *Glossophaga alticola*. However, the cerebral sulci tend to cut deeper into the mass of the cerebrum in *Leptonycteris* than in any of the species of *Glossophaga*.

Anoura (Fig. 24) has a brain similar to that of *Choeronycteris*. The cerebrum is elongate and smooth, and the pseudocentral sulci are shallow. The olfactory bulbs are relatively large, and the pseudotemporal lobes are shallow. In *Anoura*, the cerebral hemispheres are somewhat more massive than in *Choeronycteris*, and they reach the greatest relative length within this subfamily.

The brain of *Lonchophylla* (Fig. 25) has the most massive cerebrum within the Glossophaginae. The cerebrum is elongated and has relatively well-developed pseudocentral sulci and large olfactory bulbs. The pseudotemporal lobes project ventrally, and the cerebellum achieves its maximum degree of foliation within the Glossophaginae.

Subfamily Carolliinae

Brains of both genera in this subfamily have been examined. The brains of *Carollia* (Fig. 26) and *Rhinophylla* (Fig. 27) are similar in almost every detail.

The brains of *Carollia perspicillata* (Fig. 26) and *C. subrufa* (not figured) are virtually identical externally. In *Carollia*, the cerebrum is similar to that of *Micronycteris* in having relatively short and smooth hemispheres. The pseudocentral sulci are well developed, as are the sulci anterior to the pseudocentral sulci. The pseudotemporal lobes are rounded ventrally, and the inferior colliculi are not exposed dorsally. The cerebellum is simple and has only primary lobes.

The brain of *Rhinophylla* (Fig. 27) is similar to that of *Carollia*, but in *Rhinophylla*, the pseudotemporal lobes project ventrally in an angular fashion.

Subfamily Stenoderminae

This large subfamily is represented by specimens from 28 species, representing 12 genera. Brains from this subfamily normally have a deep cerebrum with pseudotemporal lobes that project ventrally in a distinctive fashion.

The genus *Artibeus* (Figs. 28-35) is represented herein by nine species. The brain of *A. aztecus* (Fig. 29) is characterized by the most shallow cerebral hemispheres within the Stenoderminae. The pseudotemporal lobes are angular and project a short distance ventrally. The pseudocentral sulci are shallow, and there are no sulci anterior to the pseudocentral sulci. The inferior colliculi are covered dorsally, and the vermiform body of the cerebellum forms a low crest. In *A. phaeotis* (Fig. 30), the cerebral hemispheres are relatively deeper than in *A. aztecus*. The pseudotemporal lobes are angular and project ventrally farther than in *A. aztecus*. The prepseudocentral gyrus is enlarged and protrudes dorsally. The posterior portions of the inferior colliculi are exposed dorsally, and the cerebellum resembles that of *A. aztecus*. The brain of *A. toltecus* (Fig. 31) is anatomically intermediate between the brains of *A. aztecus* and *A. phaeotis*. In *A. toltecus*, the cerebral hemispheres are deep and the pseudotemporal lobes project ventrally in an angular fashion. The pseudocentral sulci are shallow, as are the sulci anterior to the pseudocentral sulci. The posterior edges of the cerebral hemispheres cover all but the posterior most edges of the inferior colliculi. The cerebellum has a medial crest and small secondary foliations at the lateral edges of the vermiform body. The brains of *A. watsoni* (Fig. 32) and *A. cinereus* (Fig.

28) are indistinguishable except that *A. cinereus* has a larger brain than does *A. watsoni.* The brains of these two species are characterized by deep and relatively smooth cerebral hemispheres with shallow sulci. In both species, the inferior colliculi are not exposed, and the cerebellum is crested and without secondary foliation. The brain of *A. inopinatus* (Fig. 33) is characterized by deep cerebral hemispheres having angular and ventrally projecting pseudotemporal lobes. The pseudocentral sulci and sulci anterior to the pseudocentral sulci are well developed. The inferior colliculi are not exposed dorsally, and the cerebellum is simple and has a high medial crest. *A. hirsutus* (not figured), *A. jamaicensis* (Fig. 34), and *A. lituratus* (Fig. 35) have brains that are similar in morphology. In these species, the brain has relatively well-convoluted cerebral hemispheres and well-developed major sulci. The pseudotemporal lobes project ventrally in an angular fashion, and the inferior colliculi are not dorsally exposed. The cerebellum is well crested and has small secondary foliations at the lateral edges of the vermiform body.

The brain of *Enchisthenes* (Fig. 36) is known to me through examination of one poorly preserved specimen. The relatively smooth cerebrum with deep and angularly projecting pseudotemporal lobes resembles that of *Artibeus watsoni.* The inferior colliculi are not visible from above, and the cerebellum is simple and medially crested.

The genus *Vampyrodes* (Fig. 37) is characterized by a brain with large and anteriorly blunt cerebral hemispheres having poorly developed sulci. The pseudotemporal lobes project ventrally in an angular fashion. The posterior portions of the inferior colliculi are dorsally exposed and the cerebellum is simple. The vermiform body forms a medial crest to the cerebellum.

The brains of *Uroderma bilobatum* (Fig. 38) and *U. magnirostrum* (Fig. 39) are similar in most features. These brains have deep cerebral hemispheres with angular pseudotemporal lobes that protrude ventrally to a lesser extent than in *Artibeus.* The pseudocentral sulci and sulci anterior to the pseudocentral sulci are well developed. The inferior colliculi are not exposed dorsally, and the vermiform body of the cerebellum forms a low medial crest. There are secondary foliations at the lateral edges of the vermiform body.

Brains of *Sturnira lilium* (not figured), *S. mordax* (Fig. 40), and *S. ludovici* (Fig. 41) closely resemble each other. These brains are characterized by deep and extremely smooth cerebral hemispheres. The pseudocentral sulci and sulci anterior to the pseudocentral sulci are more poorly developed than in other stenodermine bats. The pseudotemporal lobes are angular and project ventrally. The inferior colliculi are completely covered in *S. lilium* and *S. ludovici,* but in *S. mordax,* the posterior portions of the colliculi are dorsally exposed. In all three species, the cerebellum is simple and has a medial crest.

The brain of *Ectophylla macconnelli* (Fig. 42) is similar to that of *Artibeus phaeotis.* In *E. macconnelli,* the cerebral hemispheres are deep and relatively smooth. The major sulci are well developed and the prepseudocentral gyrus protrudes dorsally. The pseudotemporal lobes are angular and protrude ventrally. The inferior colliculi are exposed dorsally, and the cerebellum is simple and crested.

The brains of *Vampyressa nymphaea* (Fig. 43) and *V. pusilla* (Fig. 44) are not alike. The brain of *V. nymphaea* is characterized by deep and somewhat domed cerebral hemispheres having well-developed major sulci. The pseudotemporal lobes project ventrally in an angular fashion. The inferior colliculi are not exposed dorsally. The cerebellum is simple and has a low medial crest. In *V. pusilla*, the cerebrum is smooth and has well-developed sulci, but it is not domed as in *V. nymphaea*. In *V. pusilla*, the inferior colliculi are exposed dorsally. The pseudotemporal lobes and cerebellum of *V. pusilla* resemble those of *V. nymphaea*.

The brains of *Chiroderma salvini* (Fig. 45) and *C. villosum* (Fig. 46) are similar and are characterized by massive cerebral hemispheres that are well sulcated, anteriorly blunt, and somewhat convoluted. The major cerebral sulci are deeper in *C. salvini*, but have small secondary fissures radiating from them in both species. The pseudotemporal lobes are massive and project ventrally in the typically angular fashion. The inferior colliculi are not exposed dorsally, and the cerebellum is crested medially and has small secondary foliations along the lateral edges of the vermiform body.

Brains of species of *Vampyrops* (Figs. 47-49) have massive cerebral hemispheres, deep sulci and high convolutions in most species, and a relatively complex pattern of foliation to the cerebellum. Among the species examined, *V. helleri* (Fig. 47) has the least convoluted cerebrum and the shallowest cerebral sulci. In *V. vittatus* (Fig. 48) and *Vampyrops infuscus* (Fig. 49), the cerebral hemispheres are deeply sulcated and well convoluted. The pseudotemporal lobes are relatively large in all three species and project ventrally in an angular fashion. In *V. helleri*, the posterior portions of the inferior colliculi are exposed dorsally, but in the other two species, the inferior colliculi are completely covered dorsally by the cerebral hemispheres. In all three, the cerebellum is crested medially, and there are secondary foliations at the lateral edges of the vermiform body.

The brain of *Centurio* (Fig. 50) is characterized by pronounced anteroposterior compression resulting in a domed brain. The cerebral hemispheres are relatively smooth and have shallow sulci. The pseudotemporal lobes are also somewhat compressed and project ventrally in a different fashion than in other members of the subfamily. The inferior colliculi are exposed dorsally, and the cerebellum is simple and slightly crested.

Ametrida (Fig. 51) has a brain similar to that of *Centurio*. The cerebrum is compressed and quite smooth, with almost no trace of the major sulci. The pseudotemporal lobes are relatively shallow, angular, and project ventrally. The cerebellum is simple and has a low crest.

The brain of *Stenoderma* (Fig. 52) also resembles that of *Centurio*. *Stenoderma* is characterized by massive cerebral hemispheres that are relatively smooth. The major cerebral sulci are shallow, and the pseudotemporal lobes are large, angular, and ventrally projecting. The inferior colliculi are exposed dorsally. The cerebellum is simple and has a low crest.

Subfamily Phyllonycterinae

Two species (*Erophylla bombifrons* and *Brachyphylla cavernarum*) were examined from this subfamily. *Phyllonycteris* is the only genus not represented.

The brain of *Erophylla* (Fig. 53) has a relatively short and smooth cerebrum, with a shallow pseudocentral sulcus and a slightly developed sulcus anterior to the pseudocentral sulcus. The pseudotemporal lobes are rounded ventrally, and there is a simple pattern of foliation of the cerebellum. The inferior colliculi are dorsally exposed and are not contiguous with each other. In *Erophylla*, the vermiform body of the cerebellum constitutes about a third of the total dorsal expression of the cerebellum.

The brain of *Brachyphylla* (Fig. 54) is characterized by relatively smooth and massive cerebral hemispheres. The major cerebral sulci are well developed, including the sulcus anterior to the pseudocentral sulcus. The pseudotemporal lobes are ventrally angular, but do not protrude ventrally. The inferior colliculi are not visible from above. The vermiform body of the cerebellum is laterally enlarged and constitutes half of the dorsal exposure of the cerebellar tissues. In addition, *Brachyphylla* has one characteristic not found in any other phyllostomatid brain in that the uvular portion of the cerebellum is greatly enlarged and forms a prominent lobe at the posterior edge of the vermiform body along the dorsal surface of the medulla.

Subfamily Desmodontinae

Brains were examined from all three genera of this subfamily. The brains of *Desmodus* (Fig. 55), *Diaemus* (Fig. 56), and *Diphylla* (not figured) are similar in that they all have large cerebral hemispheres that are deeply sulcated and well convoluted. The cerebellum is variously ornamented.

The brain of *Desmodus* (Fig. 55) is characterized by elongate and convoluted cerebral hemispheres that are deeply cut by the pseudocentral sulci and the sulci anterior to them. The pseudotemporal lobes project ventrally in an angular fashion (as in the Stenoderminae), and the inferior colliculi are not dorsally exposed. The vermiform body of the cerebellum forms a medial crest, and there are small secondary foliations along its lateral edges.

In *Diaemus* (Fig. 56), the cerebral hemispheres are less elongate than in *Desmodus* but are well convoluted and deeply sulcated. The pseudotemporal lobes are angular as in *Desmodus* and the inferior colliculi are not dorsally exposed. The cerebellum has a low medial crest and secondary foliations along the lateral edges of the vermiform body.

Diphylla has a cerebrum similar to that of *Diaemus*. The pseudotemporal lobes are angular and project ventrally. The posterior portions of the inferior colliculi are dorsally exposed, and the cerebellum is large and has a medial crest.

Internal Morphology of the Brain

General Description

Internally, the telencephalon of phyllostomatid bats (Figs. 57-61) is similar to the telencephalon of other lower mammals. The caudate nucleus appears to form a discrete body rather than the caudate-putamen complex described by Humphrey (1936) in *Tadarida*. The internal capsule is distinct and separates the putamen from the caudate nucleus as in higher mammals. The globus pallidus is well differentiated, but the laminations characteristic of higher mammals are indistinct, if present. The amygdaloid complex is well represented as in other Microchiroptera. The claustrum is normally absent in bats. Henson (1970) reviewed the extrapyramidal system of bats and noted that the basal ganglia, reticular formation, subthalamus, and tissues involved with audition or vestibular sense are well developed, but that the red nucleus, substantia nigra, pontine nuclei, and inferior olivary nuclei appear to be poorly developed. Corticobulbar and corticospinal fibers of the pyramidal system are poorly developed in all Microchiroptera. Henson (1970) also reported that in the Microchiroptera the cingulate gyrus "is not separated from the more dorsal neocortex by the sulcus splenialis (herein called the cingulate sulcus) as it is in *Pteropus* and advanced mammals." Within the Phyllostomatidae, a number of conditions occur in the development of the cingulate sulcus. This sulcus may not be present, or may be slightly developed or even highly developed. A few species also have a callosal sulcus developed along the top of the corpus callosum. The corpus callosum is well developed in the Phyllostomatidae in contrast to its poorly developed condition in other Microchiroptera. The dentate gyrus and hippocampus are well developed, but their structures appear to vary considerably. A well-developed fornix is present in this family as in other families of bats.

The diencephalon of phyllostomatid bats (Figs. 62-64) is similar to that of other bats and lower mammals. It includes a dorsal thalamus, a metathalmus, a subthalamus, an epithalamus, and a hypothalamus. In Microchiroptera, the thalamic nuclei show little of the differentiation into subgroups so characteristic of higher mammals (Iso, 1944; Kurepina, 1967). In most studies, no attempt was made to distinguish the various thalamic units beyond identification of the larger groupings and the lateral and medial geniculate bodies of the metathalamus.

The cerebellum of the Phyllostomatidae (Figs. 68-73) does not differ internally from that of other mammals. Anatomically, it appears to contain the same cell layers and many of the same fiber systems demonstrated for other mammals. The fastigial and interposital nuclei of the cerebellum are well developed, as is the pars paraflocculus of the phylogenetically more recent dentate nucleus.

The reticular formation and lemniscal systems appear to be developed in the Phyllostomatidae, but are somewhat disperse. Exceptions include the medial and lateral lemnisci, which are quite discrete in this family (Fig. 64).

The brainstem of phyllostomatids (Figs. 68-74) is similar to that of other lower mammals. Obviously, the peculiar adaptations of bats for volant locomotion and for echolocation have necessitated some departures from more "typical" mammalian brains. For instance, among mammals the nucleus gracilis is well

developed as a primary nucleus for sensory information from the hind limbs. In bats, the hind limbs are extremely reduced and, as might be expected, the nucleus gracilis also is reduced. According to Henson (1970), the general somatic sensory and general visceral sensory systems involve the spinal nucleus of V, sensory nucleus of V, solitary nucleus, and sensory nuclei of IX and X as in other mammals. He stated that the various motor systems (general somatic, general visceral, and special visceral) in bats are associated with the same brainstem nuclei as in other mammals. The gustatory, vestibular, auditory, and visual systems (special sensory) also do not differ greatly from the same systems in other mammals. In the Microchiroptera, the pyramidal tracts decussate anterior to the olives and descend lateral to them as the lateral funiculi. Pyramidal decussation is posterior to the olives in other orders of mammals.

Aspects of Variation in Internal Anatomy

Examination of serial and step sections of phyllostomatid brain tissues reveals inter and intrasubfamilial variation of a number of histological features. There has not yet been an attempt to describe completely these variations in a quantitative manner. McDaniel (1973) provided some qualitative information based on the step-sectioning of brains of 25 species of phyllostomatids. It is beyond the scope of this paper to attempt to describe completely the internal anatomy of even these 25 species. However, in order to provide the reader with at least an indication of the variation revealed by sectioning, those species studied will be commented on briefly. It should be noted that the features described represent only a small portion of the total array of structures revealed in the sections.

Subfamily Phyllostomatinae

Data are available for seven species from this subfamily: *Macrotus californicus, Micronycteris megalotis, Mimon crenulatum, Phyllostomus hastatus, Tonatia bidens, Tonatia nicaraguae*, and *Vampyrum spectrum.*

In the brain of *Macrotus* the interhemispheric sulcus forms a shallow cingulate sulcus and descends linearly to the dorsum of the corpus callosum. Cortical cells dorsal and lateral to the corpus callosum are almost uniformly dispersed. The lateral olfactory tracts are ventrally located, and the lateral thalamic nuclei protrude dorsally almost to the level of the top of the habenular nuclei. The amygdaloid nuclei are relatively large. The lateral geniculate bodies are poorly developed, but the medial geniculate bodies are well developed and form a pronounced lateral expansion of the diencephalon. The various thalamic nuclei of the diencephalon are compact and form a shallow, narrow body. The pons is deep and has a ventrally bulging floor. The inferior colliculi are large. The superior olivary nuclei are well developed, but the inferior olivary nuclei are indistinct.

The brain of *Micronycteris megalotis* is similar to that of *Macrotus*; the interhemispheric sulcus includes a shallow cingulate sulcus, below which the interhemispheric sulcus descends linearly to the roof of the corpus callosum. There is a dense layer of cortical cells dorsally adjacent to the corpus callosum and sub-

stantia alba. The lateral olfactory tracts are located on the ventral surface of the cerebrum. The amygdaloid nuclei are relatively large. The thalamic nuclei form a narrow body as in *Macrotus*. The pons projects ventrally, but less so than in *Macrotus*.

In *Mimon crenulatum*, the interhemispheric sulcus descends ventrally in a linear fashion to the roof of the corpus callosum without indication of a cingulate sulcus. The cortex dorsal to the corpus callosum is only slightly denser than the overlying cortex. The lateral olfactory tracts are ventrally located, and the amygdaloid nuclei are relatively large. The lateral thalamic nuclei project dorsally only to the level of the habenular nuclei. The thalamic nuclei form a body somewhat more compressed than in *Macrotus*. The pons is shallower and ventrally flatter than in *Macrotus*. The anterior portion of the medulla forms a deep, V-shaped structure.

The brain of *Phyllostomus hastatus* has an interhemispheric sulcus that contains an extremely well-developed cingulate sulcus (best developed within the family). From the cingulate sulcus the interhemispheric sulcus descends to the roof of the corpus callosum, terminating in a slight basal flare that forms a shallow callosal sulcus. The lateral olfactory tracts are located ventrally. The cortical cells above the corpus callosum do not form a dense layer. The lateral thalamic nuclei project dorsally to the level of the relatively small habenular nuclei. The thalamic nuclei form a wide and shallow diencephalon. The pons is a shallow, wide structure with well-developed corticospinal tracts and a rather flat ventral surface. The inferior colliculi are large (largest within the family).

In *Tonatia bidens*, the interhemispheric sulcus contains a wide, shallow cingulate sulcus, and ventrally forms a shallow callosal sulcus dorsal to the corpus callosum. The amygdaloid nuclei are large, and the cells of the cortex do not form a dense stratum along the dorsal margins of the corpus callosum and substantia alba. The lateral olfactory tracts are located on the ventral surface of the cerebrum. The lateral thalamic nuclei project dorsally almost to the level of the tops of the habenular nuclei. The thalamus is shallower and broader than in *Macrotus*. The deep, broad pons forms a nearly flat floor to the mesencephalon.

In *Tonatia nicaraguae*, the interhemispheric sulcus contains a well-formed cingulate sulcus, from which the interhemispheric sulcus descends linearly to the roof of the corpus callosum. The cingulate sulcus descends toward the corpus callosum. In the region of the anterior commissure, the cingulate sulcus rests almost upon the fibers of the corpus callosum. Cortical cells dorsal and lateral to the corpus callosum and substantia alba are rather uniformly dispersed. The amygdaloid nuclei are large, and the lateral olfactory tracts are ventrally located. The lateral thalamic nuclei project dorsally above the habenular nuclei. The thalamic nuclei form a somewhat broader body than in *Macrotus*.

In *Vampyrum*, the telencephalon includes an interhemispheric sulcus with a well-developed cingulate sulcus and a callosal sulcus dorsal to the corpus callosum. The lateral olfactory tracts are located ventrally. The corpus callosum and substantia alba are exceptionally thick, and there is a dense layer of cortex overlying the corpus callosum and substantia alba. However, this layer is not as dense

as in *Micronycteris*. The amygdaloid nuclei are relatively small in *Vampyrum*. The lateral thalamic nuclei project far above the habenular nuclei. The distance of this projection attained in *Vampyrum* is the greatest within the family. The body of the thalamus is shallow and wide as in *Phyllostomus*. The pons is wide and shallow, and forms a gently rounded venter to the mesencephalon. The corticospinal fibers coursing through the pons are large and well developed. The superior olivary nuclei are large and well developed, and the inferior olivary nuclei are small and indistinct.

Subfamily Glossophaginae

Brains of six species (*Anoura geoffroyi*, *Choeronycteris mexicana*, *Hylonycteris underwoodi*, *Leptonycteris sanborni*, *Lichonycteris obscura*, and *Lonchophylla robusta*) of this subfamily have been sectioned.

The brain of *Anoura* has an interhemispheric sulcus that bulges to form a shallow cingulate sulcus and continues in linear fashion to terminate above the corpus callosum. There is no callosal sulcus. Cortical cells dorsal to the corpus callosum and substantia alba form a denser layer than the overlying cortex. The lateral olfactory tracts are located on the ventral surface of the cerebrum. The lateral thalamic nuclei project dorsally to a level slightly above the habenular nuclei. The amygdaloid nuclei are relatively small. The thalamic nuclei form a wide shallow body. Dorsal to the superior colliculi, there is a dense layer of cell bodies along the external margin of the interhemispheric sulcus. The pons is shallow and wide and has a flat ventral surface. The superior olivary nuclei are large discrete bodies, whereas the inferior olivary nuclei are small but distinct.

In *Choeronycteris*, the interhemispheric sulcus forms a shallow cingulate sulcus as in *Anoura* and descends linearly to terminate above the corpus callosum. Cortical cells dorsal to the corpus callosum and substantia alba do not form a dense layer of cell bodies. The lateral olfactory tracts are located on the ventral aspect of the cerebrum. The lateral thalamic nuclei project dorsally a short distance above the habenular nuclei. The lateral geniculate bodies are somewhat better developed in this species than in *Anoura*, and the medial geniculate bodies are well developed. The thalamic nuclei form a shallow, wide thalamus. Cerebral cortical cells overlying the superior colliculi form a dense layer as in *Anoura*. The pons is shallow and wide, and possesses a flat ventral surface.

In *Hylonycteris*, the interhemispheric sulcus descends linearly to the roof of the corpus callosum. Anteriorly there is a short, shallow cingulate sulcus, but this structure disappears caudally. Cortical cells overlying the corpus callosum and substantia alba do not form a dense layer. The lateral olfactory tracts are ventrally located. The lateral thalamic nuclei project dorsally to a level slightly above the tops of the habenular nuclei. The amygdaloid nuclei are larger than in *Anoura*. Cortical cells overlying the superior colliculi do not form a dense layer. The pons is shallow and forms a flat floor to the mesencephalon.

In *Leptonycteris*, the interhemispheric sulcus forms a shallow cingulate sulcus and descends anteriorly almost linearly to the roof of the corpus callosum as in *Anoura*. There is an indication of a shallow callosal sulcus posteriorly. Cortical

cells above the corpus callosum and substantia alba have the same density as the overlying cells. The lateral olfactory tracts are ventrally located, but anteriorly they are more laterally placed than in *Anoura*. The lateral thalamic nuclei project dorsally above the habenular nuclei. The cerebral cortex overlying the superior colliculi is not significantly denser than in other cortical regions. The thalamus is shallow and wide; the pons is shallow, wide, and ventrally flat.

