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

Edited by
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INTRODUCTION

Because of their adaptive diversity and, in many instances, unique morphological attributes, bats of the family Phyllostomatidae long have fascinated biologists. Known only from the New World, most genera of phyllostomatids are limited distributionally to tropical environments, but some representatives occur as far north as the southwestern United States and others southward to the northern parts of Argentina and Chile; some species also are distributed on the Bahamas and islands of the Greater and Lesser Antilles. With the advent in recent years of improved methods of collecting bats, a tremendous wealth of information on phyllostomatids has 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 separately numbered as a Special Publication of The Museum at Texas Tech University. In order to establish a workable approach by which reference could be made consistently to taxa throughout the series, an annotated checklist by Jones and Carter (published in the first part of the series) was circulated to all authors. Each was asked to follow the nomenclature and systematic arrangement in the checklist or, alternatively, to document departures therefrom. This system, it is hoped, will allow readers to relate information from one chapter to another and one part to the next without the handicap of conflicting names for the same organism.

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

Even though some redundacy has resulted, we thought it best to have a section on the cited literature with each contribution. Citations to manuscripts in Part II and those scheduled for Part III of this collected series are carried in text as "this volume."

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

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

May 1977   Robert J. Baker
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ENDOPARASITES

John E. Ubelaker, Robert D. Specian, and Donald W. Duszynski

The leaf-nosed bats of the New World family Phyllostomatidae occur from the southwestern United States through tropical Central and South America. Members of this family are also found throughout the Antilles. The ecological associations of the species in this family seem to be rather broad; species are found in humid tropical to semiarid and arid subtropical environments. Diversity in feeding is readily apparent ranging from nectivores (*Glossophaga*), frugivores (*Artibeus*), sanguivores (*Desmodus*), to omnivores (*Phyllostomus*) (see review by Glass, 1970; Gardner, this volume).

To understand better the biology of phyllostomatid bats, it is worthwhile to examine their parasites. The distribution of parasites, especially endohelminths, is governed largely by climate, distribution of intermediate hosts, feeding habits of the hosts, evolutionary age, physiology, and availability of the host species. Because parasites often evolve with their host, the systematic and phylogenetic ages of particular groups of hosts can be determined, in some cases, directly from the systematics and assemblages of their parasites if appropriate precautions are taken.

The aims of this study were to collect and correlate as much information as possible concerning the endoparasites of the Phyllostomatidae and present problems for future work. Specifically, this report includes a systematic review of all parasitic species of Protozoa, Acanthocephala, Pentastomida, Platyhelminthes, and Nematoda occurring in the Phyllostomatidae; an addition of unpublished parasite collection records; and a preliminary appraisal of various factors that have influenced the dispersal and speciation in the endoparasites of leaf-nosed bats.

HISTORICAL REVIEW

Published works dealing with parasites of leaf-nosed bats are few. The earliest studies were probably those of Kolenati (1856) who examined bats in Brazil and described several nematodes of the genus *Capillaria* Zeder, 1800. Molin (1861) described and reported on the anatomy of *Histiostrongylus coronatus* from *Phyllostoma* sp. (not necessarily a species of *Phyllostomus*) collected in Brazil. Following these early reports of nematodes, Braun (1900) described several trematodes from Brazilian bats. Looss (1907) indicated, however, that Braun's descriptions were so inadequate that the species could not be identified. The trematodes of Brazilian bats were studied later in good detail by Travassos (1921, 1928, 1955).

Beginning in the 1930's, Perez-Vigueras initiated research on helminths of phyllostomatids collected in Cuba (1934, 1935, 1936, 1941a, 1941b, 1942). At about the same time, the nematodes of tropical American bats were studied ex-

tensively by Lent and Teixera de Freitas (1936, 1940) and Lent *et al.* (1945, 1946).

The first reports of helminths from North American phyllostomatids were by Caballero y Caballero (1942). His contributions to the helminth fauna of Mexican bats continued until recently. In 1960, he and Grocott reported on helminths in bats from Central American countries.

There are many reports of parasitic worms from tropical bats. The majority of these reports deal with descriptions of individual species and are presented in the systematic part of this report. In addition to the above mentioned reports, several brief surveys are available, namely, Chitwood (1938) and Stunkard (1938) in Yucatán, México, and Silva Taboada (1965) and Baruš and del Valle (1967) in Cuba.