The brain of *Lichonycteris* has a linear interhemispheric sulcus that has no indication anteriorly of a cingulate sulcus. Posteriorly there is a shallow cingulate sulcus. Cortical cells above the corpus callosum and substantia alba are not stratified. The lateral olfactory tracts are ventrally located. The lateral thalamic nuclei project dorsally to a level slightly higher than the tops of the habenular nuclei. The thalamus is wide and shallow. A dense lamination of cerebrocortical cells overlies the superior colliculi. The pons is shallow and has concavities in its ventral surface beneath the corticospinal tracts.

The brain of *Lonchophylla* has an interhemispheric sulcus that descends almost linearly to the roof of the corpus callosum. There is a short, shallow cingulate sulcus rostral to the anterior commissure. Cortical cells overlying the corpus callosum and substantia alba do not form a particularly dense stratum. The lateral olfactory tracts are ventrally located, and the lateral thalamic nuclei project dorsally slightly above the habenular nuclei. The thalamus is wide and shallow. The pons is shallow and ventrally flat.

Subfamily Carolliinae

Data are available for brains of two species from the Carolliinae, *Carollia perspicillata* and *Rhinophylla pumilio*.

The brain of *Carollia* has an interhemispheric sulcus that includes a shallow cingulate sulcus and a shallow callosal sulcus. Cortical cells dorsal to the corpus callosum and substantia alba do not form a dense layer. The lateral olfactory tracts are located on the ventral aspect of the cerebrum. The lateral thalamic nuclei project dorsally to the level of the tops of the habenular nuclei. The amygdaloid nuclei are relatively large as in the Phyllostomatinae. The thalamus is relatively narrow and deep. The pons is shallow, wide, and ventrally flattened. The superior olivary nuclei are large and distinct, and the inferior olivary nuclei reach the largest relative size within the family.

The brain of *Rhinophylla* is similar to that of *Carollia*. The interhemispheric sulcus is anteriorly linear, but caudally develops a shallow cingulate sulcus and a shallow callosal sulcus. Cortical cells above the corpus callosum and substantia alba do not form a dense layer. The lateral olfactory tracts are ventrally located. The lateral thalamic nuclei project dorsally to the level of the habenular nuclei. The amygdaloid nuclei are large. The thalamus is deep and narrow. The pons is shallow, wide, and ventrally flattened. The superior olivary nuclei are large, and the inferior olivary nuclei are relatively large and distinct as in *Carollia*.

Subfamily Stenoderminae

Brains of six species of this subfamily, *Artibeus jamaicensis*, *Artibeus phaeotis*, *Centurio senex*, *Chiroderma salvini*, *Vampyressa nymphaea*, and *Vampyrops helleri*, have been sectioned and examined.

The brain of *Artibeus jamaicensis* has an interhemispheric sulcus containing a shallow cingulate sulcus and a shallow callosal sulcus just dorsal to the corpus callosum. The callosal sulcus deepens as it courses caudally, and, in the region of the habenular nuclei, it is deeper than the cingulate sulcus. Cells of the cortex do not form a dense layer dorsal to the corpus callosum and substantia alba. The lateral olfactory tracts are ventrally located, but anteriorly they are in a more lateral position than in the phyllostomatines. The amygdaloid nuclei are smaller than in the Phyllostomatinae. The anterior thalamic nuclei project dorsally to the level of the habenular nuclei. The nuclei of the thalamus form a shallow, wide structure. The pons is shallow, well nucleated, and ventrally flattened.

In *Artibeus phaeotis*, the interhemispheric sulcus forms a distinct cingulate sulcus and a smaller callosal sulcus above the corpus callosum. The callosal sulcus is less well developed than in *Artibeus jamaicensis*. Cortical cells overlying the corpus callosum and substantia alba form a slightly denser zone than is formed by other layers of the cortex. The lateral olfactory tracts are ventrally located. The lateral thalamic nuclei project dorsally almost to the level of the habenular nuclei. The thalamus is narrow and deep. The pons is deep and ventrally flattened.

The brain of *Centurio senex* has an interhemispheric sulcus that contains a shallow cingulate sulcus and a somewhat deeper callosal sulcus above the corpus callosum. Cells of the cortex do not form a dense layer dorsal to the corpus callosum and substantia alba. The lateral olfactory tracts are located on the ventral side of the cerebrum. The amygdaloid nuclei are larger than in *Artibeus*. The lateral thalamic nuclei project dorsally a slight distance above the tops of the habenular nuclei. The thalamic nuclei form a deep, relatively narrow body. The pons is wide, shallow, and ventrally flattened.

In *Chiroderma salvini*, the interhemispheric sulcus descends to form a shallow cingulate sulcus and a slightly deeper callosal sulcus. There is no dense layer of cortical cells above the corpus callosum and substantia alba. The lateral olfactory tracts are ventrally located. The amygdaloid nuclei are larger than those of *Artibeus*. The lateral thalamic nuclei project dorsally almost to the level of the habenular nuclei. The thalamic nuclei form a wide, shallow thalamus. The pons is deep and wide, and has a flat ventral surface.

The brain of *Vampyressa nymphaea* has an interhemispheric sulcus containing a well-developed cingulate sulcus and a callosal sulcus that deepens caudally. Cortical cells dorsal to the corpus callosum and substantia alba do not form a dense layer. The lateral olfactory tracts are ventrally located. The lateral thalamic nuclei project dorsally to the level of the habenular nuclei. The thalamus is deep as in *Centurio*. The pons is shallow and has well-formed corticospinal tracts coursing through it. The ventral surface of the pons is flat.

The brain of *Vampyrops helleri* has an interhemispheric sulcus that descends linearly into a well-developed cingulate sulcus. There is a callosal sulcus above the corpus callosum. Cells of the cortex do not form a dense layer of cell bodies above the corpus callosum and substantia alba. The lateral olfactory tracts are located on the ventral surface of the cerebrum. The lateral thalamic nuclei project dorsally above the tops of the habenular nuclei. The thalamic nuclei form a narrow, deep body. The pons is shallow and has a flat ventral surface.

Subfamily Phyllonycterinae

Brains of two species of this subfamily, *Erophylla bombifrons* and *Brachyphylla cavernarum*, were studied.

The brain of *Erophylla* has an anteriorly linear interhemispheric sulcus. Posteriorly, the interhemispheric sulcus includes a shallow cingulate sulcus and a shallow callosal sulcus. Cortical cells overlying the corpus callosum and substantia alba form a shallow layer. The lateral olfactory tracts are located on the ventral surface of the brain. The thalamic nuclei project dorsally to the level of the habenular nuclei. The amygdaloid nuclei are large as in the phyllostomatines. The lateral geniculate bodies are possibly the shallowest in the family, and the medial geniculate bodies are large and well developed. The thalamus is wide and shallow. The pons is shallow, wide, and ventrally curved. The superior olivary nuclei are large and distinct, and the inferior olivary nuclei are relatively large and distinct as in the Carolliinae.

The brain of *Brachyphylla* differs in some features from those of other phyllostomatids. In cross-section, the cerebrum is remarkably circular. Anteriorly, the interhemispheric sulcus includes only a well-developed cingulate sulcus. Posteriorly, there is a shallow cingulate sulcus and a callosal sulcus similar to that of the Desmodontinae. Cortical cells dorsal to the corpus callosum and substantia alba do not form a dense layer distinct from the overlying cortex. This brain offers the only example in the family of lateral olfactory tracts, which are located on the lateral aspects of the cerebrum. The lateral thalamic nuclei project no higher than the habenular nuclei. The amygdaloid nuclei are large as in the phyllostomatines. The pons is deep, wide, and ventrally flattened.

Subfamily Desmodontinae

Data are available for brains of two species from the Desmodontinae, *Desmodus rotundus* and *Diaemus youngii.*

In *Desmodus*, the interhemispheric sulcus includes a cingulate sulcus and a callosal sulcus just above the corpus callosum. Cortical cells above the corpus callosum and substantia alba do not form a dense stratum. The lateral olfactory tracts are located on the ventral surface of the cerebrum. The amygdaloid nuclei are relatively large as in the Phyllostomatinae. The anterior ends of the habenular nuclei are widely separated. The lateral thalamic nuclei project dorsally only to the level of the habenular nuclei. The lateral geniculate bodies are somewhat larger in *Desmodus* than in most members of the family. The medial geniculate bodies are large and deep. The thalamus is wide and shallow. The pons is

relatively deep and narrow, with sides that rise steeply to the level of the cerebellar peduncles. The floor of the pons is flat. The superior olivary nuclei are large and distinct. The inferior olivary nuclei are small (although larger than in most members of the family) and distinct.

The brain of *Diaemus* is much like that of *Desmodus*. The interhemispheric sulcus descends to a well-formed cingulate sulcus, and descends farther and flares laterally just above the corpus callosum to form a callosal sulcus. The cingulate lobes of the cerebrum protrude ventrally into the interhemispheric sulcus. Cortical cells above the corpus callosum and substantia alba do not form a dense layer. The lateral olfactory tracts are located on the ventral surface of the brain. The lateral thalamic nuclei project dorsally to the level of the habenular nuclei. The lateral geniculate bodies are developed as in *Desmodus*, and the medial geniculate bodies are large and deep. The thalamus is wide and shallow. The amygdaloid nuclei are large. The anterior ends of the habenular nuclei are not as distant from each other in *Diaemus* as in *Desmodus*. The pons is deep and narrow, with a flat floor. The sides of the pons rise steeply to the level of the cerebellar peduncles.

Phylogenetic Implications of Neuroanatomical Variation

Small quantitative variations in brain structure may be due to dietary or experience factors (Bennett *et al.*, 1964; Neville and Chase, 1971). However, distinctive variations and patterns of a more qualitative nature above the level of individual variation are likely to be the result of genetic variation. Certainly, features of brain anatomy have been modified to facilitate the various feeding habits among the Phyllostomatidae. Although these modifications have occurred, certain structures have apparently been modified at a much slower rate than have others, and these can be used to demonstrate relationships that are otherwise obscure.

Subfamily Phyllostomatinae

Within the Phyllostomatinae, several trends are evident in the progression of complexity. The cerebral hemispheres tend to elongate from a short and stubby appearance in *Mimon* as indicated by the following series: *Mimon* (Fig. 2), *Micronycteris nicefori* (Fig. 3), *Tonatia bidens* (Fig. 12), *Trachops* (Fig. 10), and *Vampyrum* (Fig. 17). There is also a tendency for cerebral sulcation to deepen and to become more complex in pattern, as shown by the following series: *Macrophyllum* (Fig. 9), *Mimon* (Fig. 2), *Micronycteris minuta* (Fig. 4), *Tonatia bidens* (Fig. 12), *Phyllostomus hastatus* (Fig. 14), and *Phylloderma* (Fig. 16). Another trend involves coverage of the tectum by cerebral and cerebellar tissues. In *Mimon* (Fig. 2), a large portion of the tectum is exposed anterior to the inferior colliculi. This condition is characteristic of primitive bats such as the family Emballonuridae (Schneider, 1957), but occurs in only one phyllostomatid. In *Lonchorhina*, a small strip of tectum is exposed anterior to the inferior colliculi, but in all other phyllostomatids none of the tectum anterior to the inferior colliculi is exposed. Two types of tectal coverage exist within the remainder of the

Phyllostomatinae. In most, the inferior colliculi are dorsally exposed, but in *Phylloderma* (Fig. 16), *Vampyrum* (Fig. 17), and two species of *Phyllostomus* (Figs. 14 and 15) the inferior colliculi are covered dorsally by cerebral and cerebellar tissues. Still another trend is the increasing depth of the cerebellar foliations and the addition of small secondary lobes along the lateral aspects of the vermiform body as in *Macrophyllum* (Fig. 9) and *Vampyrum* (Fig. 17).

Within the Phyllostomatinae, the species of *Micronycteris* (Figs. 3-7) segregate as a group apart from other phyllostomatines. Brains of members of this genus are more complex externally than those of *Mimon* and *Lonchorhina* because the brains of *Micronycteris* have deeper sulci, more elongate cerebral hemispheres, and more complete coverage of the tectum. A distinctive feature of the members of the genus *Micronycteris* thus far examined is that the dorsally exposed inferior colliculi are not contiguous. This condition is not found in any other phyllostomatine, but is found generally in those bats of other subfamilies in which the inferior colliculi are dorsally exposed (*Artibeus phaeotis*, *Vampyrodes caraccioloi*, *Vampyressa pusilla*, *Stenoderma rufum*, and *Diphylla ecaudata*). *Erophylla* appears to be the only member of the family not a phyllostomatine to have dorsally exposed and contiguous inferior colliculi.

Internally, brains of the Phyllostomatinae are varied and indicate derivation from an ancestral type similar to that of *Mimon*. Thus, *Mimon* has the simplest interhemispheric sulcus (Fig. 75)—linear and without evidence of either a cingulate or callosal sulcus. In *Macrotus*, *Tonatia nicaraguae*, and *Micronycteris*, a shallow cingulate sulcus is present (Fig. 76). *Tonatia bidens* has both a shallow cingulate sulcus and a callosal sulcus (Fig. 77), and *Vampyrum* shows even greater development of the same structures (Fig. 79). The cingulate sulcus attains its maximum depth for all Phyllostomatidae in *Phyllostomus hastatus* (Fig. 78). The lateral thalamic nuclei rise above the habenular nuclei in *Phyllostomus*, *Tonatia nicaraguae*, and *Vampyrum*. The thalamus is compressed and fairly symmetrical in *Mimon*, shallow and narrow in *Macrotus* and *Micronycteris*, and shallow and broad in *Phyllostomus*, *Tonatia*, and *Vampyrum*. The pons is altered from the deep and ventrally bulging condition in *Macrotus* into a shallow and ventrally flat structure in *Phyllostomus*. As with external features, the species of *Micronycteris* are distinguished among the Phyllostomatinae in internal anatomy. In *Micronycteris*, there is a dense layer of cell bodies in the cortex overlying the superior colliculi. This layer of cortex is slightly developed in *Vampyrum*, but not in other phyllostomatines.

Aspects of brain anatomy indicate the following relationships within the Phyllostomatinae (Figs. 89, 90). *Mimon* and *Lonchorhina* appear to have the least modified brains among the group and appear to represent a stage from which other species of phyllostomatines are derived. *Macrotus*, *Macrophyllum*, *Micronycteris*, *Trachops*, and *Tonatia* seem to represent one line of evolution from the basal form, but *Micronycteris* diverges rather early from the remainder of this line. *Tonatia* and *Trachops* have the most highly modified brains in this line, those of *Macrotus* and *Macrophyllum* being much less modified. A second line of evolution is indicated by the brains of *Phyllostomus* and *Phylloderma*. Within

this second line, *Phyllostomus elongatus* appears to be an early branch. *Vampyrum* shares features with both major lines of evolution and cannot be assigned easily to either on the basis of features examined in this study.

Subfamily Glossophaginae

Examination of the subfamily Glossophaginae reveals two basic brain types with many features in common. The genera *Choeroniscus*, *Glossophaga*, *Hylonycteris*, *Leptonycteris*, and *Lonchophylla* are similar in having a rather short, stubby cerebrum with relatively small olfactory bulbs. A longer and shallower cerebrum with larger olfactory bulbs is characteristic of *Anoura*, *Choeronycteris*, and *Monophyllus*.

Of these two general types, brains of the group characterized by a short, stubby cerebrum bear some resemblance to brains of some of the smaller Phyllostomatinae such as *Macrotus* or *Macrophyllum*, with the exception that the inferior colliculi are not exposed dorsally in the Glossophaginae.

The extent of elongation and shallowness of the cerebrum in the second group renders brains of its members unlike those of any other phyllostomatid bats. The brain of *Anoura* represents the extreme in terms of cerebral elongation and dorsoventral compression.

A similar dichotomy is evident from examination of the internal anatomies of the brains of several of these species. Again, the brains of *Anoura* and *Choeronycteris* (*Monophyllus* was not sectioned) resemble each other closely, but are somewhat different from brains of other glossophagines. *Anoura* and *Choeronycteris* have a shallow but definite cingulate sulcus (Fig. 81) and a dense layer of cell bodies along the margin of the interhemispheric sulcus above the superior colliculi. Brains of *Hylonycteris*, *Leptonycteris*, *Lichonycteris*, and *Lonchophylla* have only a hint of a cingulate sulcus (*Leptonycteris* has the most definite sulcus). The brains of these genera do not have a dense layer of cell bodies along the margin of the interhemispheric sulcus (Fig. 80).

Compared with variations found in the Phyllostomatinae and Stenoderminae, brains of glossophagine bats reveal little variation. Although this undoubtedly is a reflection of the small number of characters investigated, it also may result from the imposition of severe restrictions placed on brain development by the elongation and streamlining of the skull as an adaptation to nectar-feeding.

Data on brain anatomy indicate subgroups of glossophagine bats unlike the groups indicated by Baker's chromosomal data (1967) or the groups indicated by Phillips' study of dentitions(1971).

Subfamily Carolliinae

Brains within this small subfamily show little interspecific variation and almost as little variation between the two genera.

The brain of *Carollia* (Fig. 26) is similar to those of the smaller phyllostomatines. *Carollia* has relatively short cerebral hemispheres with shallow sulcations, a simple pattern of cerebellar foliation, and rounded pseudotemporal lobes on the cerebrum. *Carollia* differs from the small phyllostomatines by not

having dorsally exposed inferior colliculi. Internally, the brain of *Carollia* also resembles that of the small phyllostomatines, except that the cingulate and callosal sulci resemble those of the Stenoderminae (Fig. 82). The thalamus of *Carollia* resembles that of *Macrotus*, but the pons is more like that of *Tonatia.*

The brain of *Rhinophylla* shows many of the same relationships indicated by that of *Carollia.* However, *Rhinophylla* differs from *Carollia* in having more angular pseudotemporal lobes (as in the Stenoderminae) and a less well-developed cingulate sulcus.

Phylogenetically, the Carolliinae appear to have arisen from a small phyllostomatine ancestor with a brain probably not far removed from the condition seen in *Macrotus. Rhinophylla* is probably derived relative to *Carollia* in light of the more pronounced similarities between *Carollia* and some smaller phyllostomatines.

Subfamily Stenoderminae

Although the subfamily Stenoderminae is exceptionally large, brains of its members have a rather conservative degree of variation among genera. The amount of variation is not substantially greater than that found among the species of the single genus *Artibeus.* Brains of this subfamily are characterized by a deep cerebrum having large pseudotemporal lobes that project ventrally in a pronounced angular fashion. The major cerebral sulci are well developed in most species. The cerebellum tends to have small secondary foliations at the lateral edges of the vermiform body. In most species, the vermiform body is expanded dorsally to form a medial cerebellar crest. Intrageneric variation exists in cerebral surface topography and in dorsal exposure of the inferior colliculi.

Anatomical trends within this subfamily include a gradual elongation of the cerebrum as reflected in the series: *Artibeus toltecus* (Fig. 31), *Artibeus watsoni* (Fig. 32), *Uroderma bilobatum* (Fig. 38), and *Chiroderma salvini* (Fig. 45). A deepening of cerebral sulcation is found in the progression from *Artibeus watsoni* (Fig. 32), to *Vampyrodes caraccioloi* (Fig. 37), to *Uroderma bilobatum* (Fig. 38), attaining the greatest depth in *Vampyrops vittatus* (Fig. 48). There is also a trend for ornamentation to increase along the lateral lobes of the cerebellum (compare *Artibeus watsoni* (Fig. 32) with *Vampyrops helleri* (Fig. 47)).

Smaller species of the genus *Artibeus* appear to have the least modified brains in this subfamily. These brains are among the least sculptured within the Stenoderminae, but even the brains of larger species of this genus are only slightly modified from those of *Artibeus cinereus* (Fig. 28), *A. aztecus* (Fig. 29), *A. toltecus* (Fig. 31), and *A. watsoni* (Fig. 32). The brain of *Artibeus phaeotis* (Fig. 30) differs from those of other species of *Artibeus* in having short and deep cerebral hemispheres, a somewhat domed profile, and dorsally exposed inferior colliculi.

Within the Stenoderminae, the genera *Centurio* (Fig. 50), *Ametrida* (Fig. 51), and *Stenoderma* (Fig. 52) are characterized by the presence of an anteroposteriorly compressed brain and skull. In these genera, the brain is externally much like that of *Artibeus phaeotis* in having short and deep cerebral hemispheres, a domed

profile, and dorsally exposed inferior colliculi. The degree of similarity among these brains suggests that *Centurio*, *Ametrida*, and *Stenoderma* are derived from an ancestor anatomically much like *Artibeus phaeotis*.

Externally, most of the remaining stenodermine genera vary only slightly from the general *Artibeus* type of brain. More exceptional variation is found in *Vampyrodes* (Fig. 37), *Sturnira mordax* (Fig. 40), *Ectophylla macconnelli* (Fig. 42), and *Vampyressa pusilla* (Fig. 44). In these species, the inferior colliculi are exposed dorsally. Other features of the brains of these species are similar to those of most *Artibeus*.

Aspects of internal anatomy were examined for six species of the Stenodermi-nae and only slight variation was found. The interhemispheric sulcus is among the most consistent structures within this subfamily. All species have a cingulate sulcus and a flared callosal sulcus similar to that of *Vampyrops* (Fig. 83). The thalamus is narrow and deep in *Artibeus phaeotis*, *Centurio senex*, *Vampyressa nymphaea*, and *Vampyrops helleri*; it is wide and shallow in *Artibeus jamaicensis* and *Chiroderma salvani*. The lateral thalamic nuclei project dorsally above the habenular nuclei in *Centurio* and *Vampyrops*, but in *Artibeus* (two species), *Chiroderma*, and *Vampyressa* they project only to the level of the top of the habenular nuclei.

Aspects of internal anatomy do not appear to vary in a significant pattern within the Stenoderminae.

Subfamily Phyllonycterinae

It is unfortunate that a brain of *Phyllonycteris* was unavailable for examination during the course of this study, because even a cursory examination of the brains of *Erophylla* and *Brachyphylla* reveals pronounced differences in anatomy. The magnitude and nature of these differences suggest greater divergence within this subfamily than within any other subfamily of phyllostomatids.

The brain of *Erophylla* (Figs. 53, 84, 87) resembles that of *Macrotus* in several features: short smooth cerebrum; ventrally rounded pseudotemporal lobes; primitive foliation of the cerebellum; dorsally exposed inferior colliculi that are narrowly contiguous; shallow cingulate sulcus; lateral olfactory tracts on the ventral surface of the cerebrum; and relatively large amygdaloid nuclei. This relationship is similar to that which Walton and Walton (1968) reported between *Phyllonycteris* and *Macrotus* on the basis of pelvic and pectoral osteology.

The brain of *Brachyphylla* (Figs. 54 and 85) is more desmodontine or stenodermine in appearance. It has massive cerebral hemispheres, ventrally angular pseudotemporal lobes, inferior colliculi that are not exposed dorsally, a well-developed cingulate sulcus, and a well-developed callosal sulcus. *Brachyphylla* differs from all other phyllostomatid bats in two features—the lateral olfactory tracts are located on the lateral aspect of the cerebral hemispheres (Fig. 88), and the uvula is enlarged to form a shelf of cerebellar tissue above the medulla. Aspects of brain anatomy do not support the conclusions of Silva-Taboada and Pine (1969), but indicate instead that *Brachyphylla* is most closely allied to the Desmodontinae or possibly the Stenoderminae as indicated by Dobson (1878).

Subfamily Desmodontinae

The three genera of this subfamily have brains that are similar in anatomical structure. *Desmodus* (Fig. 55) has relatively longer cerebral hemispheres than does *Diaemus* (Fig. 56) or *Diphylla* (not figured), but *Diphylla* has dorsally exposed inferior colliculi, whereas *Desmodus* and *Diaemus* do not. In all three genera, the cerebrum is similar to that of the larger stenodermines.

Internally, the Desmodontinae are stenodermine in most features, but the interhemispheric sulcus of vampire bats is modified somewhat from the typical stenodermine sulcus. In vampires, the cingulate gyrus protrudes into the callosal sulcus and the base of the interhemispheric sulcus (Fig. 86).

Phylogenetically, the Desmodontinae appear to be derived from stenodermine ancestry (Fig. 89). At this point, all three genera appear to be equally modified from any stenodermine ancestor. No attempt at aligning the genera can be made until the brain of *Diphylla* has been sectioned.

In general, aspects of brain anatomy reveal expected phylogenetic relationships within and among subfamilies of the Phyllostomatidae (Figs. 89 and 90), and indicate the possibility of some rather interesting new relationships. It appears that a constellation of characters (certainly greater than considered here) will be necessary to describe satisfactorily relationships at the generic and specific levels. In retrospect, it seems likely that brain anatomy will prove more difficult to utilize in other mammalian families in which there is considerably less diversity among species.

SUMMARY

Variations of external and internal brain anatomy of phyllostomatid bats support many of the phylogenetic relationships that have been hypothesized on the basis of characteristics of dentition and skull morphology. In a few cases, features of brain anatomy suggest relationships contrary to those currently accepted.

Within the subfamily Phyllostomatinae, features of the brain indicate that insectivorous taxa, such as *Mimon* and *Lonchorhina*, are the least modified from a hypothetical generalized and primitive type. This finding is consistent with existing concepts of chiropteran evolution in which insectivory is considered the "primitive" feeding habit of bats. Brains of slightly modified insect eaters characteristically have short, stubby, relatively smooth cerebral hemispheres, dorsal exposure of the tectum anterior to the inferior colliculi, and a simple pattern of cerebellar foliation. Two lines of evolution apparently have developed from the primitive type. One of these lines, which includes the genera *Phyllostomus* and *Phylloderma*, is characterized by the presence of massive and deeply sulcated brains. The other line of phyllostomatine evolution, which includes *Micronycteris*, *Macrotus*, *Tonatia*, and similar species, have brains that resemble those of *Mimon* and *Lonchorhina*, but reveal complex development of some features. Interestingly, brains of the genus *Micronycteris* vary only slightly among themselves, but segregate easily from those of other phyllostomatines on the basis of a number of external and internal characteristics. This contiguity

within the genus *Micronycteris* is of considerable interest, because some doubt previously has existed as to the validity of this genus as a natural taxonomic unit. Internal histological examination is needed for several members of this genus not yet studied.

Brains from the nectar-feeding Glossophaginae indicate the possibility of two major directions of development within that subfamily, but present data do not support the diphyletic lines proposed by Baker (1967). The brains of *Anoura*, *Choeronycteris*, and *Monophyllus* are extremely elongate and shallow as compared with those of *Choeroniscus*, *Glossophaga*, *Hylonycteris*, *Leptonycteris*, and *Lonchophylla*. Brains from the latter group are rather stubby, and are most likely derived from those of small phyllostomatine type. Brains from the former group are so modified that, although they bear some resemblance to the brains of other glossophagines, the exact nature of the existing relationship is obscure and will require further investigation. There is little indication of external brain requirements for nectar-feeding. However, massive cerebral hemispheres have not evolved, and it is clear that nectar-feeding may be accommodated by both short and long-cerebrum brains. Internally, a few differences were observed between the two subgroups of glossophagines. Most nectar-feeders have no cingulate sulcus, but a shallow cingulate sulcus does develop in the case of the long-cerebrum group. The small amount of internal variation in glossophagine brain structure is possibly explained as a result of the severe anatomical restrictions encountered by nectar feeders.

Brains of *Carollia* and *Rhinophylla* (subfamily Carolliinae) are similar. The two genera comprising this subfamily show many affinities with a *Macrotus*-like ancestor (small phyllostomatine).

The Stenoderminae, although the most diverse subfamily within the Phyllostomatidae in number of species, evidently does not have as much diversity in aspects of brain anatomy as that found in the Phyllostomatinae. Additionally, except for a few internal features, variation among stenodermine bats is confined to those features found also to vary among the Phyllostomatinae. This peculiarity perhaps further substantiates a phyllostomatine ancestry for the Phyllostomatidae. It is of interest that the spectrum of variation encountered within the Stenoderminae is no greater than that found within the single stenodermine genus *Artibeus*.

A final comment concerns the development of the vermiform body of the cerebellum. In the Stenoderminae and the Desmodontinae, the vermiform body tends to be enlarged dorsally, forming a pronounced cerebellar crest, especially when compared with its more reduced state among the Glossophaginae. These opposing conditions are possibly a direct reflection of conditions imposed by different feeding habits. The enlargement of the relatively less-derived vermiform body may correlate directly with a habit involving active terrestrial locomotion (stenodermine bats crawl or forage in fruit trees, and vampires often crawl onto their prey from the ground). In glossophagine bats, concentrated development of the phylogenetically more recent lateral lobes of the cerebellum may correlate with specialized hovering behavior.

Within the Phyllonycterinae, the brain of *Brachyphylla* differs greatly from the brain of *Erophylla*, and differs significantly in some features from the brains of all other phyllostomatid bats. The magnitude of difference between the brains of *Brachyphylla* and *Erophylla* is such that the validity of considering *Brachyphylla* as an aberrant phyllonycterine must be questioned seriously. On the basis of features of brain anatomy, *Erophylla* appears to be derived from a *Macrotus*-like (phyllostomatine) ancestor, whereas *Brachyphylla* shows more similarity to the Desmodontinae than to any other subfamily.

Brains of the Desmodontinae show definite specialization towards an enlarged cerebrum with well-developed gyri and sulci. Some intergeneric variation is evident, but the brains of vampires suggest a subgroup of specialized bats of probable stenodermine ancestry.

Acknowledgments

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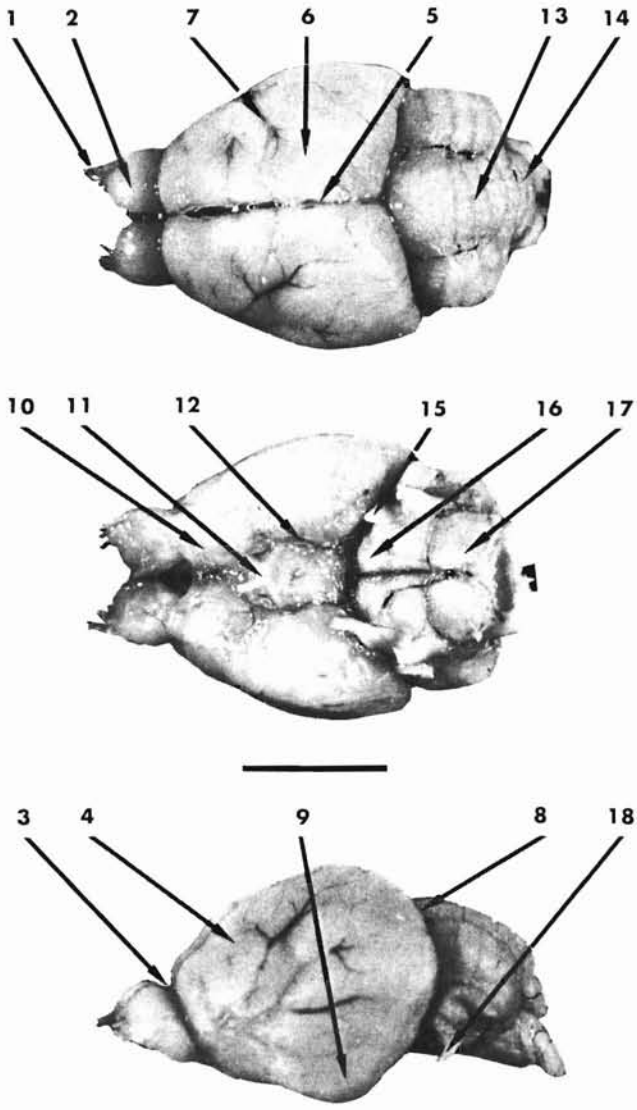
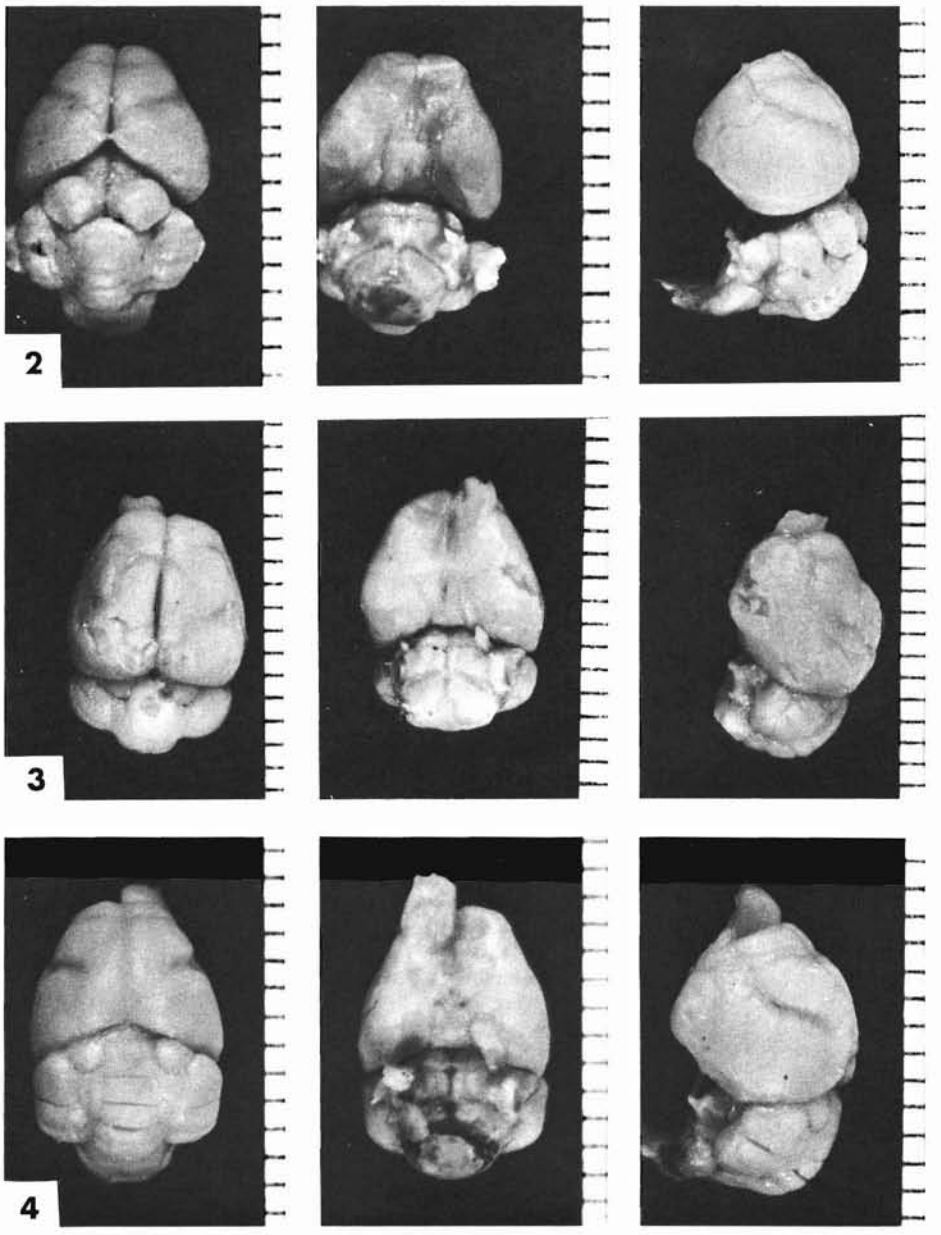
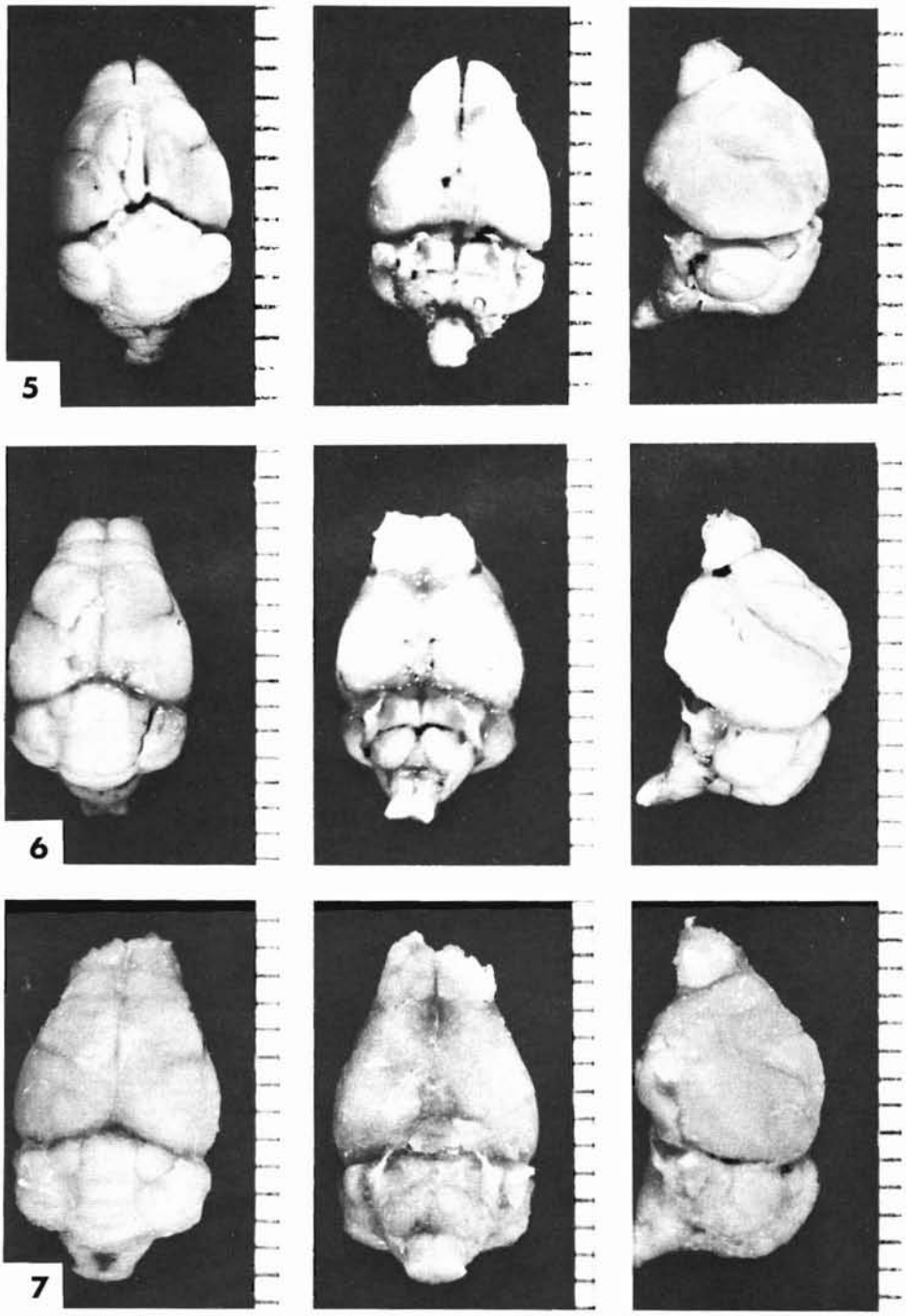


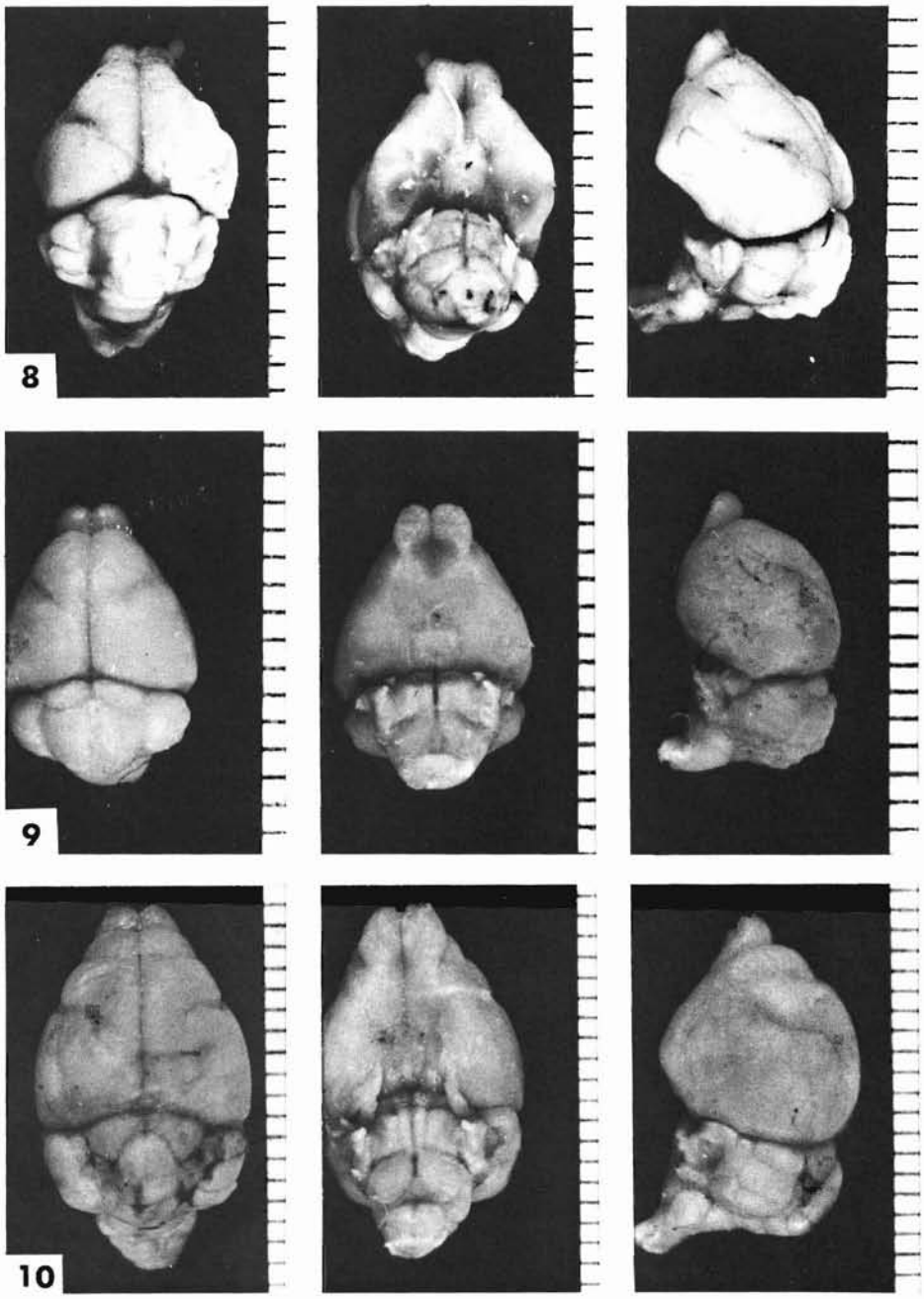
FIG. 1.—Dorsal, ventral, and lateral views of a phyllostomatid brain (*Leptonycteris sanborni*). Line between ventral and lateral views represents 5 mm. Labeled structures are: 1, olfactory nerve; 2, olfactory bulb; 3, anterior rhinal fissure; 4, frontal lobe of telencephalon; 5, interhemispheric sulcus; 6, parietal portion of telencephalon; 7, pseudocentral sulcus; 8, occipital portion of telencephalon; 9, pseudotemporal lobe of telencephalon; 10, lateral olfactory tract; 11, optic chiasma; 12, hippocampal sulcus; 13, vermiform body of cerebellum; 14, uvula of cerebellum; 15, trigeminal nerve; 16, pons; 17, olive; 18, vestibulocochlear nerve.



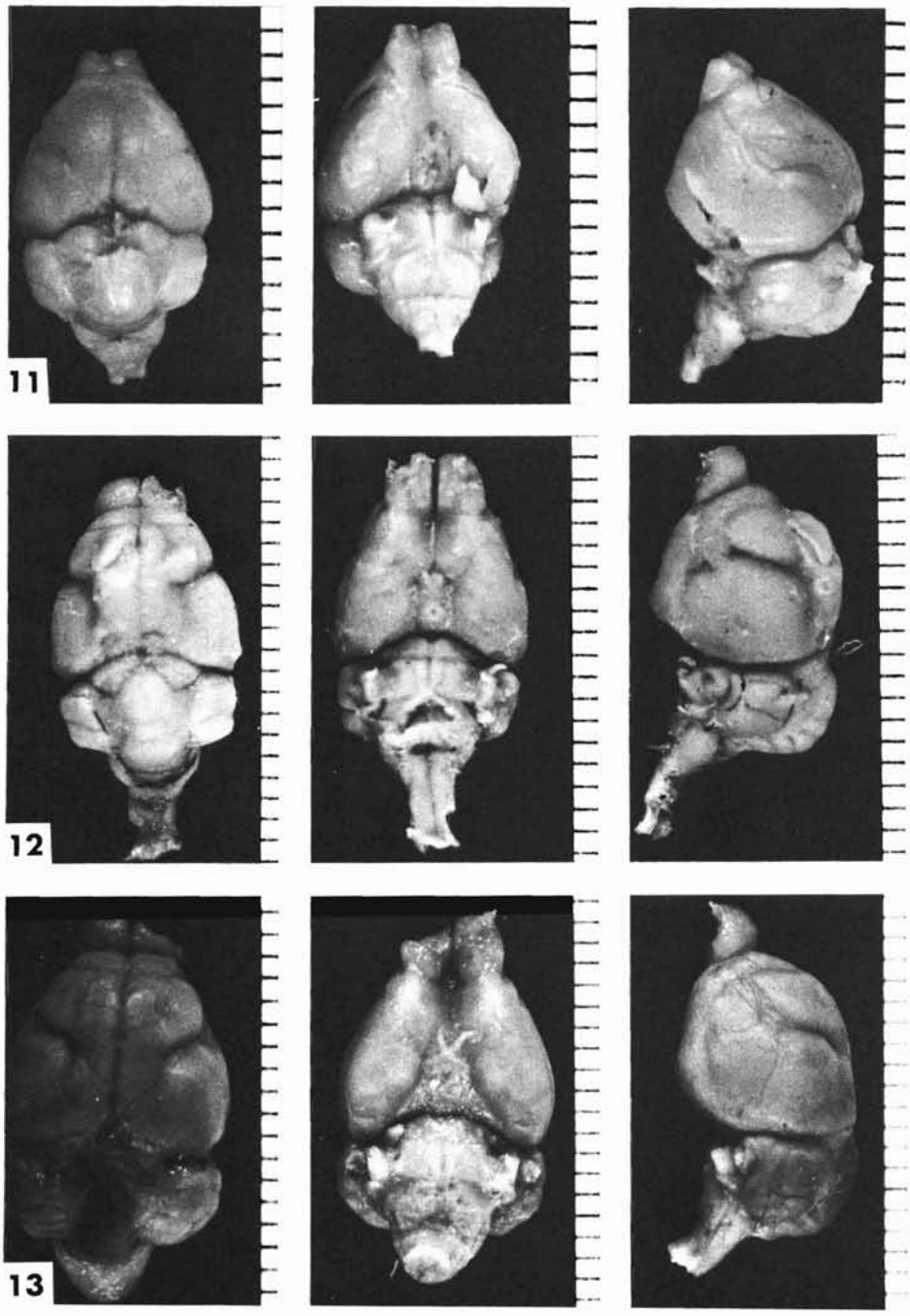
FIGS. 2-4.—Dorsal, ventral, and lateral views of the brains of: 2, *Mimon crenulatum*; 3, *Micronycteris nicefori*; and 4, *Micronycteris minuta*.