With the exception of the haemoflagellates, the protozoan parasites of bats have not been studied well. Most published parasite surveys of phyllostomatid bats are concerned only with their parasitic helminths, as noted above, or with zoonotic bacterial, viral, and fungal organisms (for example, Grose and Marinkelle, 1966, 1968; Grose *et al.*, 1968; Marinkelle and Grose, 1966). In only a few instances have general survey reports included information of the protozoan parasites of phyllostomatids and these are usually of a public health nature in which attention is given to zoonotic forms.

Several reviews of parasites from bats in general are available. Stiles and Nolan (1931) listed all known parasites of bats, including ecto and endoparasitic forms. A general account of parasites of bats was presented by Allen (1939). Caballero y Caballero and Grocott (1960) published a significant work reviewing the trematodes from bats. Ubelaker (1970) published a general account of parasites from bats and in the following year, Barus and Rysavy (1971) analyzed the biogeography of nematodes of the family Trichostrongylidae occurring in microchiroptera. Webster (1973) reviewed the helminths of bats north of the United States-México border.

METHODS

The majority of the specimens obtained for study were acquired by three collecting trips to Southern México and Central America. Collectors on these trips included Cesar Estrada R. (CER), Lawrence M. Hardy (LMH), J. Knox Jones, Jr. (JKJ), Timothy E. Lawlor (TEL), James D. Smith (JDS), Delbert L. Kilgore, Jr. (DLK) and John E. Ubelaker (JEU). Specimens indicated by DWD were collected by Donald W. Duszynski in Costa Rica.

Specimens collected in México or Nicaragua were fixed in formalin or acetic acid-formalin-alcohol (AFA) and stored in 70 per cent ethanol; those collected in Costa Rica were fixed in warm 70 per cent ethanol and stored in 70 per cent ethanol and 5 per cent glycerine until studied.

Wherever possible, museum accession numbers are given for host specimens. The designation (KU) refers to the mammalogy collection, the Museum of Natural History, The University of Kansas, Lawrence. Due to the misidentification or name changes of hosts, the practice of depositing hosts in reputable museum collections is strongly encouraged.

[Editors' note: Because the use of host names in the older parasitological literature often obscures host-parasite relations for those ill acquainted with the nomenclatural history of host taxa, we routinely replaced a junior synonym with a senior one. When some notation of such changes seemed necessary, we enclosed a brief explanation in brackets; otherwise, none was made. Also, misspelled names were corrected. We made no attempt to verify the identification of any species, although a notation was inserted when the identity of a host was improbable. A host name was enclosed in quotation marks to indicate that its original use in the parasitological literature could not be applied with certainty to any known taxon.]

All specimens to be studied by light microscopy were stored in 70 per cent ethanol and subsequently mounted on glass microscope slides. Soft-bodied specimens were stained in acetocarmine, cleared in xylene, and mounted in Canadian balsam prior to study. Nematode specimens were cleared either in warmed lactophenol or glycerine prior to study.

Specimens studied by scanning electron microscopy were prepared in the following manner. Fixed specimens were dehydrated in an ascending series of ethanol solutions to 70 per cent, transferred to 5 per cent glycerine-95 per cent ethanol solution from which the alcohol was allowed to evaporate, and cleared in 96.6 per cent glycerol-0.05 per cent potassium chloride-3.35 per cent distilled water, 24 to 48 hours prior to examination. Whole specimens or dissected portions of the helminths were mounted on metal specimen stubs with Duco cement, out-gassed in a vacuum evaporator for one hour or more, rotary coated with gold palladium (200 Å or less), and examined with an AMR 1000 scanning electron microscope.

Phylum PROTOZOA

The best present classification of the Protozoa is that proposed by Honigberg *et al.* (1964), as presented by Levine (1973), though we prefer not to use the latter's "uniform endings of higher taxa" (Levine, 1958). Of the five subphyla utilized in this classification, two of these, Ciliophora and Sarcomastigophora, contain both free-living and parasitic forms, whereas in the remaining three, Apicomplexa, Microspora, and Myxospora, all species are parasitic. Only two of these subphyla (Apicomplexa, the coccidia, malaria, and toxoplasma-type organisms; Sarcomastigophora, the flagellates and amoebae) contain parasites frequently found in mammals. Unfortunately, there is a considerable paucity of information on the protozoan parasites of all bats, worldwide, and such studies would provide much new information to future workers.

Subphylum APICOMPLEXA Levine, 1970
Class SPOROZOA Leukart, 1879
Family Eimeriidae

Eimeria sp.
Type host.—Any phyllostomatid bat.