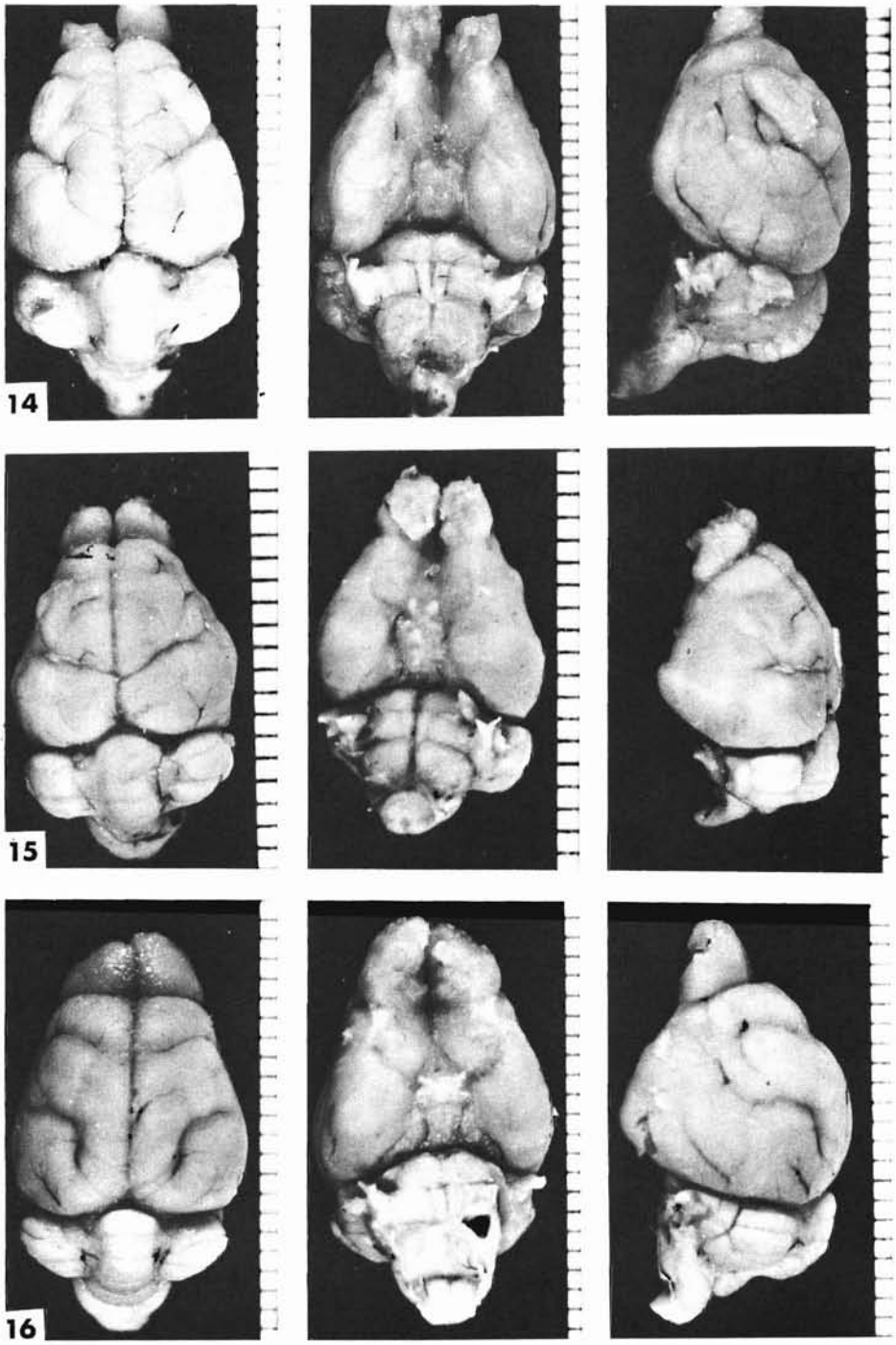
FIGS. 5-7.—Dorsal, ventral, and lateral views of the brains of: 5, *Micronycteris schmidtorum*; 6, *Micronycteris megalotis*, and 7, *Micronycteris hirsuta*.



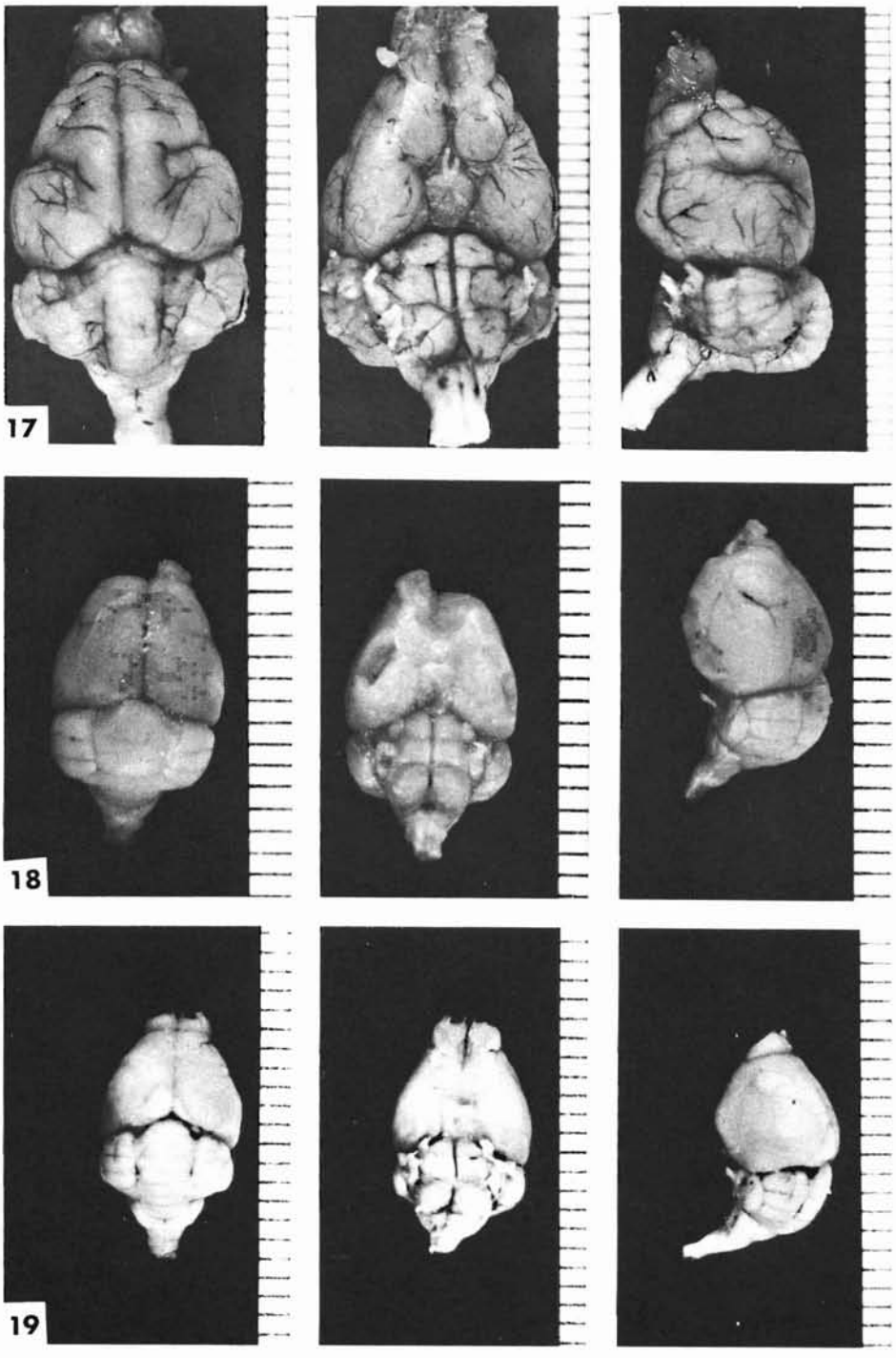
FIGS. 8-10.—Dorsal, ventral, and lateral views of the brains of: 8, *Macrotus californicus*; 9, *Macrophyllum macrophyllum*; and 10, *Trachops cirrhosus*.



FIGS. 11-13.—Dorsal, ventral, and lateral views of the brains of: 11, *Tonatia nicaraguae*; 12, *Tonatia bidens*; and 13. *Phyllostomus elongatus*.



FIGS. 14-16.—Dorsal, ventral, and lateral views of the brains of: 14, *Phyllostomus hastatus*; 15, *Phyllostomus discolor*; and 16, *Phylloderma stenops*.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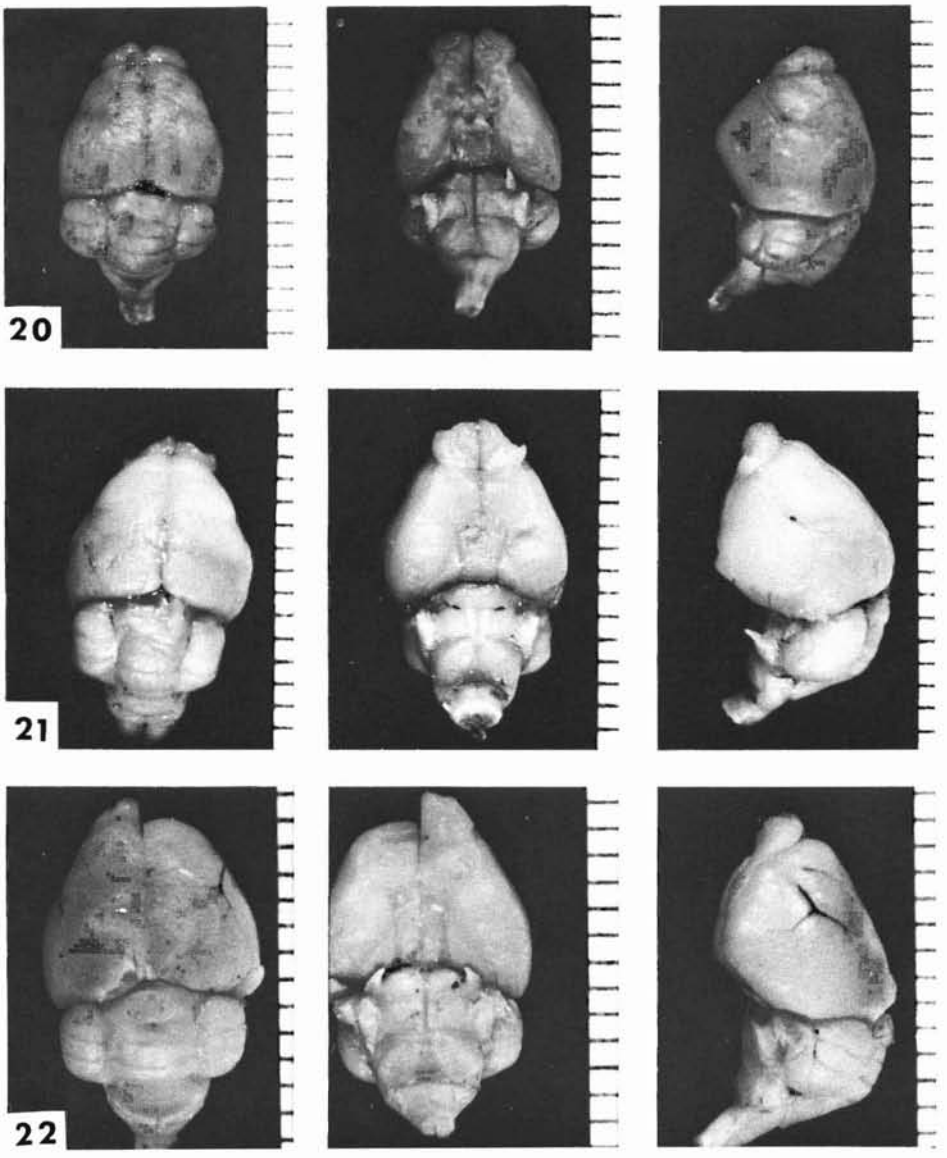
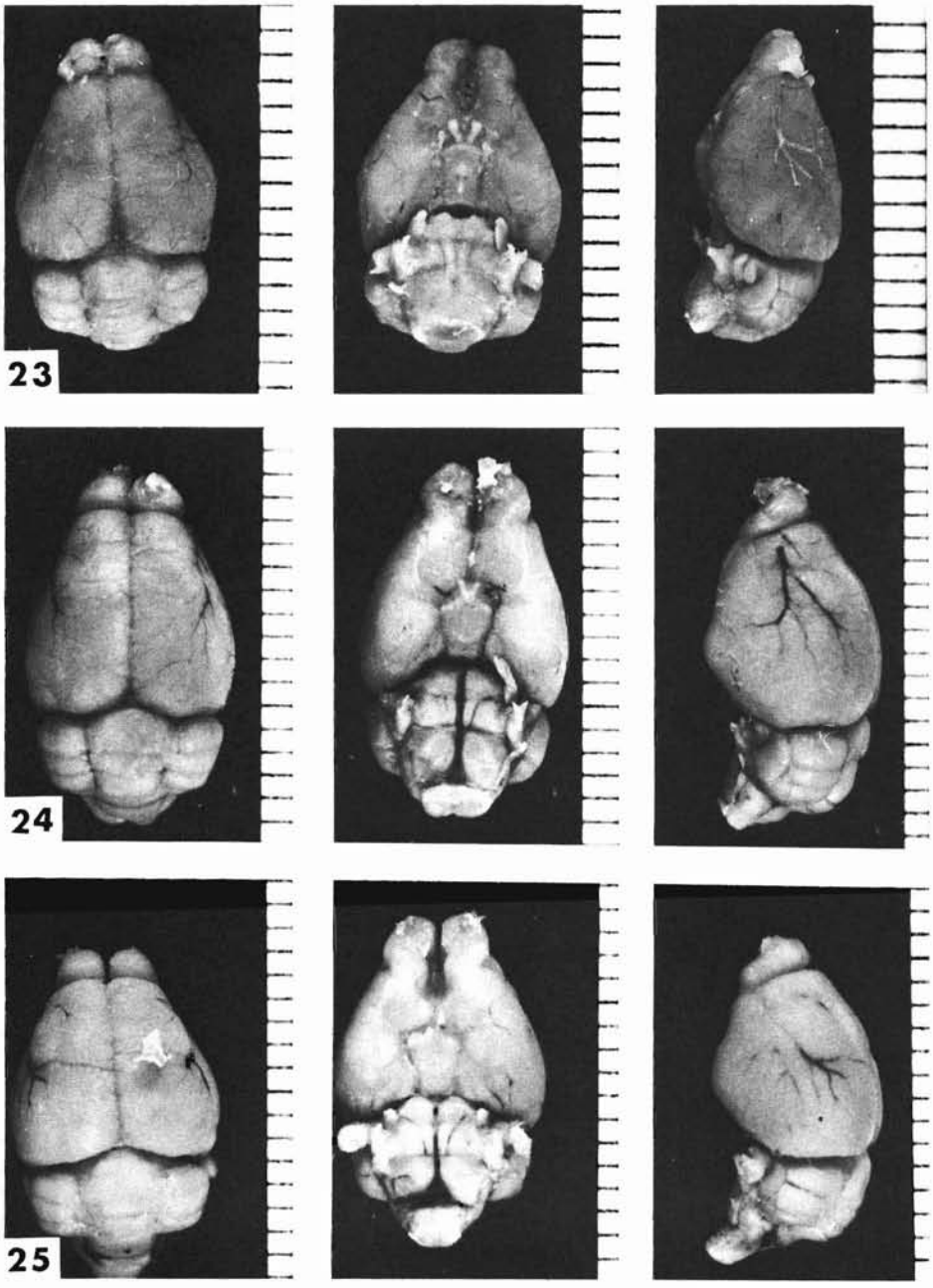


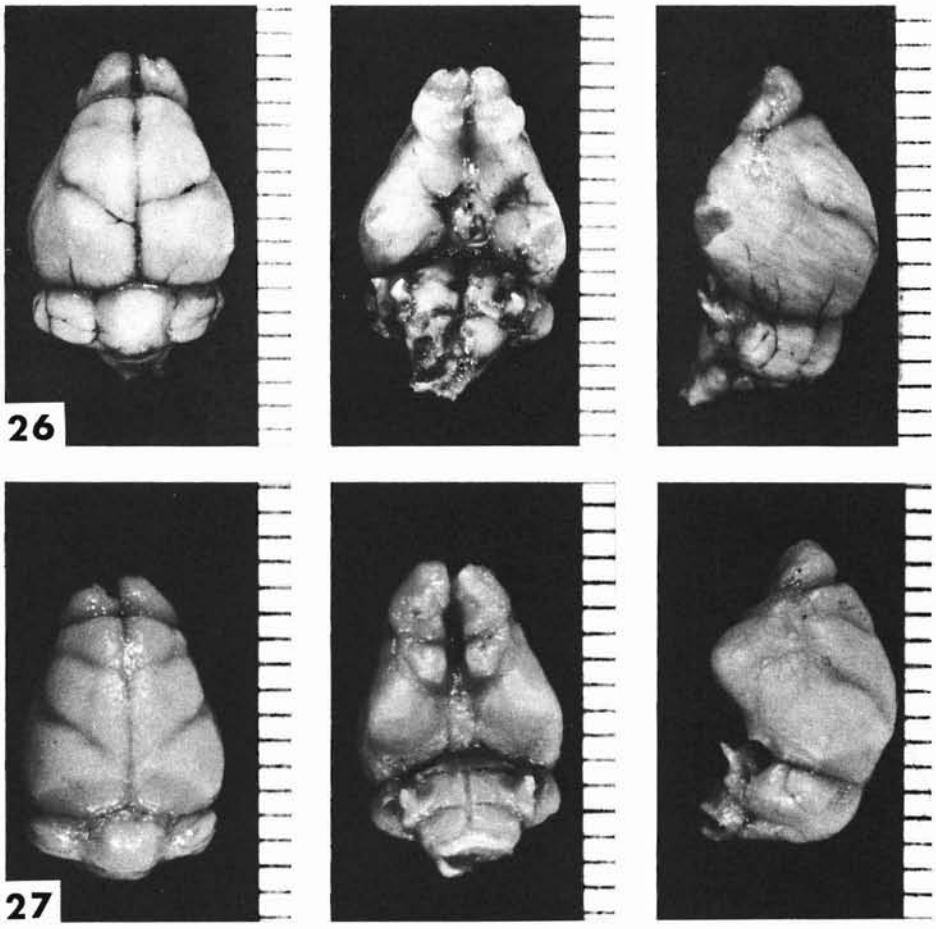
FIGS. 20-22.—Dorsal, ventral, and lateral views of the brains of: 20, *Lichonycteris obscura*; 21, *Glossophaga alticola*; and 22, *Glossophaga commissarisi*.

←

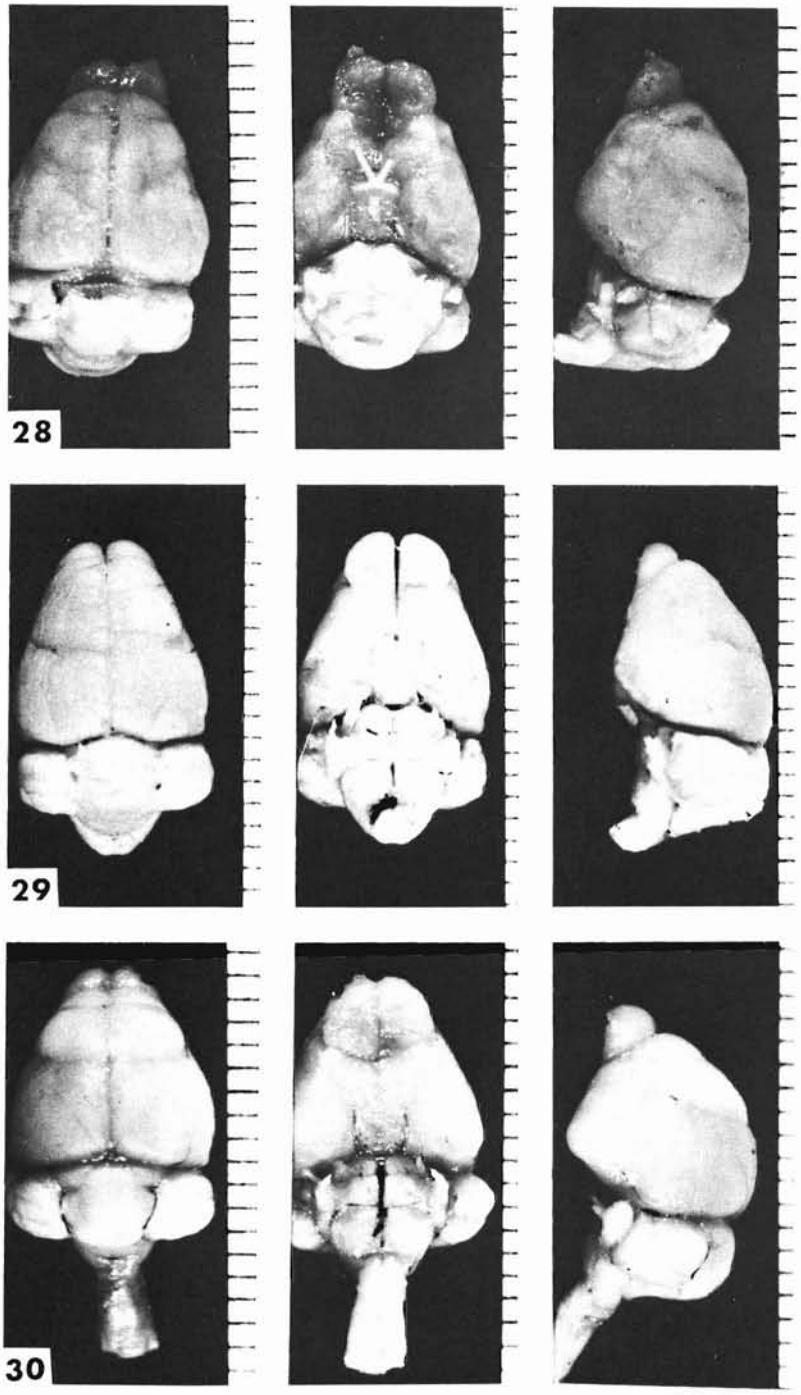
FIGS. 17-19.—Dorsal, ventral, and lateral views of the brains of: 17, *Vampyrum spectrum*; 18, *Choeroniscus godmani*; and 19, *Hylonycteris underwoodi*.



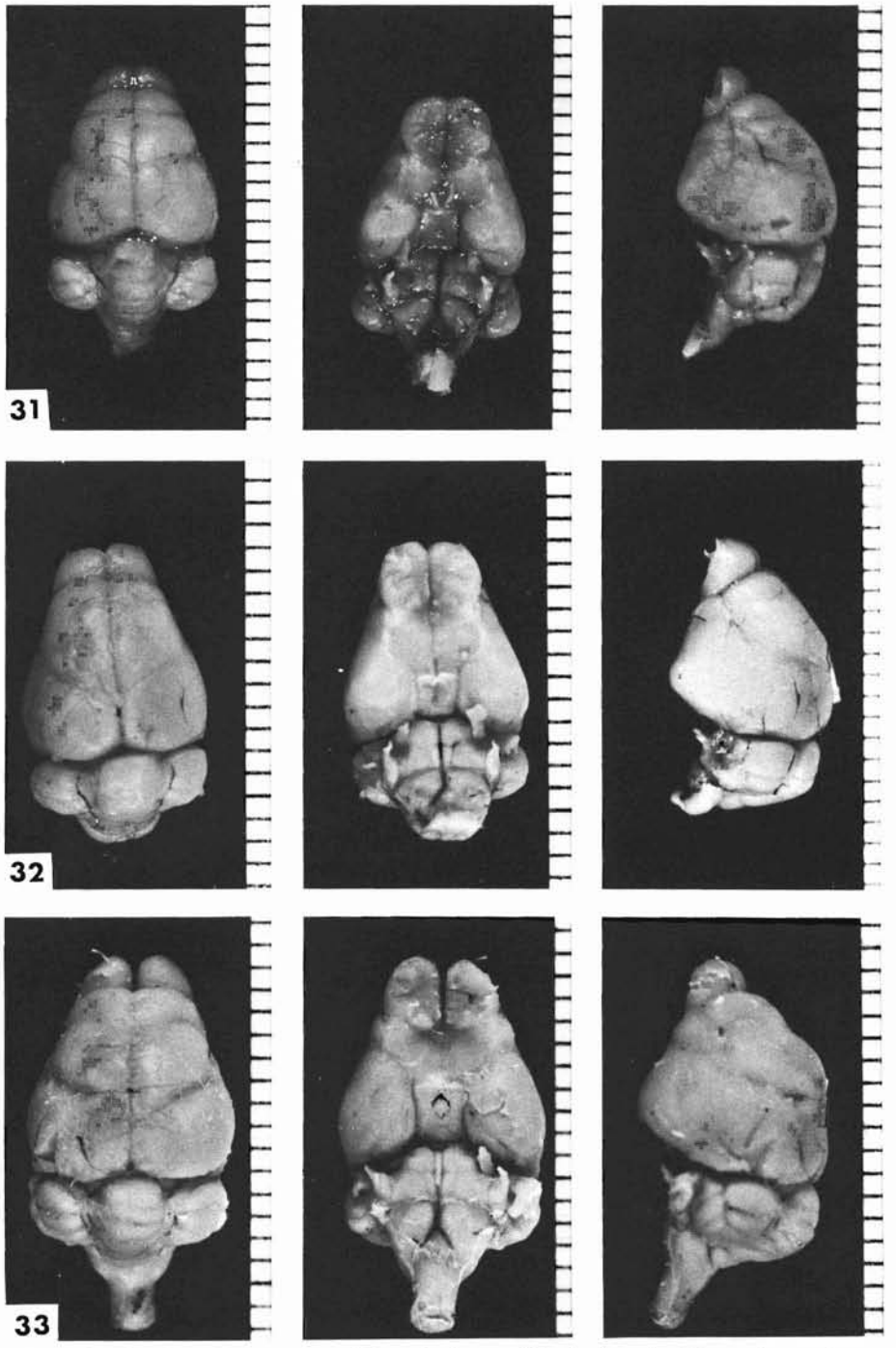
FIGS. 23-25.—Dorsal, ventral, and lateral views of the brains of: 23, *Choeronycteris mexicana*; 24, *Anoura geoffroyi*, and 25, *Lonchophylla robusta*.



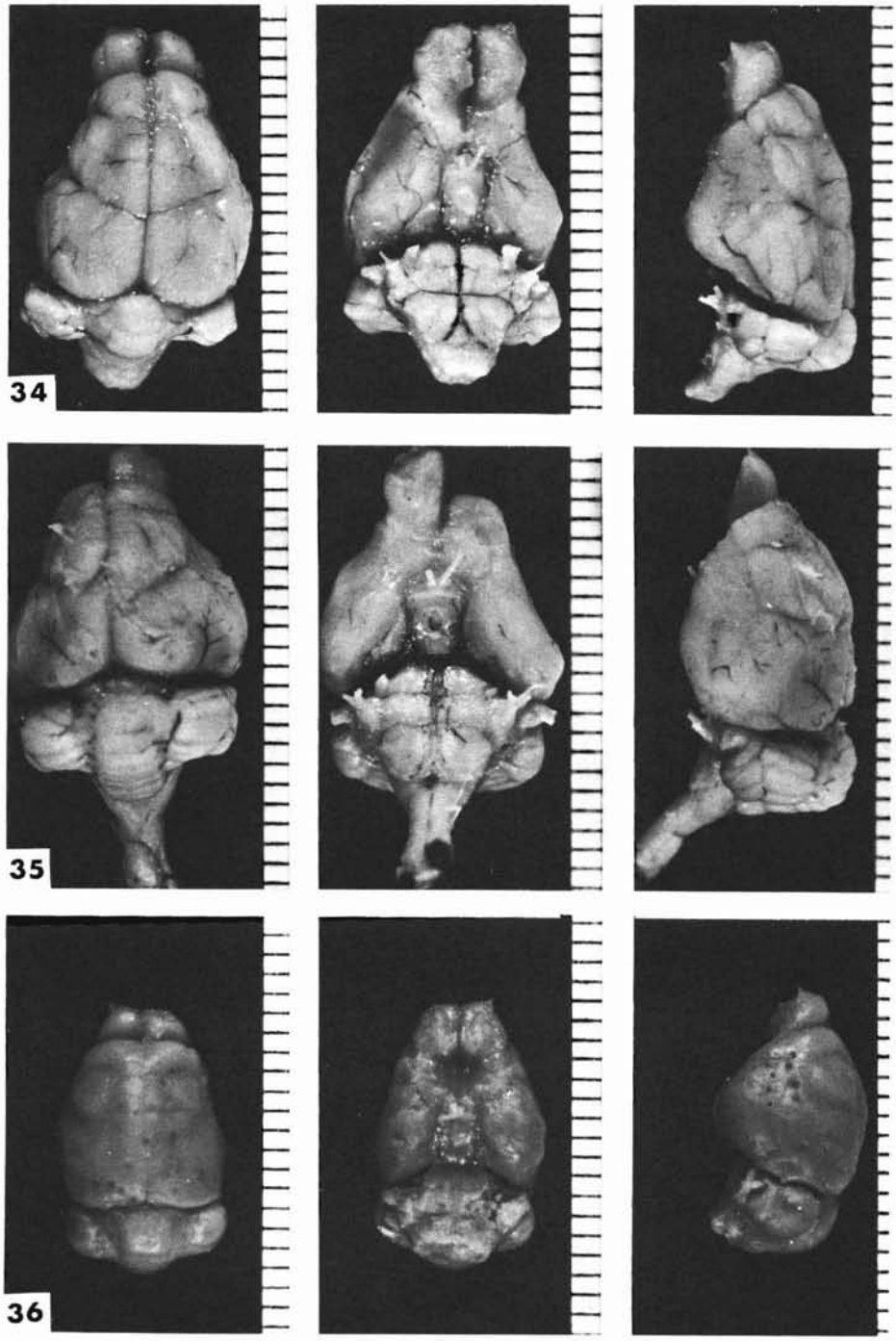
FIGS. 26-27.—Dorsal, ventral, and lateral views of the brains of: 26, *Carollia perspicillata*; and 27, *Rhinophylla pumilio*.



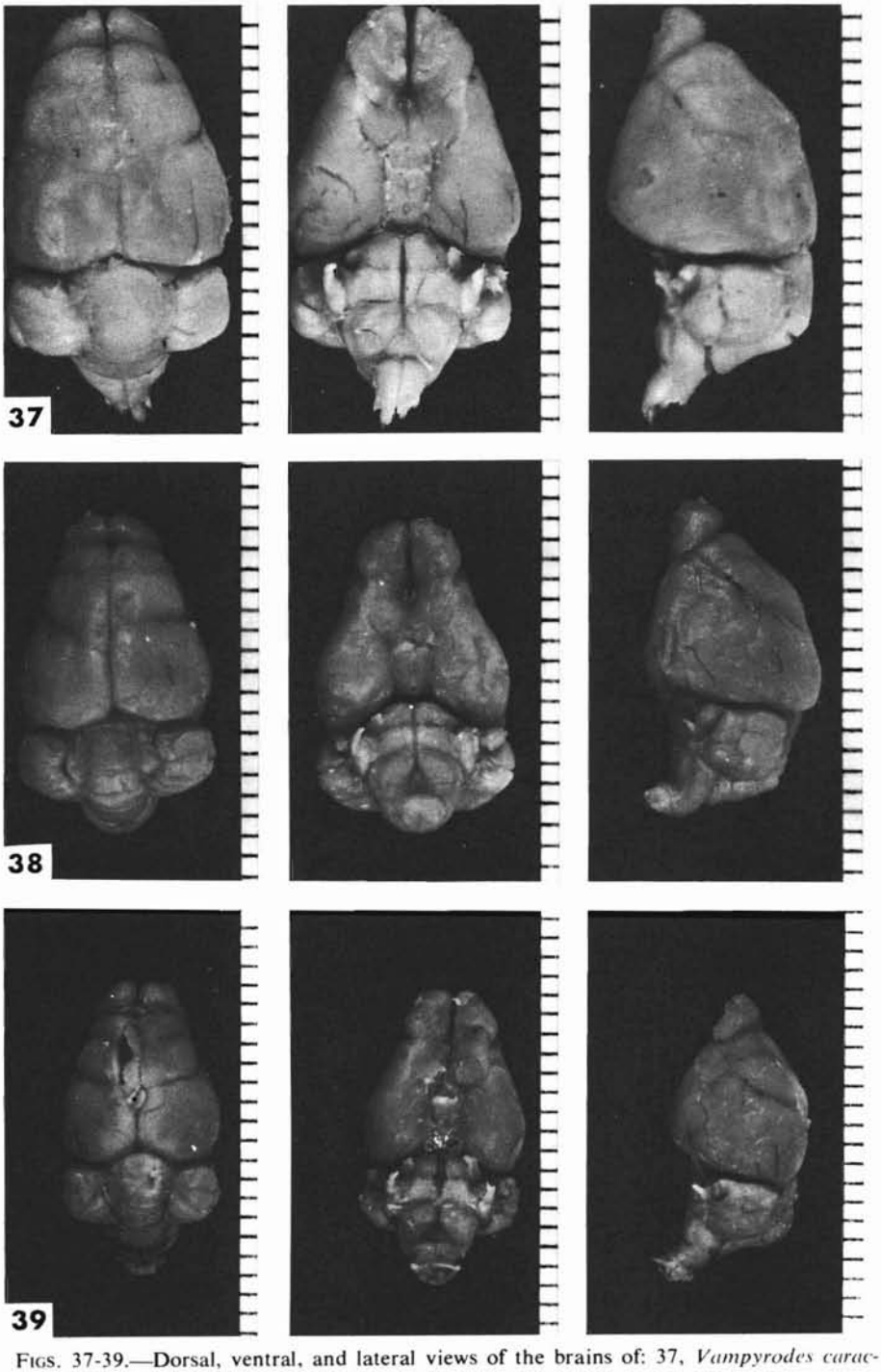
FIGS. 28-30.—Dorsal, ventral, and lateral views of the brains of: 28, *Artibeus cinereus*; 29, *Artibeus aztecus*; and 30, *Artibeus phaeotis*.



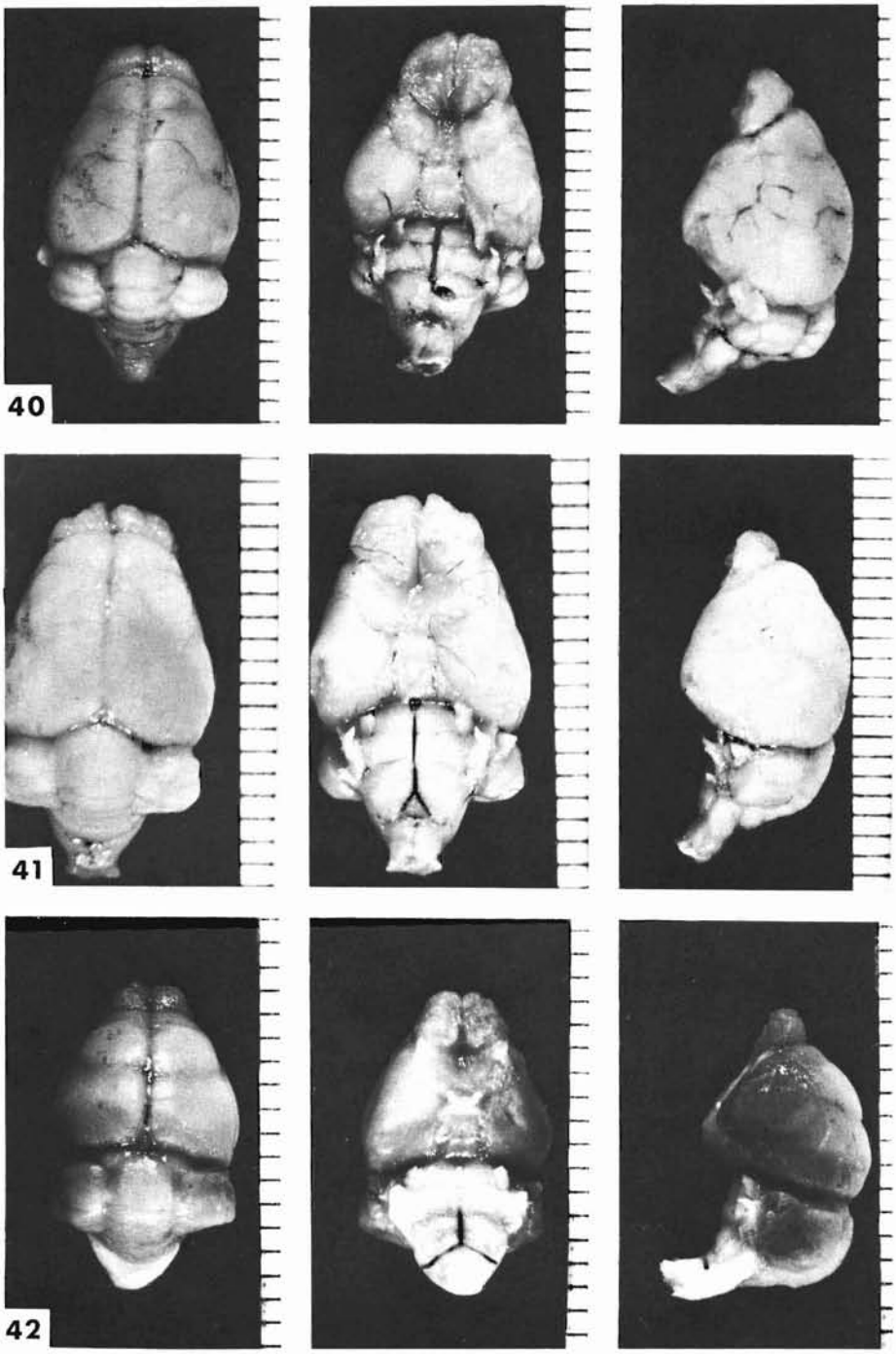
FIGS. 31-33.—Dorsal, ventral, and lateral views of the brains of : 31, *Artibeus toltecus*; 32, *Artibeus watsoni*; and 33, *Artibeus inopinatus*.



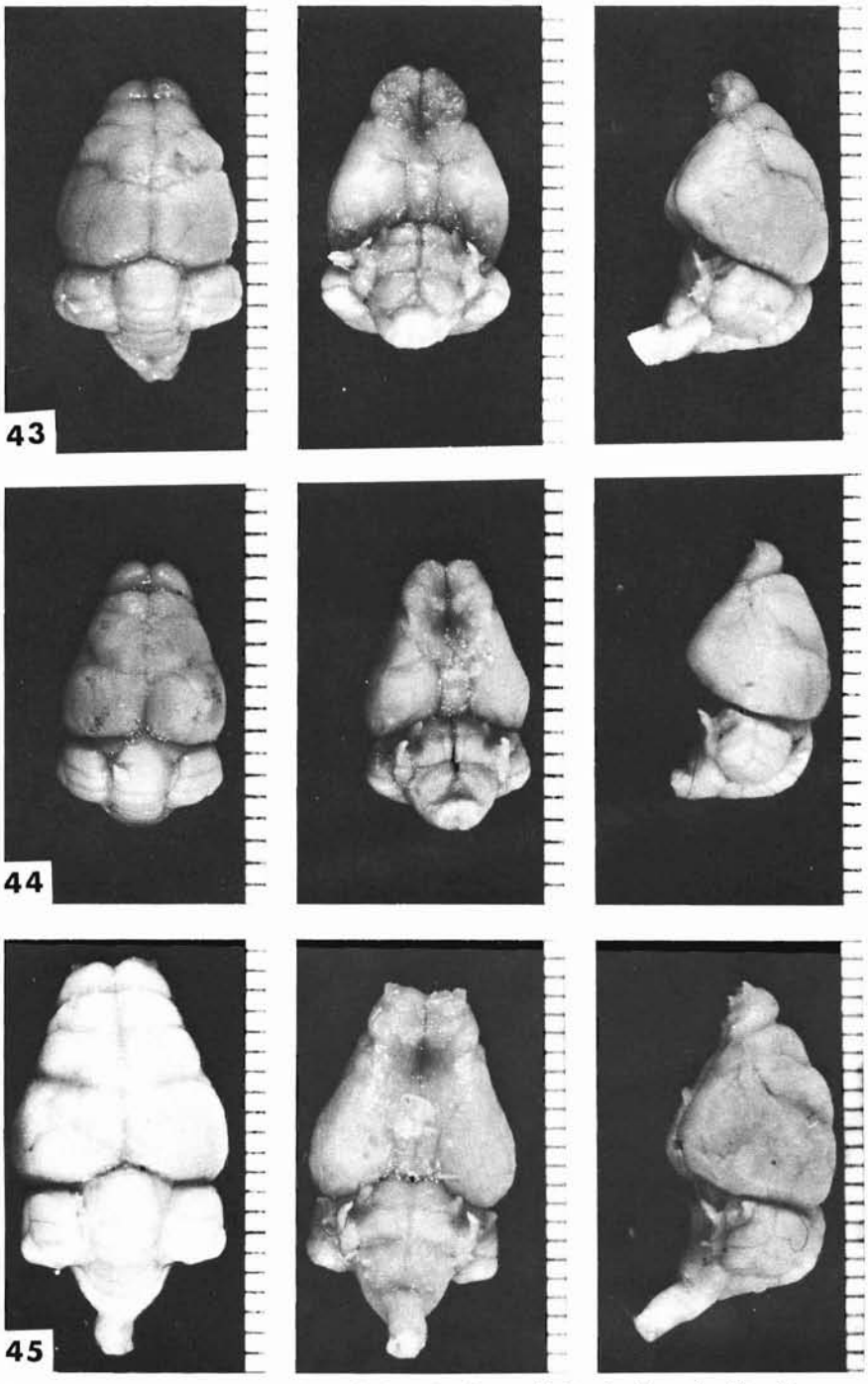
FIGS. 34-36.—Dorsal, ventral, and lateral views of the brains of: 34, *Artibeus jamaicensis*; 35, *Artibeus lituratus*; and 36, *Enchisthenes hartii*.



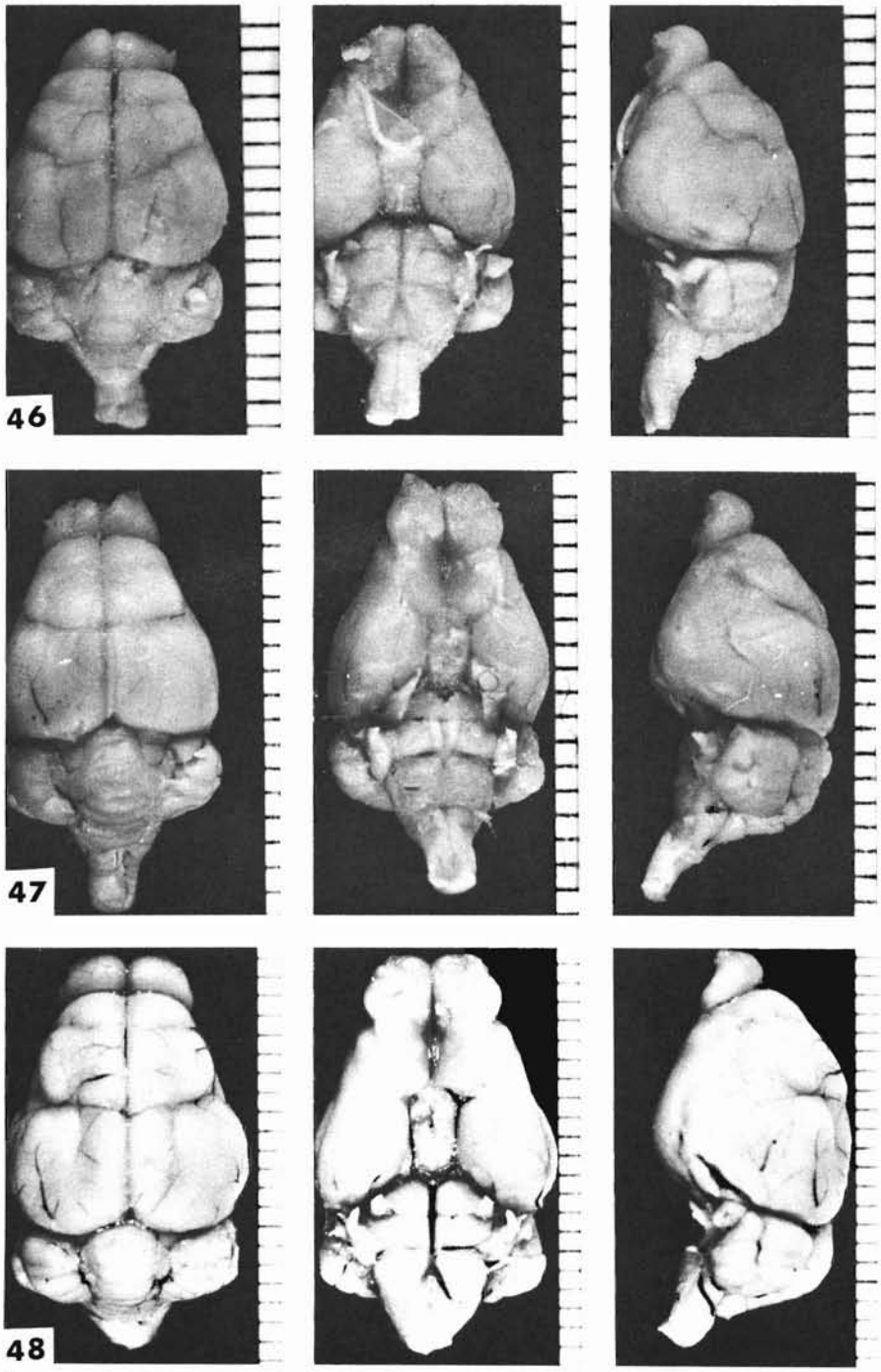
FIGS. 37-39.—Dorsal, ventral, and lateral views of the brains of: 37, *Vampyrodes caraccioloi*; 38, *Uroderma bilobatum*; and 39, *Uroderma magnirostrum*.



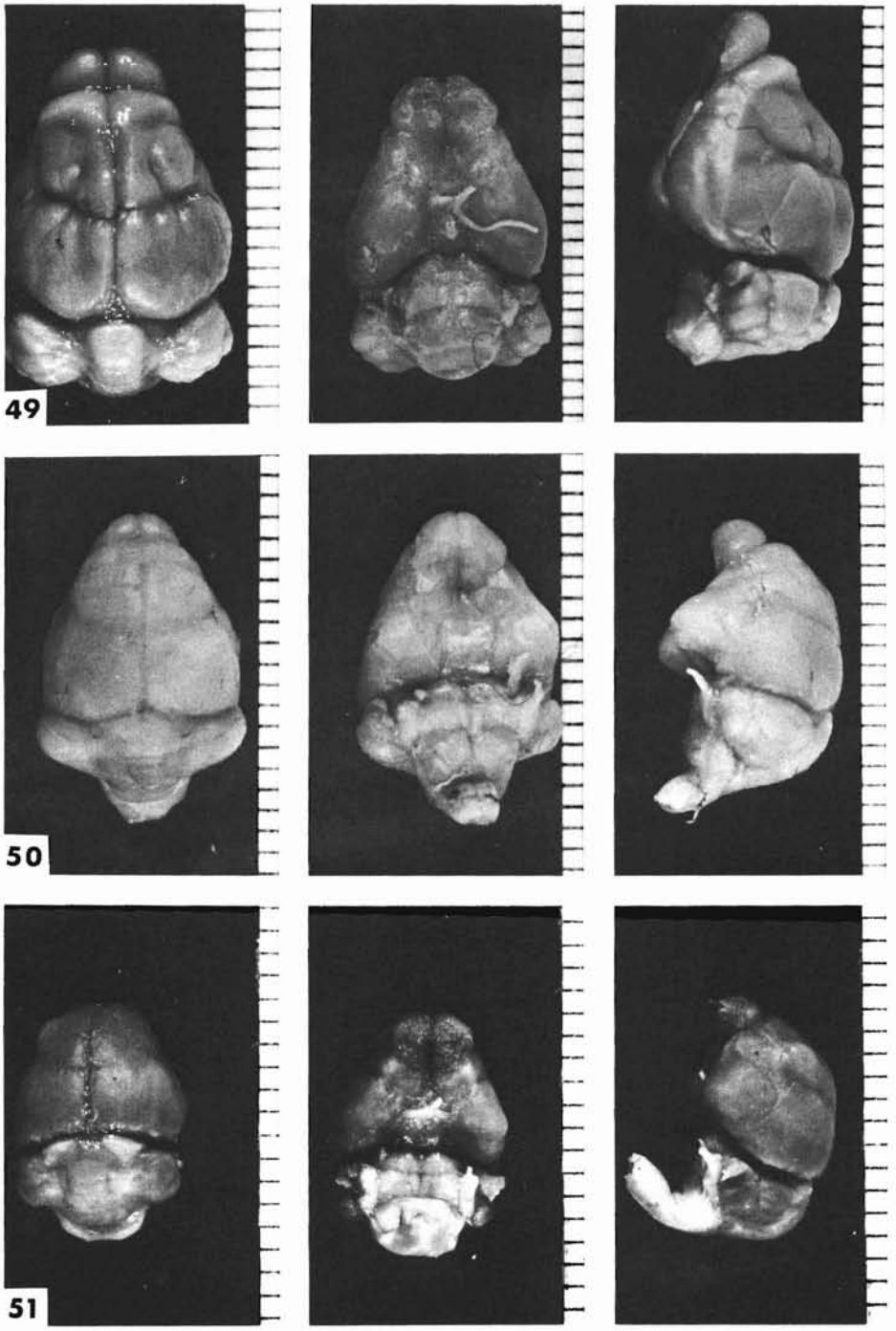
FIGS. 40-42.—Dorsal, ventral, and lateral views of the brains of: 40, *Sturnira mordax*; 41, *Sturnira ludovici*; and 42, *Ectophylla macconnelli*.