Site of infection.—Endogenous stages usually in the intestinal epithelial cells; oocysts are found in the feces.

Remarks.—Although there are no records of Coccidia from phyllostomatid bats, we include this section to point out the immediate need for work in this area. Inasmuch as the Coccidia tend to be particularly host specific, the information from such studies could provide data to indicate and help us understand certain phylogenetic relationships.

There are 13 named species of bat eimerians, but it is questionable whether all should be considered valid species (Pellérdy, 1974; Wheat, 1975). Of these 13 species, only *Eimeria eumops* from *Eumops trumbulii* (Colombia), *E. macyi* from *Pipistrellus subflavus* (Alabama), and *E. rhynchonycteridis* from *Rhynchonycteris naso* (British Honduras) have been reported in the Western Hemisphere (Lainson, 1968; Marinkelle, 1968a; Wheat, 1975). Presumably, eimerians and related taxa (for example, *Klossia variabilis*, see Levine *et al.*, 1955) have not been found in phyllostomatids because no one has bothered to look for them. The 13 reported species of bat eimerians are only a fraction of the number which must actually parasitize these mammals; *Eimeria* spp. have been described from only 12 of the 168 Recent genera (7 per cent) and 14 of the 853 living species (1.6 per cent) of bats recognized by Vaughan (1972). Although some species of *Eimeria* occur in more than one host, we also know that many hosts harbor two or more species that may be unique to them. If we conservatively assume that there is a least one *Eimeria* species per bat species, as was done for rodents (Levine and Ivens, 1965), we can estimate that there may be about 900 species of *Eimeria* alone in bats. The number described already is only 1.5 per cent of this number.

Family Plasmodiidae

Polychromophilus deanei Garnham *et al.*, 1971

Type host.—*Myotis nigricans.*
Site of infection.—Red blood cells.
Type locality.—Pará, Brazil.
Other records.—This species was seen in the blood of *Glossophaga soricina* from Pará, Brazil, by Deane and Deane (1961), but their identification was both incorrect and incomplete (Garnham *et al.*, 1971; Garnham, 1973).

Remarks.—Haemosporidian parasites of any sort are rare in New World mammals. According to Garnham (1973), the haemosporidian parasites of bats fall into at least four genera, *Plasmodium, Hepatocystis, Nycteria,* and *Polychromophilus,* with the first three being found only in bats of the Old World. The first report of a bat "malaria" on the American continent was by Wood (1952) in which he found what he called *Plasmodium* sp. in five *Antrozous pallidus* (Vespertilionidae) in California and in one *A. pallidus* and one *Pipistrellus hesperus* (Vespertilionidae) from the Chisos Mountains in Texas. He did not specify whether the California and Texas parasites were the same or different species.

Only one report exists of a haemosporidian in phyllostomatid bats, and that was by Deane and Deane (1961), who found what they also described as *Plas-*

modium sp. After describing and picturing the parasite in considerable detail, they concluded their paper by stating they weren't sure whether the forms they saw belonged to the genus *Plasmodium* or to some other genus within the "Haemoproteidae." Garnham *et al.* (1971) described *P. deanei* from *M. nigricans* (Vespertilionidae) caught in the same general area of Pará as the bats examined by Deane and Deane (1961) and speculated that the general morphological features of *P. deanei* and the *Plasmodium* sp. seen by the Deanes were quite similar. In a later report, Garnham (1973) synonymized *P. deanei* and the form seen a decade earlier by Deane and Deane (1961) and, after reviewing the original slides made by Wood (1952), also placed that "malarial parasite" into the genus *Polychromophilus*. Thus, *Polychromophilus* has been reported three times in the New World, twice from the Amazon region and once from California and Texas. The latter parasite is longer and more oval than *P. deanei* and the pigment in the female is more abundant.

Family Toxoplasmatidae

Toxoplasma gondii Nicolle and Manceaux, 1908

> *Type host.*—*Ctenodactylus gondi.*
> *Site of infection.*—Trophozoites and cysts throughout the host's tissues.
> *Type locality.*—Foothills and mountains, Southern Tunisia, North Africa.
> *Other records.*—Roever-Bonnet *et al.* (1969), using the Sabin-Feldman dye test for toxoplasmosis, found the sera of two *Artibeus literatus* from Tibú, Santander, Colombia to be positive for this parasite.
> *Remarks.*—Literally thousands of records of *T. gondii* from over 50 vertebrate species have appeared in the literature since this parasite first was described (for review, see Frenkel, 1973). However, information on the incidence of *T. gondii* in bats is meager as few such surveys have been conducted worldwide (for example, Rifaat *et al.*, 1967; Kaliakin, 1970) and we find only one report documenting, serologically, the incidence of *T. gondii* in phyllostomatid hosts (Roever-Bonnet *et al.*, 1969). *Toxoplasma gondii* is almost ubiquitous in nature and the role of bats in the ecology and distribution of this most important parasite certainly should merit immediate future investigation.