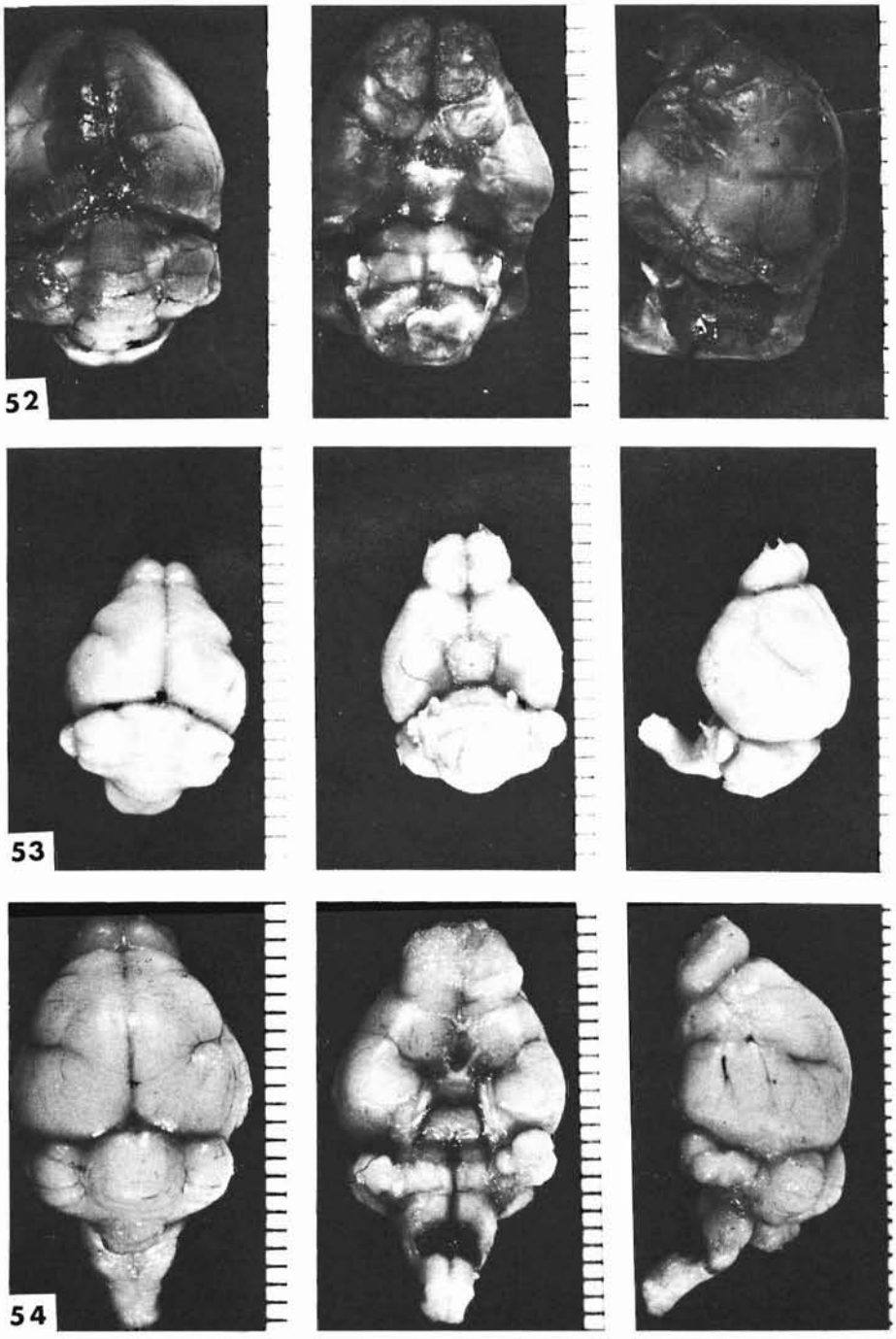
FIGS. 43-45.—Dorsal, ventral, and lateral views of the brains of: 43, *Vampyressa nymphaea*; 44, *Vampyressa pusilla*; and 45, *Chiroderma salvini*.



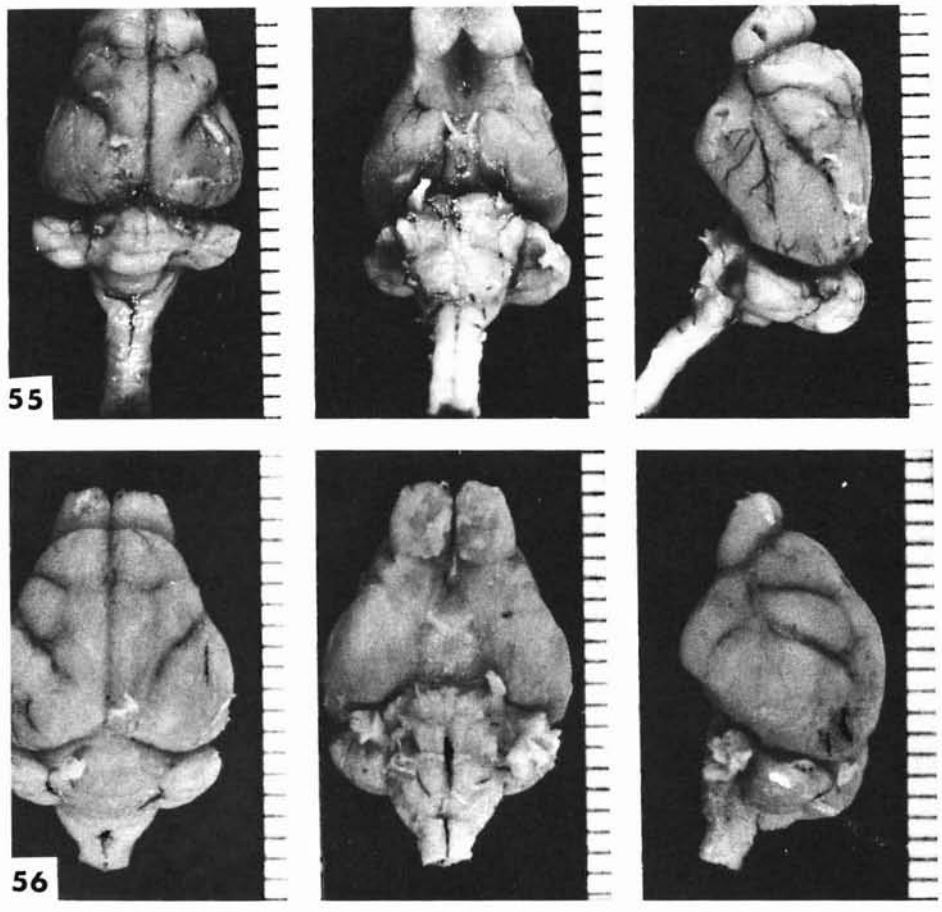
FIGS. 46-48.—Dorsal, ventral, and lateral views of the brains of: 46, *Chiroderma villosum*; 47, *Vampyrops helleri*; and 48, *Vampyrops vittatus*.



FIGS. 49-51.—Dorsal, ventral, and lateral views of the brains of: 49, *Vampyrops infuscus*; 50, *Centurio senex*; and 51, *Ametrida centurio*.

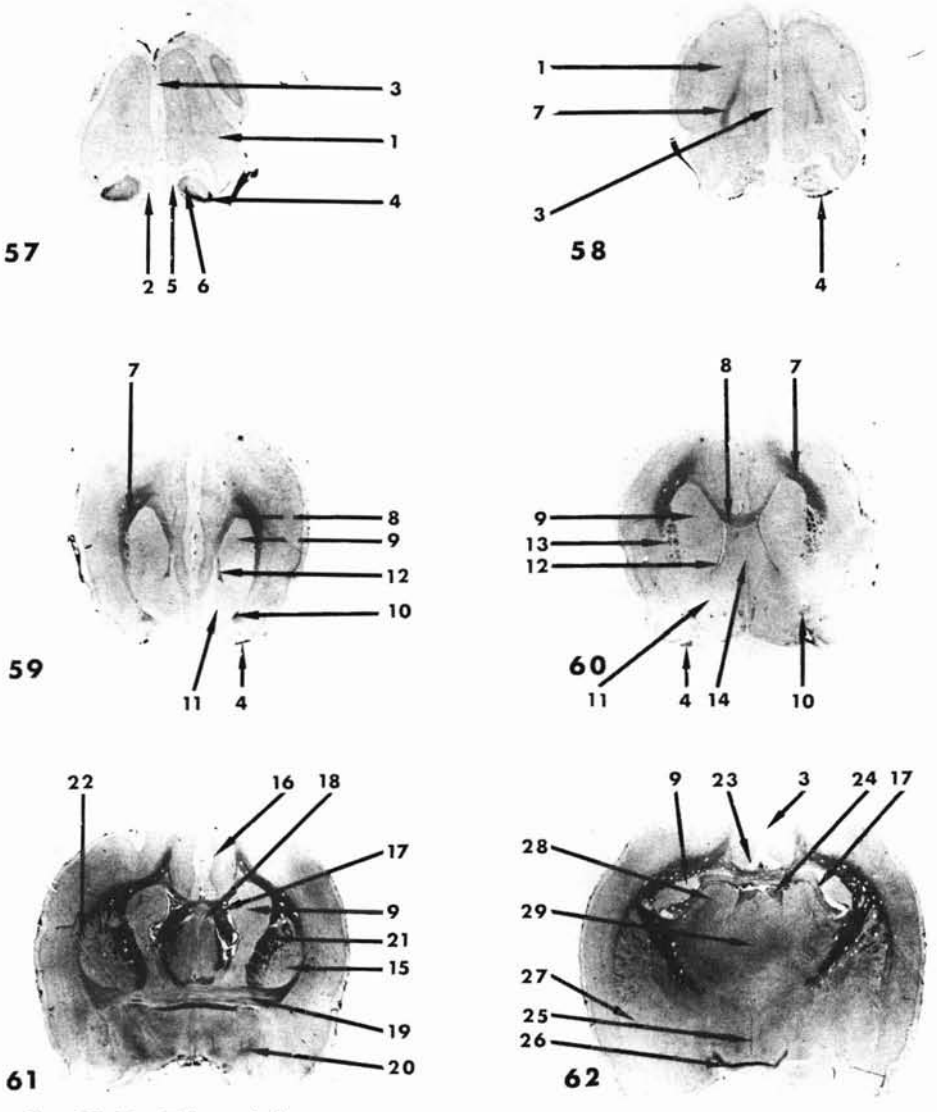


FIGS. 52-54.—Dorsal, ventral, and lateral views of the brains of: 52, *Stenoderma rufum*, 53, *Erophylla bombifrons*; and 54, *Brachyphylla cavernarum*.

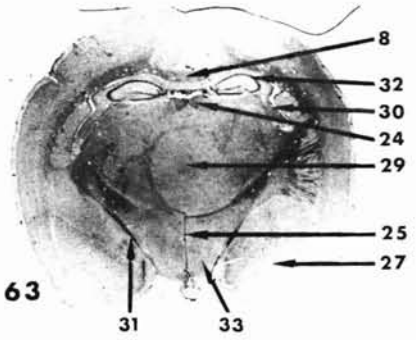


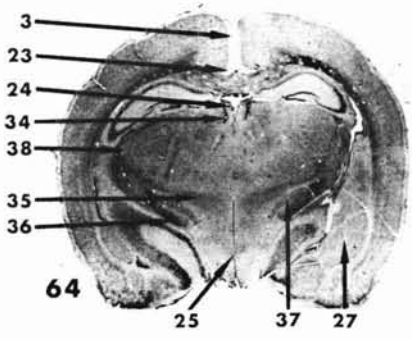
FIGS. 55-56.—Dorsal, ventral, and lateral views of the brains of: 55, *Desmodus rotundus*; and 56, *Diaemus youngii*.

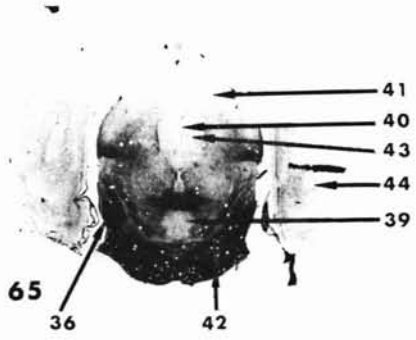
FIGS. 57-74.—Cross-sections through the brain of *Tonatia bidens*. Sections are shown from anterior to posterior end of the brain, and are selected as an aid in identification of features discussed in this study. Labeled structures are: 1, frontal lobe of telencephalon; 2, glomerular stratum of olfactory bulb; 3, interhemispheric sulcus; 4, lateral olfactory tract; 5, plexiform layer of olfactory bulb; 6, internal granular layer of olfactory bulb; 7, substantia alba; 8, corpus callosum; 9, caudate nucleus; 10, intermediate olfactory tract; 11, nucleus accumbens septi; 12, lateral ventricle; 13, fibers of internal capsule; 14, septum; 15, putamen; 16, cingulate sulcus; 17, column of fornix; 18, epithalamus; 19, anterior commissure; 20, medial telencephalic fasiculus; 21, globus pallidus; 22, external capsule; 23, callosal sulcus; 24, habenular nuclei; 25, third ventricle; 26, optic chiasma; 27, amygdaloid nuclei; 28, lateral thalamic nuclei; 29, medial thalamic nuclei; 30, fimbria of hippocampus; 31, optic tract; 32, dentate gyrus; 33, hypothalamus; 34, thalamic stria medullaris; 35, medial lemniscus; 36, crus cerebri; 37, subthalamic nucleus; 38, lateral geniculate body; 39, interpeduncular nucleus; 40, cerebral aqueduct; 41, superior colliculus; 42, pons; 43, central gray matter; 44, telencephalon; 45, inferior colliculus; 46, pyramis; 47, facial colliculus; 48, cerebellum; 49, trapezoid body; 50, dorsal cochlear nucleus; 51, locus ceruleus; 52, lateral superior olivary nucleus; 53, medial superior olivary nucleus; 54, superior cerebellar peduncle; 55, ventral cochlear nucleus; 56, fourth ventricle; 57, medial longitudinal fasiculus; 58, inferior cerebellar peduncle; 59, inferior olivary nucleus; 60, dentate nucleus; 61, reticular formation; 62, raphe; 63, fastigial nucleus; 64, nucleus of the spinal tract of the trigeminal nerve; 65, spinal tract of the trigeminal nerve; 66, fasiculus cuneatus; 67, anterior column; 68, anterior funiculus; 69, posterior column.

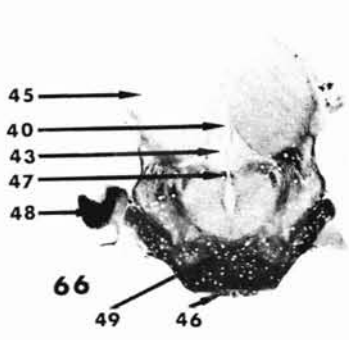


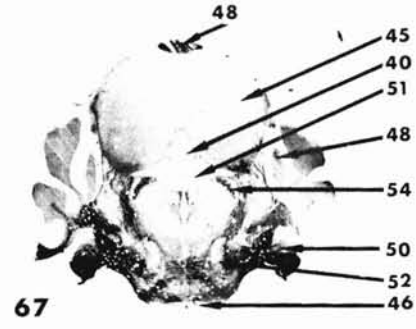
FIGS. 57-61.—Telencephalon.
FIG. 62.—Diencephalon.

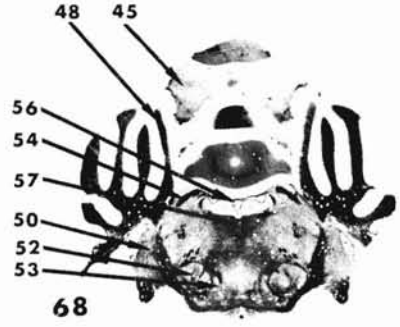




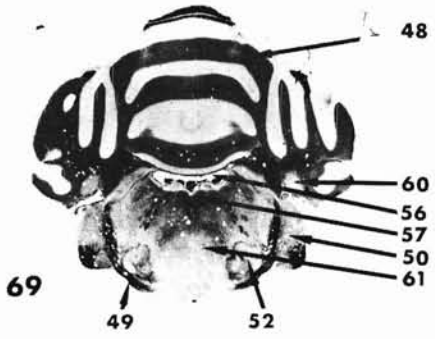


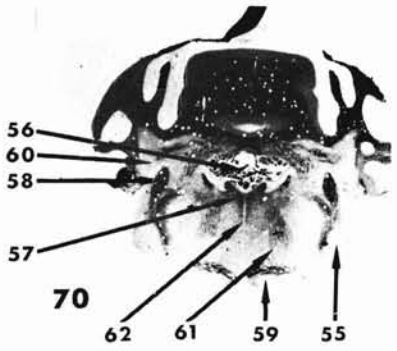


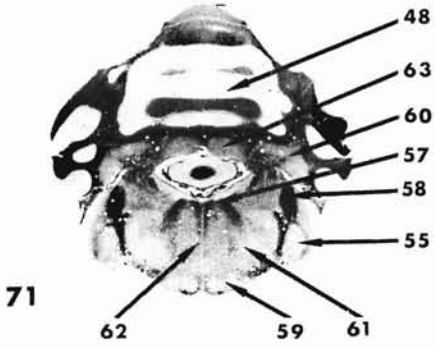


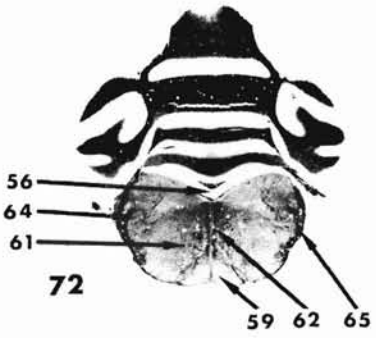


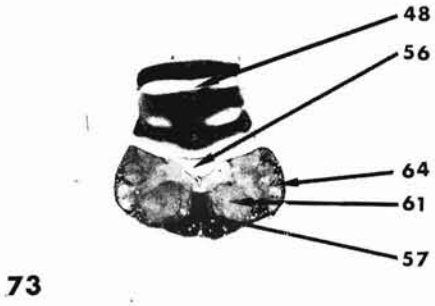
FIGS. 63-64.—Diencephalon.
FIGS. 65-66.—Mesencephalon.
FIG. 67.—Mesencephalon and anterior medulla.
FIG. 68.—Cerebellum and medulla.

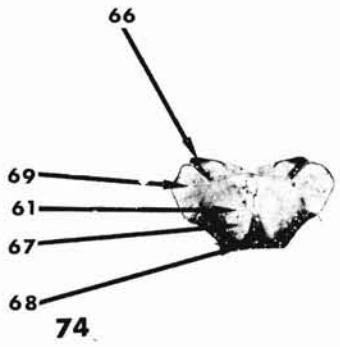




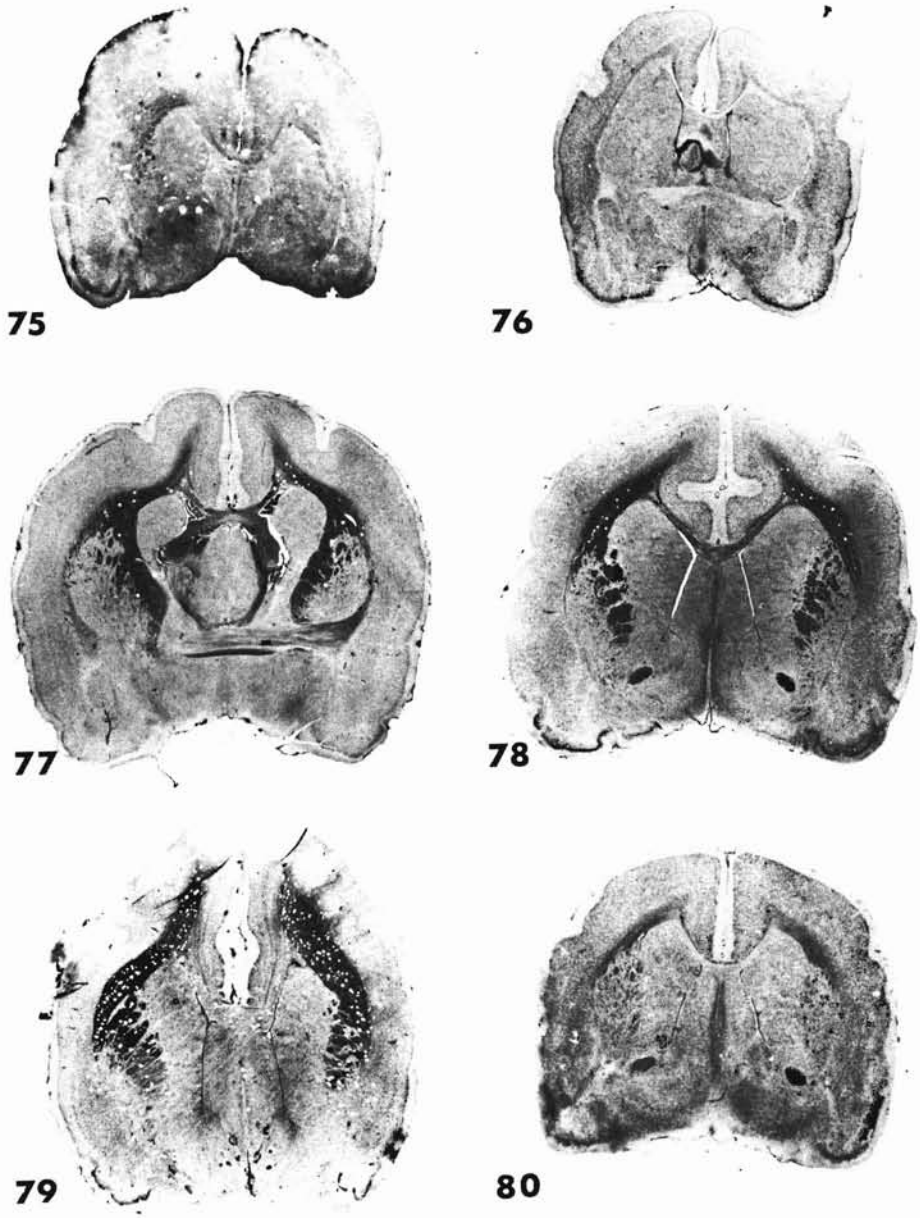




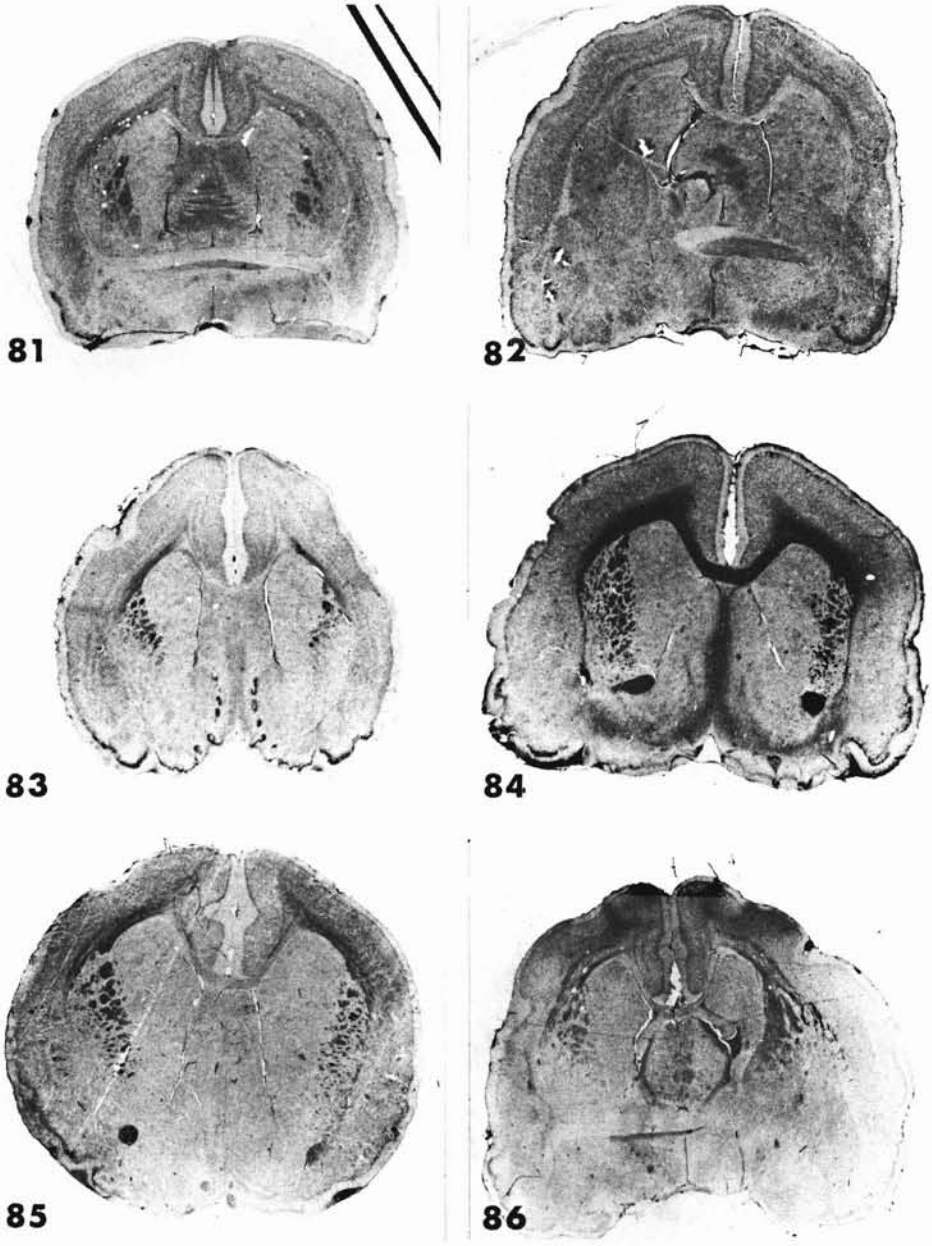




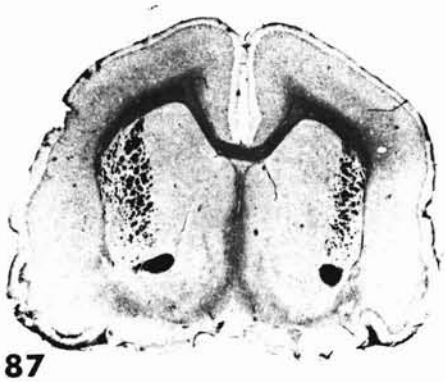
FIGS. 69-73.—Cerebellum and medulla.
FIG. 74.—Posterior medulla.



FIGS. 75-80.—Cross sections through the telencephali of selected species of phyllostomatid bats. Sections are at the level of the corpus callosum and demonstrate variation in the interhemispheric and cingulate sulci. Cingulate sulci in: 75, *Mimon crenulatum*; 76, *Micronycteris megalotis*; 77, *Tonatia bidens*; 78, *Phyllostomus hastatus*; 79, *Vampyrum spectrum*; and 80, *Lichonycteris obscura*.



FIGS. 81-86.—Cingulate sulci in: 81, *Anoura geoffroyi*; 82, *Carollia perspicillata*; 83, *Vampyrops helleri*; 84, *Erophylla bombifrons*; 85, *Brachyphylla cavernarum*; and 86, *Diaemus youngii*.



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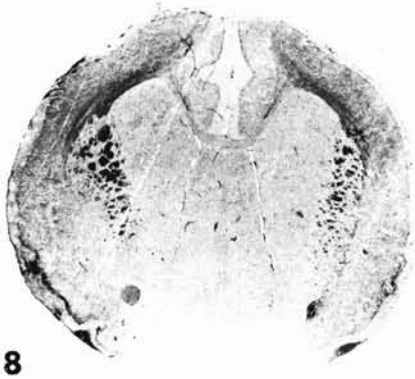

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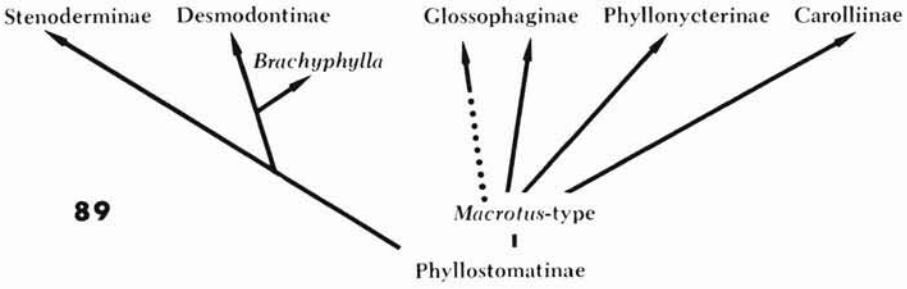

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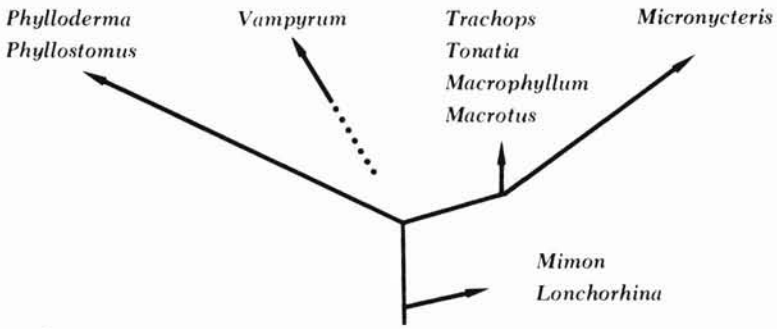

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FIG. 87.—Cross-section of the telencephalon of *Erophylla*. Section is at the level of the corpus callosum and demonstrates the ventral position of the lateral olfactory tracts.

FIG. 88.—Cross-section of the telencephalon of *Brachyphylla*. Section is at the level of the corpus callosum and demonstrates the lateral position of the lateral olfactory tracts.

FIG. 89.—Schematic representation of a possible phylogeny of the family Phyllostomatidae, based on selected features of brain anatomy.

FIG. 90.—Schematic representation of a possible phylogeny of the subfamily Phyllostomatinae, based on selected features of brain anatomy.

LACTATION AND MILK

ROBERT JENNESS, AND EUGENE H. STUDIER

Lactation, one of the most distinctive characteristics of mammals, involves a special cell type that produces a product unique in nature. Milk is a balanced, multicomponent dietary system, which supplies the young mammal with energy, amino acids, minerals, and vitamins. It also supports the growth of symbiotic bacteria and in some species transmits passive immunity. Milk contains an amazing array of constituents. Some are organ and species specific, such as certain proteins and fats; others are organ but not species specific, such as lactose; certain proteins, such as serum albumin and immunoglobulins, are species but not organ specific; and finally such constituents as water, salts, carotenoids, sterols, and vitamins are neither species nor organ specific. Formation of milk involves both biosynthetic processes in the mammary tissue and active and passive transport of constituents from the blood. The quantitative composition of milk varies greatly among species and races of mammals, with the course of lactation and to some extent with the composition of the diet. There are also marked qualitative differences among species in the proteins, lipids, and carbohydrates (other than lactose). Present knowledge of milk composition is virtually overwhelmed by numerous and detailed studies of six domestic species (*Bos taurus*, *Bubalus bubalis*, *Capra hircus*, *Ovis aries*, *Equus caballus*, and *Sus scrofa*) and man, *Homo sapiens*. There are miscellaneous and scattered data on about 200 species and no data at all on nearly 4000 species. Available data have been reviewed (Jenness and Sloan, 1970; Jenness, 1974*a*, 1974*b*).

Obviously, the differences in milk composition among species result from different rates of synthesis of some constituents and different rates of transfer of others across the barriers of the mammary cell from blood to milk. The mechanisms by which these processes are controlled are not well understood, but a number of restrictions are evident. Some of these are: 1) the diet of the animal, which influences the supply of precursors furnished to the mammary cells via the blood; 2) the necessity for maintaining the osmolality of milk close to that of blood; 3) the relative insolubility of salts of calcium and phosphate; and 4) the necessity for milk fat to be liquid at body temperature.

Mammals are born at widely different stages of development, and if it is presumed that their nutritive requirements depend on their physiological maturity, it is easy to reason rather teleologically that the milk of a given species is best adapted to nourish the young of that species. Thus it is tempting to speculate that nutritive requirements of the young have exerted an important selective influence on the evolution of composition of milk. Presently available data, however, do not seem to show a general correlation between milk composition and physiological maturity of young at birth (Jenness, 1974*a*). The nutritional adequacy of milk for the young depends not only on the composition but also on the quantity produced. Available data on milk production and composition in 22 widely

different species indicate a daily milk yield of 0.126 ± 0.0169 kg./kg.$^{0.75}$ body weight and daily energy output of 140 ± 15.7 kcal./kg.$^{0.75}$ body weight (Linzell, 1972).

Because milk production varies as the 0.75 power of body weight, it is obvious that small animals produce more milk per unit weight than do large animals. Linzell (1972) has shown that this is due to the fact that small animals have more mammary tissue per unit weight. The demands of lactation on small mammals are met by huge increases in food consumption (about three-fold in the case of *Rattus norvegicus*—Brody, 1945:433).

In many species, milk yield is probably less than sufficient to support the maximum rate of growth of young (Blaxter, 1961), but it is by no means certain that a maximum growth rate is evolutionarily optimal. Furthermore, the degree of nutritive dependence of young on milk during the nursing period and hence the strength of selective forces operating on milk composition varies markedly among species.

Lactation in Phyllostomatids

Seasonality

The extent of our knowledge of reproductive cycles of phyllostomatids has been thoroughly reviewed in this volume (see Wilson, this volume) as well as in a few recent publications (Fleming *et al.*, 1972; Wilson, 1973). Most Neotropical phyllostomatids exhibit a reproductive cycle described as bimodal polyestry, with *Artibeus jamaicensis*, at least, showing an interesting slight modification of that pattern (Fleming, 1971). A seasonal polyestry is evident in vampires. Finally, although no Neotropical phyllostomatids appear to exhibit seasonal monestry, this pattern obtains in a temperate genus, *Macrotus* (Bradshaw, 1962), and possibly occurs also in some *Leptonycteris*. In view of these patterns and because phyllostomatids routinely give birth to a single young, the reproductive potential of Neotropical phyllostomatids certainly appears to be greater than that of the more temperate representatives.

Duration

The lactation period for a large number of temperate-zone vespertilionids is four to eight weeks (Kleiman, 1969; Kunz, 1971; Bogan, 1972; O'Farrell and Studier, 1973). A similar lactation period is demonstrated by some Neotropical vespertilionids (Wilson and Findley, 1970; Medway, 1972). In the insectivorous temperate phyllostomatid, *Macrotus californicus*, lactation lasts about one month (Bradshaw, 1962), whereas it lasts approximately four to eight weeks in the nectar-feeding *Leptonycteris* (personal observation). In the sanguivorous common vampire, *Desmodus rotundus*, lactation lasts at least three months (Schmidt and Manske, 1973).

One can interpret figures 4 and 5 of Fleming *et al.* (1972) in a manner slightly modified from that described by Kunz (1971) to estimate length of lactation. Kunz estimated the period of lactation to last from the time 50 per cent of ob-

served females began lactation until 50 per cent of observed females were in postlactation stages. Because the reproductive cycles of most Neotropical phyllostomatids are not so well synchronized as those of the temperate vespertilionids, Fleming *et al.* (1972) recorded no instance when all females were lactating. However, the time span from the point when half the maximum percentage of observed bats began lactation until half were in postlactation is two to four months for many Neotropical frugivorous phyllostomatids.

Captive *Carollia* lactate for nearly two months (Bleier *et al.*, this volume). These data suggest that the length of lactation may be more closely related to the normal feeding habits of the species than to their latitude of residence. Bats appear to lactate for a longer period than do rodents of comparable size.

Milk Composition

Gross Composition

Data on the composition of the milk of bats are meager. To our knowledge, milk specimens have been analyzed from only 23 species. These are all New World bats and include seven species of the Phyllostomatidae—*Glossophaga soricina*, *Leptonycteris sanborni*, *Carollia perspicillata*, *Vampyrodes caracccioloi*, *Artibeus jamaicensis*, *A. cinereus*, and *Diphylla ecaudata*. Huibregtse (1966) and Stull *et al.* (1966) compared some aspects of the composition of milk of *Leptonycteris sanborni* with that of *Tadarida brasiliensis*; all other data are in publications of Jenness and Sloan (1970), Glass and Jenness (1971).

It is not especially difficult to secure milk from bats in full lactation. Individuals of many species are so small, however, that specimens from several females must be pooled to have an amount sufficient for analysis. Data thus far available allow no more than a general summary of the composition and properties of chiropteran milk. The gross analyses are not of high precision because of necessity of dealing with small samples.

Table 1 presents data for the composition of milks of phyllostomatids and of some other species for comparative purposes. Except for the milk of *Glossophaga*, phyllostomatid milks are high in fat content. Nectar and fruit-eating species produce milk with higher carbohydrate (calculated as lactose) and lower protein contents than do insectivorous bats. Like milks of all other mammals that have been examined, bat milk contains both casein (acid precipitable) and whey (acid soluble) proteins although the proportion of the two classes varies considerably among species. In a number of mammalian milks, caseins have been shown to be present in the form of particles or micelles, which bind considerable calcium and phosphate and thus enhance the ability of milk to carry these important minerals to the young. Presumably they are present in this form in bat milk as well.

Bat milk contains concentrations of citrate comparable to those in the milk of domestic cows and many other species. Citrate also enhances the calcium carrying capacity of milk by forming soluble complexes with it. A few genera, notably *Rattus* and *Mus*, degrade citrate in the mammary cells and channel the

TABLE 1.—*Composition of milks of phyllostomatids and some other species*[1].

Species	Specimens	Females per specimen	Fat g./100g.	Lactose g./100g.	Casein g./100g.	Whey protein g./100g.	Citrate g./100g.	Energy[2] kcal./g.
Glossophaga soricina	2	5, 7	5.2	3.9	1.1	0.75	0.08	0.74
Leptonycteris sanborni[3]	2	6, 7	18.5	4.8	2.5	1.8	0.15	2.1
Carollia perspicillata	1	2		4.1	*ca.* 7		0.16	
Vampyrodes caraccioloi	2	1, 1	29.0	4.1	0.83	2.3	0.09	3.0
Artibeus jamaicensis	2	1, 1	18.6	7.3	1.1	3.6	0.11	2.3
Artibeus cinereus	1	4	23.0	3.8	0.57	3.4	0.06	2.5
Myotis lucifugus	2	4, 5	6.0	3.1	3.8	3.5	0.19	1.1
Tadarida brasiliensis[4]	2	5, 5	16.3	2.8	3.0	3.2	0.21	2.0
Mus musculus	5	1	13.1	3.0	7.0	2.0	0.005	1.9
Homo sapiens	compilation		3.8	7.0	0.4	0.6	0.05	0.68
Bos taurus	compilation		3.7	4.8	2.8	0.6	0.17	0.73

[1]Data from Jenness and Sloan (1970) and unpublished data.

[2]Calculated using factors as follows: lactose = 3.95 kcal./g., protein = 5.86 kcal./g., and fat = 9.20 kcal./g.

[3]Huibregtse (1966) reported 5.39 per cent carbohydrate, 4.37 per cent protein, and 0.63 per cent ash for milk of this species.

[4]Huibregtse (1966) reported 3.70 per cent carbohydrate 11.07 per cent protein, and 0.73 per cent ash for milk of this species.

products to the synthesis of fatty acids; evidently the bats examined do not employ this pathway.

Not much is known about mineral constituents in bat milk. Huibregtse (1966) reported 0.63 and 0.73 per cent ash in milks of *Leptonycteris sanborni* and *Tadarida brasiliensis*, respectively. R. Jenness, R. L. Glass, and E. H. Studier (unpublished data) found milk of *Glossophaga soricina* to have 0.09 per cent Ca and 0.08 per cent P, whereas that of *L. sanborni* had three times as much—0.27 per cent Ca and 0.24 per cent P.

Table 1 shows that the milks of phyllostomatids, except for *Glossophaga*, are of high calculated energy content. The value for *Glossophaga*, due to low fat and protein contents, should be checked by additional sampling and analyses. For milks in general, Jenness (1974*a*) pointed out that the protein and carbohydrates supply 0.30 to 0.65 kcal./g., while additional energy, up to totals as high as 5.0 kcal./g. in some species, is supplied by fat. Bat milks fall into this pattern.

The high energy content of bat milks are in accordance with the suggestion of Ben Shaul (1962) that mammals that nurse their young on a scheduled basis produce milk of higher energy content than do those that nurse continuously or on demand. They also agree with Blaxter's (1961) proposal that small mammals produce milks of higher energy content than do large species because the stomach capacity of the young is proportional to body weight and the metabolic requirements are more nearly proportional to body surface (actually proportional to $W^{0.75}$ according to Kleiber, 1961).

Howell (1972) found that the nectarivorous phyllostomatid *Leptonycteris* can maintain nitrogen balance through ingestion of nectar and pollen. The observation that milk of *Leptonycteris* contains protein levels comparable to those of other bats (Table 1) further indicates that this species readily maintains nitro-

TABLE 2.—*Fatty acid composition of milk fats*[1] *(per cent by weight).*

Species	*12:0*[2]	*14:0*	*16:0*	*16:1*	*18:0*	*18:1*	*18:2*	*18:3*	*Other*
Glossophaga soricina	0.2	12.0	37.4	10.7	2.2	35.1	2.1		1.2
Leptonycteris sanborni	2.0	25.6	31.2	11.4	2.1	24.9	0.6	1.8	2.3
Carollia perspicillata		9.4	32.6	7.6	2.5	44.0	3.5		0.4
Vampyrodes caraccioloi		6.0	30.2	2.9	5.4	33.0	6.3	15.9	
Artibeus jamaicensis		5.6	34.6	6.6	5.4	44.2	3.4	2.5	2.4
Artibeus cinereus		7.5	38.0	6.5	5.2	41.0	0.4		2.0
Diphylla ecaudata		4.0	37.2	6.6	4.9	43.1	4.2		
Myotis lucifugus		1.8	22.3	7.0	4.6	37.8	16.5	5.6	4.8
Tadarida brasiliensis		0.5	31.7	7.1	2.6	48.2	6.0	3.9	
Mus musculus	8.1	11.9	23.2	3.9	2.9	25.7	16.3	2.0	6.0
Homo sapiens	3.1	5.1	20.2	5.7	2.9	46.4	13.0	1.4	1.3
Bos taurus	3.1	9.5	26.3	2.3	14.6	29.8	2.4	0.8	9.7[3]

[1]Data from Jenness (1974*a*) and unpublished data from R. Jenness, R. L. Glass, and E. H. Studier.

[2]Fatty acids are designated by carbon number and number of double bonds; thus, 12:0 refers to a chain of 12 carbons with no double bonds.

[3]3.3 per cent 4:0, 1.6 per cent 6:0, 1.3 per cent 8:0, 3.0 per cent 10:0.

gen balance on its natural diet and that suckling young are not nutritionally stressed by low levels of protein in the ingested milk.

Milk Fat

Bat milk is characterized by prominent amounts of palmitic (16:0) and oleic (18:1) fatty acids (Table 2). Note that fatty acids are designated by carbon number and number of double bonds; thus, 16:0 refers to a chain of 16 carbons with no double bonds. Myristic acid (14:0) is also much more prominent in the phyllostomatids, particularly *Leptonycteris*, than in the insectivorous *Myotis lucifugus* and *Tadarida brasiliensis*. Stull *et al.* (1966) also reported a high concentration (21 per cent) of myristic acid in the milk fat of *Leptonycteris sanborni*. The milk fat of *Vampyrodes caraccioloi* differs markedly from that of the other phyllostomatids in its low concentration of palmitoleic acid (16:1) and high concentrations of 18:2 and 18:3 acids. The bat milk fats analyzed to date contained only small amounts of short chain (less than 14 carbons) fatty acids. Such acids generally are prominent in ruminants and some rodents and primates. They are synthesized by the mammary cells and their absence from bat milk implies that bats derive their milk fatty acids largely from food fat rather than by biosynthesis in the mammary gland.

Carbohydrates

The carbohydrate contents reported in Table 1 were determined by a nonspecific method and are calculated and expressed as lactose. However, paper chromatography of the soluble carbohydrates of bat milks reveals that lactose actually is the predominant constituent (Fig. 1). Although not shown in Fig. 1, the dialyzable carbohydrate fraction of the milks of the other phyllostomatids tested (*Carollia perspicillata*, *Vampyrodes caraccioloi*, *Artibeus cinereus*, and *Diphylla*

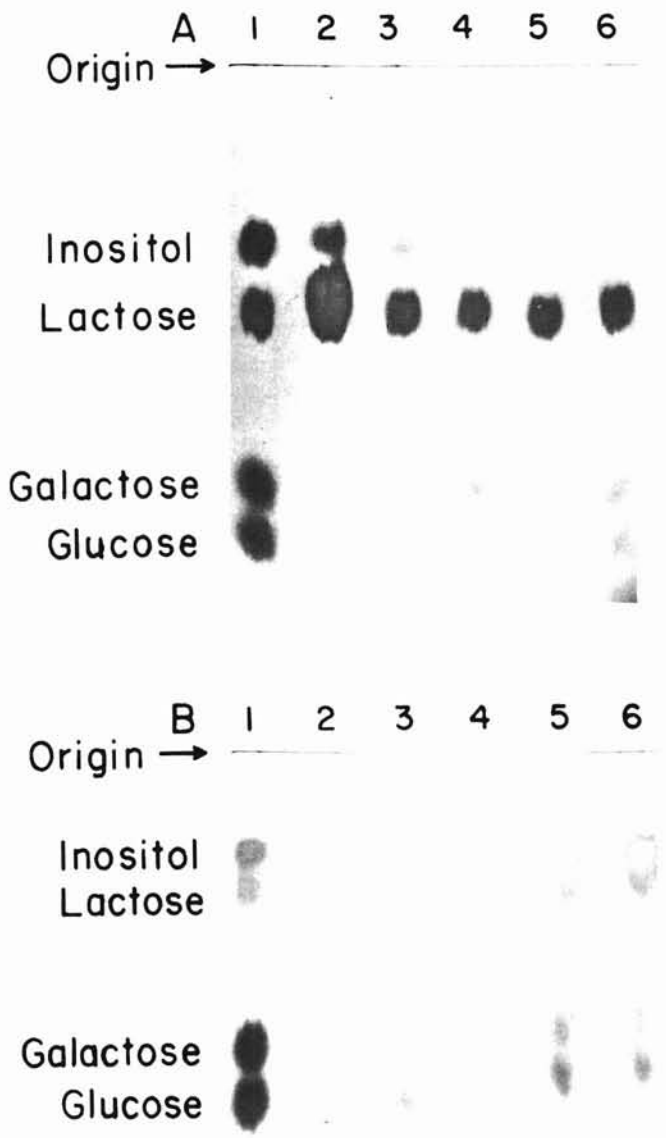

FIG. 1.—Paper chromatograms of sugars of bat milks (run on Whatman no. 1 filter paper for 16 to 20 hours with ethyl acetate, pyridine, water 10:4:3). A: 1, standard (glucose, galactose, lactose, *myo*-inositol); 2, *Glossophaga soricina*; 3, *Myotis lucifugus*; 4, *Tadarida brasiliensis*; 5, *Myotis yumanensis*; 6, *Leptonycteris sanborni*. B: 1, standard; 2, *Balantiopteryx plicata*; 3, *Molossus ater*; 4, *Myotis nigricans*; 5, *Artibeus jamaicensis*; 6, *Artibeus jamaicensis*.

ecaudata) also have been found to contain a prominent component identified as lactose. Significant concentrations of glucose and galactose sometimes occur (as shown in Fig. 1 for *Artibeus jamaicensis*). These vary from specimen to speci-

men, however, and may in part represent hydrolysis of lactose occurring after the specimen was drawn.