Subphylum SARCOMASTIGOPHORA Honigberg and Balamuth, 1963

Class ZOOMASTIGOPHOREA

Family Trypanosomatidae

Before beginning a discussion on the haemoflagellates, we must point out that the classification of the various species and the terminology associated with their developmental stages has changed considerably in the last several years. Thus, to be consistent with current trends of thought, we will follow the classification of the Trypanosomatidae as outlined by Levine (1973) and the uniform terminology of body forms introduced by Hoare and Wallace (1966).

The study of trypanosomes of bats is important because bats often live in proximity to humans and can migrate great distances; thus, they can act as links

between sylvatic, rural, and urban populations. According to Dias (1936a), trypanosomes of bats have been known since 1898 when Dionisi in Italy first isolated and described, but did not name, haemoflagellates that he found in the blood of three species of vespertilionid bats (*Miniopterus schreibersii, Vespertilio murinus, Vesperugo noctula*). Dias (1936a) also stated that in 1900 Durham examined the stomach contents of a mosquito that had just fed on the blood of *Phyllostomus* sp. from the state of Pará, Brazil, and found numerous trypomastigote forms. Durham, apparently, did not describe these forms nor specifically identify the host.

The first name given to a bat haemoflagellate was in 1904 when Battaglia, in Italy, identified a very small trypomastigote form from the blood of *Pipistrellus* sp. (Vespertilionidae) as *Trypanosoma vespertilionis*. This name has persisted and has been assigned since to trypanosomes of bats from Africa, the Americas, and Europe. Six years later, Cartaya (1910) in Cuba described the first trypanosome from bats in the Americas when he named *T. phyllostomae* from *Carollia perspicillata* (reported as "*Artibeus perspicillatus*"). However, the validity of this species is, today, suspect by many authors (Table 1). Since then, several reports have documented the occurrence of trypanosomes in phyllostomatids, but in most, the information presented was scanty or specific identification of those forms was not made. Thus to date, only six valid specific names (*T. cruzi, T. equinum, T. evansi, T. pessoai, T. pifanoi,* and *T. vespertilionis*) and two of questionable value (*T. lineatus, T. phyllostomae*) have been attributed to trypanosomes from American phyllostomatids. When specific identifications were not made, the haemoflafellates from these hosts were identified as *Trypanosoma* sp., *T. cruzi*-like or *T. rangeli*-like.

In his review of bat trypanosomes, Dias (1936a) established two main groups: 1) the *vespertilionis* group—small trypomastigote blood forms (14 to 20 microns) with a very large, round subterminal kinetoplast and a narrow undulating membrane; this group includes, among others, *T. cruzi, T. lineatus* (?), *T. phyllostomae* (?), and *T. vespertilionis*; and 2) the *megadermae* group—large and broad trypomastigote forms (25 to 40 microns) with a small, round, or rod-shaped kinetoplast located far from the posterior end of the body, closer to the nucleus, and a broad, wavy, undulating membrane (Deane and Sugay, 1963); this group includes, among others, *T. pessoai* and *T. pifanoi.* In addition to these two main groups of bat trypanosomes, there are other large trypanosomes that do not fit well into either group: *T. pteropi* from Australian flying foxes (from Marinkelle and Duarte, 1968); *T. rangeli*-like forms from *Artibeus lituratus* and *Glossophaga soricina* in Colombia (Marinkelle, 1966b); *T. evansi* from *Desmodus rotundus* in Panamá and Colombia (Ayala and Wells, 1974; Clark, 1948; Clark and Dunn, 1933; Dunn, 1932; Johnson, 1936a, 1936b); and *T. equinum* from *D. rotundus* in Argentina (Acosta and Romaña, 1938).

The trypanosomes that have been described from phyllostomatid hosts and the countries in which they were found are listed in Table 1. Additional pertinent information for each species is presented below.