Milks of many species of rodents and carnivores and some insectivorous bats contain considerable concentrations of components migrating more slowly than lactose in paper chromatography. In some species, at least, this has been shown to be *myo*-inositol (Byun, 1973). Such constituents are not usually prominent in milks of phyllostomatids, although one specimen of *Glossophaga soricina* milk exhibited it (Fig. 1).

Milk Proteins

As pointed out previously (Table 1), both caseins and whey proteins are present in bat milk. The caseins of all species of mammals thus far examined consist of a number of distinct kinds of polypeptide chains, which are separable by electrophoresis (Jenness, 1974*a*). The only information on bat caseins is the report by Huibregtse (1966) that caseins of *Tadarida brasiliensis* and *Leptonycteris sanborni* are resolved, although not distinctly, into a number of fractions on electrophoresis on paper.

The noncasein or whey proteins of bat milk are readily resolvable into a number of distinct entities upon electrophoresis in polyacrylamide gel (Fig. 2). Comparison of the patterns for whey proteins with those of blood serum of the same species shows that the milk always contains a protein component having the same mobility as blood serum albumin. Some species of bats (notably molossids) have many whey protein components moving considerably faster than blood serum albumin, but only two such cases have been noted in the phyllostomatids yet examined (in *Glossophaga soricina* and *Artibeus jamaicensis*). Several whey protein components of slower mobility than blood serum albumin are present; their number and mobilities differ a geat deal among species. The data currently available do not permit conclusions as to intraspecific variability or interspecific homology of these proteins. They merely suggest that the milk proteins of bats exhibit considerable evolutionary divergence. It would be interesting to identify the component designated "α-lactalbumin," which is specifically involved in the biosynthesis of lactose and appears to be present in all milks containing lactose (Jenness, 1974*a*).

Bioenergetics of Lactation and Growth

It is convenient and instructive to integrate the processes of lactation and growth by considering the transfer of energy involved. It must be remembered, however, that integration on an energetic basis neglects the important role of biosynthesis of proteins and the transfer of proteins and minerals for which nutritive value does not depend on their energy contents.

Methods

Several methods have been used to estimate energetic costs of pregnancy and lactation in wild mammals. These are most often based on the tenet that total in-

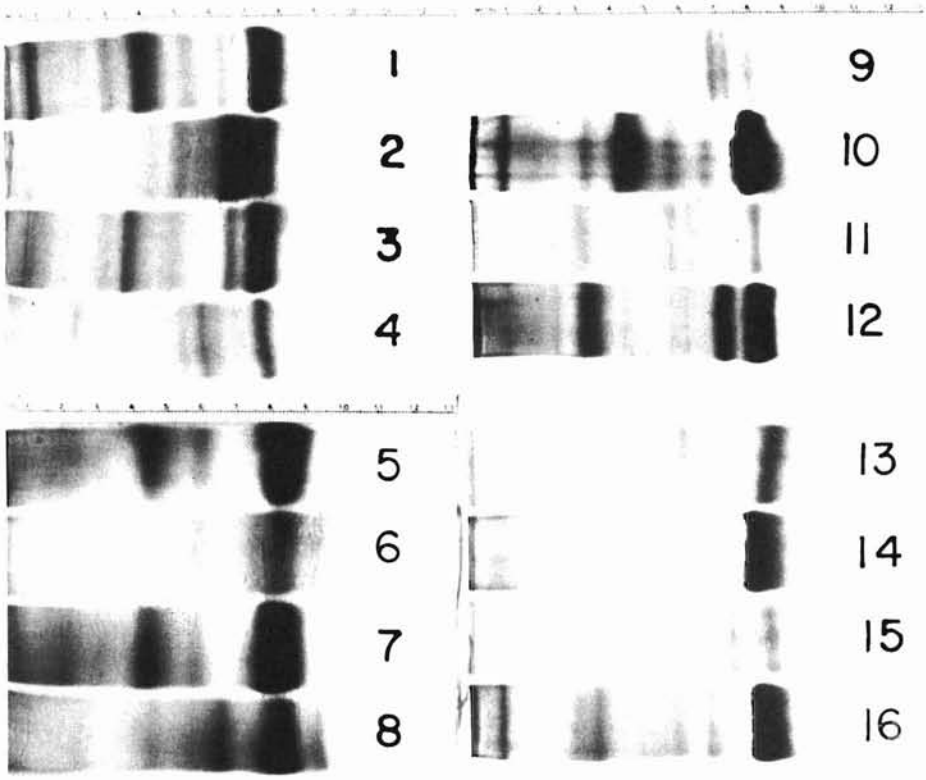

FIG. 2.—Acrylamide gel electrophoretic patterns of whey proteins and blood serums (5 per cent acrylamide, veronal buffer pH 8.6, ionic strength = 0.02): *Vampyrodes caraccioloi* (1 serum, 2 W.P.); *Vampyrodes caraccioloi* (10 serum, 9 W.P.); *Artibeus cinereus* (3 serum, 4 W.P.); *Artibeus jamaicensis* (5 serum, 6 W.P.); *Artibeus jamaicensis* (7 serum, 8 W.P.); *Carollia perspicillata* (12 serum, 11 W.P.); *Glossophaga soricina* (14 serum, 13 W.P.); *Myotis lucifugus* (16 serum, 15 W.P.).

gested energy is partitioned by the organism for growth and maintenance, or is lost in urine or feces. This relationship can be expressed as:

$$I = M + G + E,$$

where I is total ingested energy/time, M is energy used in maintenance/time, G is energy stored as mass increase/time, and E is energy egested or wasted/time. Many studies on small (less than 30 grams) rodents and insectivores (Barrett, 1969; Gebczynski *et al.*, 1972) and bats (Brisbin, 1966; Neuhauser and Brisbin, 1969; O'Farrell *et al.*, 1971; Pagels and Blem, 1973) uniformly yield an assimilation efficiency—$100\ (I - E)/I$—approximating 90 per cent. Although we have found no specific information on phyllostomatids, it seems safe to assume that, on a natural diet, at least the smaller leaf-nosed bats would use about 90 per cent of ingested energy for maintenance and growth and would waste about 10 per cent (in males and anaestrus females). Several studies utilizing a wide variety of organisms indicate that the portion of assimilated energy used for

growth or increase in biomass is dependent upon endogenous thermoregulatory performance of the species. Ectotherms channel a maximum of about 15 per cent of ingested energy to growth (Odum and Odum, 1955; Slobodkin, 1959; Wiegert, 1964, 1965), whereas for endotherms the percentage is much lower (Golley, 1960; Odum, *et al.*, 1962). Overall partitioning of ingested energy for phyllostomatids should be roughly 10 per cent egested or wasted, 75 to 89 per cent used in maintenance, and one to 15 per cent contributing to growth. Such partitioning will vary with some predictibility for individuals depending on age and reproductive condition.

One obvious complication of the equation above occurs during lactation, in which case the equation must be modified to include milk production, that is,

$$I_m = M_m + G_m + E_m + \text{milk energy}$$

where subscript m is used to designate maternal values. Furthermore, a second equation is generated for the nursing young:

$$\text{milk energy} = I_n = M_n + G_n + E_n$$

where subscript n refers to neonatal values.

We shall discuss three of the several methods employed for estimating one or more of the variables in the first equation above.

Assimilated Energy Method

Several investigators have determined total ingested energy (I) or assimilated energy ($I - E$) for rodents during anaestrus periods, pregnancy, and lactation (Kaczmarski, 1966; Migula, 1969). The increase of total energy ingested or assimilated relative to anaestrus levels provides an estimate of energy costs of pregnancy and lactation. This method has the following limitations:

1) It cannot differentiate the assimilated energy into growth or maintenance categories during pregnancy or into growth, maintenance, and milk production categories during lactation.

2) It assumes that maintenance, growth, and waste energy for the female alone are constant throughout anaestrus, pregnancy, and lactation—a situation known to be untrue for small rodents (Trojan and Wojciechowska, 1967).

3) It is valid only for those species that remain homeothermic throughout pregnancy and lactation, and, further, that maintain the same level of regulated body temperature and thermal conductance throughout the reproductive cycle.

4) It is useful only for those animals that can be maintained in captivity and will reproduce there.

5) It assumes that rates of embryonic and neonatal growth in captivity are similar to those under field conditions and that the investigators can provide a reasonably natural diet yielding a relatively normal assimilation efficiency.

Feeding habits of phyllostomatids are extremely diverse inasmuch as the family includes insectivorous, frugivorous, nectarivorous, sanguivorous, carnivorous, and omnivorous representatives (McNab, 1969, 1971; Fleming *et al.*, 1972). Several species of leaf-nosed bats have been maintained in captivity for extended periods, and some of them reproduce successfully in captivity (Wimsatt and

Guerriere, 1961; McNab and Morrison, 1963; Novick, 1963; Rasweiler and de Bonilla, 1972; Rasweiler and Ishiyana, 1973). Surprisingly, the amount of food consumed is detailed for only one species (Wimsatt and Guerriere, 1962). This study dealt with a sample of vampires with sexes pooled and in various reproductive conditions. It is thus a rather marginal use of the assimilated energy method.

Metabolic Rate Method

A second technique used in estimating energetic parameters involves the determination of average daily metabolic rate (ADMR) (Hansson and Grodzinski, 1970; Drozdz *et al.*, 1972; Gebczynski *et al.*, 1972). This method is useful in estimating energy costs of pregnancy and lactation through the determination of ADMR of females throughout the stages of the reproductive cycle (Trojan and Wojciechowska, 1967). It provides an assessment of the maintenance costs of the female but it ignores energy of growth and energy wasted and is, of course, complicated during the period of lactation by maintenance energy required by the offspring. This method has the same limitations involving thermoregulation of females and captivity as the preceding method. When both methods are combined, however, values for I, M, and E are generated for captive animals and thus energy devoted to growth can be calculated.

In principle, the ADMR of free living animals can be measured by the double labeled water (D_2 $^{18}0$) method (see Gessaman, 1973; Mullen, 1973). This method requires that the animal be captured, injected with D_2 $^{18}0$, released, and then recaptured after an interval for determination of blood levels of the isotopes in water and carbon dioxide. It is expensive and has not yet been applied to bats or to any lactating mammal. It has been used to show that the metabolic rate is considerably greater in free-living rodents than in those in captivity (Mullen, 1970, 1971).

Actually no ADMR method has been used to estimate the bioenergetic costs of pregnancy and lactation in phyllostomatids. Several studies have dealt with the relationship of metabolic rates to ambient temperature (Carpenter and Graham, 1967; Lyman and Wimsatt, 1966; McNab, 1969) as well as energetics of flying bats (Thomas and Suthers, 1972). Morrison and McNab (1967) reported diel cycling of metabolic rates in a few caged phyllostomatids. There are, however, no other literature references concerned with measured daily metabolic rates. This is, of course, understandable in view of the natural volant locomotion of bats.

The use of either the assimilated energy method or the ADMR method is complicated by variability in ability to regulate temperature. Thus, temperate and Neotropical leaf-nosed bats have been reported to be homeothermic after a period of laboratory acclimation (Carpenter and Graham, 1967; Arata and Jones, 1967; McNab, 1969), occasionally to exhibit thermolability (Morrison and McNab, 1967; LaVal, 1969), and to be variably thermolabile immediately after capture (Studier and Wilson, 1970). Similar variations have been reported in pteropodids (Bartholomew *et al.*, 1964, 1970; Kulzer, 1963*a*, 1963*b*; Jones, 1972). Two ves-

pertilionids (*Myotis thysanodes* and *M. lucifugus*) exhibited marked cycling of tendency to regulate temperature during different stages of the reproductive cycle (Studier and O'Farrell, 1972).

Energy Accretion Method

The third procedure that may be useful in estimating energy costs of pregnancy and lactation involves the determination of the rate of energy incorporation by the developing foetus or neonate (Studier *et al.*, 1973), and is, therefore, a measure of only the minimal amount of energy required for embryonic or neonatal growth. This procedure ignores energy costs of maintenance and waste and requires embryos or neonates of known age. It has the advantages, however, of being unaffected by thermoregulatory performances of females or neonates and does not require that animals be kept in captivity.

This method for estimating energetics during reproduction has been applied to two vespertilionid species (Studier *et al.*, 1973) and could be applied to phyllostomatids because it is independent of thermoregulatory performance of either adult females or suckling young. It requires adequate data on pre and postnatal growth patterns. Such information has only recently become available (Schmidt and Manske, 1973; Bleier *et al.*, this volume).

Energy Requirements of Desmodus rotundus

Unfortunately, it must be concluded from the discussion in the preceding section that some methods for estimating energy requirements for reproduction are of questionable applicability to phyllostomatids and satisfactory experiments remain to be performed. The construction of energy budgets for pregnancy and lactation is tenuous at present because of lack of satisfactory data; however, some insight may be gained through such an attempt. The best available and useable literature relates to common vampires; thus, an attempt will be made to estimate roughly energy costs of lactation in this species. Results of the calculations are given in Table 3. Vampires, like most phyllostomatid bats, regularly deliver only one young per pregnancy, which simplifies estimates of energy costs of lactation because growth rates of young are influenced by the number of litter mates (Miller and Parsonage, 1971).

Neonates

The growth rate of vampires from day 5 (7.0 grams) to day 20 (12.0 grams) after birth is approximately 0.33 grams per day (calculated from Schmidt and Manske, 1973). For older animals, growth rates calculated from the same source are 0.17 grams per day (days 20 to 50), 0.1 grams per day (days 50 to 100) and 0.035 grams per day (days 100 to 200). The initial growth rate for vampires (days 5 to 20) is identical to that of *Myotis thysanodes* (O'Farrell and Studier, 1973). If the energy content is constant on a dry weight base throughout the nursing period as it is in laboratory mice (Brisbin, 1970) and *Myotis thysanodes* (Studier *et al.*, 1973), and the percentage of body water in developing vampires

TABLE 3.—*Approximated bioenergetic parameters of neonatal and lactating vampires* (Desmodus rotundus). *See text for further explanation.*

	$T_a = 32°C$					$T_a = 22°C$				
	Age of neonates (days)									
	5	20	50	100	200	5	20	50	100	200
	Weight of neonates (grams)									
Samples	7.0	12.0	17.0	22.0	25.5	7.0	12.0	17.0	22.0	25.5
	Neonates									
	G_n (kcal.)									
	0.35	0.35	0.19	0.11	0.04	0.35	0.35	0.19	0.11	0.04
	M_n (kcal.)									
a	0.3	0.5	0.5	0.6	0.7	0.3	0.4	0.5	0.5	0.6
b	1.7	2.5	3.3	4.0	4.4	5.1	6.3	6.6	8.0	8.9
c	3.4	5.1	6.6	8.0	8.9	10.1	12.7	13.1	16.0	17.8
	E_n (kcal.)									
a	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
b	0.2	0.3	0.4	0.5	0.5	0.6	0.7	0.8	0.9	1.0
c	0.4	0.6	0.8	0.9	1.1	1.2	1.4	1.5	1.8	2.0
	Milk energy (kcal.)									
a	0.7	0.9	0.8	0.8	0.8	0.7	0.8	0.8	0.7	0.7
b	2.3	3.2	3.9	4.6	5.0	6.0	7.4	7.5	9.0	9.9
c	4.1	6.0	7.5	9.0	9.9	11.7	14.4	14.8	17.9	19.8
	Utilization efficiency (per cent)									
a	47.9	37.6	23.2	13.8	5.0	50.7	40.2	25.3	15.1	5.6
b	15.5	10.9	4.9	2.4	0.8	5.8	4.7	2.5	1.2	0.4
c	8.5	5.8	2.5	1.2	0.4	3.0	2.4	1.3	0.6	0.2
	Lactating Females									
	Basic requirements (grams of blood)									
	17.8	17.8	17.8	17.8	17.8	23.8	23.8	23.8	23.8	23.8
	Milk (grams)									
a	0.3	0.4	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.3
b	0.9	1.3	1.5	1.8	2.0	2.4	3.0	3.0	3.6	4.0
c	1.7	2.4	3.0	3.6	4.0	4.7	5.8	5.9	7.1	7.9
	Additional blood needed (grams)									
a	0.7	0.9	0.8	0.7	0.7	0.6	0.8	0.7	0.7	0.7
	1.4	1.7	1.5	1.5	1.5	1.3	1.6	1.4	1.4	1.4
b	2.1	3.0	3.6	4.2	4.6	5.6	6.9	6.9	8.3	9.2
	4.2	5.9	7.2	8.4	9.2	11.2	13.7	13.9	16.7	18.4
c	3.8	5.6	6.9	8.3	9.2	10.8	13.4	13.7	16.5	18.3
	7.7	11.2	13.9	16.7	18.4	21.6	26.8	27.4	33.1	36.6

is roughly similar to that of *Myotis thysanodes* during initial postnatal growth, then the minimum amount of energy necessary for growth from days 5 through 20 is approximately 0.35 kcal./day (G_n in equation 3). Similar G_n values were calculated for older ages with slight modifications upwards due to presumed gradual decrease in percentage of body water.

Maintenance energy (M_n) values for neonates were calculated on three alternative bases as follows:

1) Ectothermy is assumed. Bartholomew and Tucker's (1964) equation for lizards at 30°C was used to estimate M_n at 32°C, and a value 10 per cent less was used for 22°C.

2) Homeothermy at minimum metabolic rate is assumed. Kleiber's (1961:212) equation ($M = 70W^{0.75}$) provided an estimate of M_n at 32°C. Values for 22°C were obtained by multiplying the 32°C values by 3.0 for age 5 days, by 2.5 for age 20 days, and by 2.0 for older ages.

3) Values twice those of category 2 were calculated. This probably represents a more realistic energy demand for a wild mammal.

The energy in the ingested milk (I_n) and energy wasted (E_n) were then computed on the assumption that $G_n + M_n$ represent 90 percent of I_n and 10 per cent is wasted. Finally, the efficiency of food utilization (100 G_n/I_n) was computed.

The maintenance requirements of neonates will, of course, be affected by the degree to which the above assumptions of homeothermy, optimal thermal environment, and basal metabolic status' are fulfilled. Heat loss of the sparsely furred newborns will require greater heat production than for fully furred animals, but the lack of fur will be partially offset by contact with the mother and with other young in the roost. These effects are difficult to quantify although the magnitude of the effect of hairlessness is suggested by Mount's (1971) report that hairless mice have a weight-specific oxygen consumption about 25 per cent higher than do haired mice of similar weight (32 to 35 grams).

In adult bats an ambient temperature (T_a) of 10°C below the thermal neutral zone results in at least a doubling of metabolic rate (McNab, 1973). The increase would undoubtedly be considerably greater for neonates if they regulate deep body temperature (T_b). It is highly unlikely, however, that newborn vampires do so. Most small mammal neonates, including several vespertilionids, fail to regulate T_b during the first few days of postnatal life (Eedy and Ogilvie, 1970; McManus, 1971; Studier and O'Farrell, 1972; Weigold, 1973). Of course lack of thermoregulation would greatly reduce the daily energy requirements for maintenance.

Lactating Females

On the basis of published information (Crespo *et al.*, 1961; Wimsatt and Guerriere, 1962; Wimsatt, 1969; McFarland and Wimsatt, 1969; Tucker, 1970) and data of his own, McNab (1973) calculated the daily energy budget of a 42-gram male vampire to be 25.7 kcal./day at an average roost temperature of 22°C. This would require a blood meal of 23.8 grams because a gram of blood is equivalent to 1.08 kcal. (McNab, 1973). It can be assumed that a lactating female will

have a similar basal energy requirement plus an additional requirement for milk production. The figures presented in Table 3 were computed on the basis of McNab's (1973) value of 23.8 grams of blood for maintenance at 22°C and the assumption that the requirement is 33 per cent less at 32°C.

Daily milk production required to meet the needs (I_n) of the neonates was calculated on the basis of 2.5 kcal./gram of milk (the average for phyllostomatids, excluding *Glossophaga*, see Table 1). A 30-gram female (0.072 $kg.^{0.75}$) secreting 10 kcal. of milk energy per day is producing at the rate of 139 kcal. per day per $kg.^{0.75}$, which is close to the value calculated by Linzell (1972) for 22 species. Such production is similar to that of *Mus musculus*, an animal of similar size.

The additional dietary blood required for lactating females is given at the bottom of Table 3. The upper figure represents the amount of extra blood required if it could be transferred with 100 per cent energetic efficiency into milk, whereas the lower figure represents estimates of additional blood required if it were transferred into milk at 50 per cent efficiency. Brody (1945:792-852) calculated gross energetic efficiency of milk production to be 28 to 34 per cent for cattle, 32 to 40 for goats, 41 to 47 for humans, and 44 to 48 for rats. The numbers shown in Table 3 should not be construed to represent actual, but only relative, values. On this basis, it is apparent that ectothermy on the part of neonates results in by far the least energy cost to the lactating female and most efficient energy use on the part of the neonate independent of roost temperature. Furthermore, if the neonate is endothermic, T_a has a profound effect on energy requirements, again emphasizing the importance of roost site selection. Finally, neonatal thermoregulatory level appears to affect energy demand more profoundly than age or weight (that is, values rise more rapidly reading down data sets rather than across).

If apparent blood requirements for lactating females are roughly correct, in view of the load lifting capacity of vampires (Crespo *et al.*, 1970) and observed feeding capacities (Wimsatt and Guerriere, 1962), it is unlikely that lactating females nursing homeothermic neonates feed only once nightly as has been reported (Wimsatt, 1969).

An interesting observation of Schmidt and Manske (1973) was that after about three months after birth, females regurgitated small amounts of blood, which were eaten by the offspring. To our knowledge, this sort of feeding behavior has not been reported previously for bats and would greatly decrease the energy requirements of the female after about day 100 of lactation. This behavior of vampires suggests the possibility that other phyllostomatid species may not feed their young entirely on milk but may regurgitate nectar (for example, *Leptonycteris*) or transport or regurgitate fruit (for example, *Artibeus*).

Postnatal growth in *Carollia* is nearly linear (Bleier *et al.*, this volume) with initial growth rates of about 0.22 grams per day (days 1 to 20) and a later growth rate of 0.20 grams per day (days 20 to 50). Adult weight is reached about 60 to 70 days after birth. Assuming that a single young is suckled, initial (days 1 to 20) bioenergetic demands for lactation are probably less than those of vampires. If milk is not supplemented by other food, lactation energy demands late in the lactation period (days 20 to 50) would certainly be higher than those of vampires.

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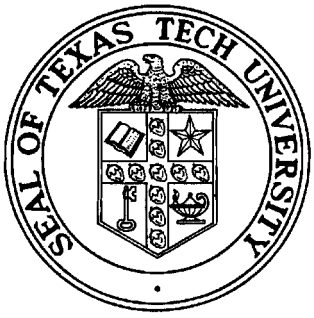
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