TABLE 1.—*The trypanosomes of phyllostomatid bats. Experimental infections are indicated by an asterisk.*

Bat hosts	Locality	References
MEGADERMAE		
Trypanosoma pessoai		
Artibeus cinereus, *Artibeus jamaicensis*	Jarco, San José, Costa Rica	Esquival *et al.*, 1967
Carollia perspicillata, *Choeroniscus minor*	Pará, Brazil	Deane, 1964*b*
Desmodus rotundus	Guararema, São Paulo, Brazil	Deane and Sugay, 1963
Desmodus rotundus	Cali, Colombia	Ayala and Wells, 1974
Trypanosoma pifanoi		
Artibeus lituratus, *Phyllostomus hastatus*	Tibú and Tolima, Colombia	Marinkelle and Duarte, 1968
Trypanosoma spp.		
Carollia perspicillata, *Choeroniscus minor,* *Glossophaga soricina*	Pará, Brazil	Deane, 1964*b*
Carollia perspicillata, *Glossophaga soricina*	Pará, Brazil	Dias *et al.*, 1942; Deane and Sugay, 1963
Carollia perspicillata, "*Lonchoglossa ecaudata*"	Rio de Janeiro, Brazil	Dias, 1940 (not *T. heybergi*-like, see Deane, 1964*b*)
Desmodus rotundus	San José, Costa Rica	Zeledón and Vieto, 1957
Desmodus rotundus	Pará, Brazil	Romaña, 1940 (*in* Dias *et al.*, 1942)
VESPERTILIONIS		
Trypanosoma cruzi		
Artibeus jamaicensis, *Uroderma bilobatum*	Canal Zone, Panamá	Clark and Dunn, 1932
Artibeus lituratus, *Carollia perspicillata,* *Desmodus rotundus,* *Glossophaga soricina,* *Phyllostomus discolor,* *Phyllostomus hastatus*	Western and central Colombia	Marinkelle, 1966*b*; Marinkelle and Grose, 1966
Carollia perspicillata*, *Phyllostomus hastatus*	Chilibrillo Caves, Panamá	Clark and Dunn, 1932
Glossophaga soricina	Bella Vista, Panamá	Clark and Dunn, 1932
Phyllostumus hastatus, *Carollia perspicillata*	Brazil	Dias, 1936*a*
Trypanosoma cruzi-like		
Artibeus cinereus, *Artibeus lituratus,* *Artibeus jamaicensis,*	Western and central Colombia	Marinkelle, 1966*b*, 1968*b*; Deane, 1967

TABLE 1.—*Continued.*

Carollia perspicillata, *Desmodus rotundus,* *Glossophaga soricina,* *Mimon bennettii,* *Phyllostomus discolor,* *Phyllostomus hastatus,* *Uroderma bilobatum,* *Vampyrum spectrum*		
Artibeus jamaicensis, *Phyllostomus hastatus*	French Guiana	Floch *et al.,* 1942
Carollia perspicillata	Colombia	Renjifo-Salcedo *et al.,* 1952; Marinkelle, 1966*b*
Carollia perspicillata	Guarativana, Yaracuy, Venezuela	Dias and Pifano, 1941
Carollia perspicillata, *Choeroniscus minor,* *Glossophaga soricina,* *Lonchophylla mordax,* *Micronycteris megalotis,* *Phyllostomus elongatus*	Marajo Island, Belem and Pará, Brazil	Dias *et al.,* 1942; Deane, 1961, 1964*a*
Carollia perspicillata, *Choeroniscus minor,* *Phyllostomus hastatus*	Pará, Brazil	Deane, 1964*a,* 1964*b*; Dias, 1940
Desmodus rotundus	Panamá	Wood and Wood, 1941
Glossophaga soricina, *Lonchophylla thomasi*	Pará, Brazil	Garnham *et al.,* 1971
Phyllostomus elongatus	Venezuela	Dias and Pifano, 1942
Phyllostomus hastatus	Brazil, Colombia, Venezuela	Carini, 1932; Deane, 1961, 1964*a,* 1967; Dias, 1933, 1936*a,* 1936*b*; Dias and Romaña, 1939; Marinkelle, 1966*b*; Pifano, 1964; Renjifo-Salcedo, 1948; Renjifo-Salcedo *et al.,* 1950
Trypanosoma lineatus		
Vampyrops lineatus	Caracas, Venezuela	Iturbe and Gonzalez, 1916; W.Y., 1917
Trypanosoma phyllostomae		
Carollia perspicillata	Brazil	Dias, 1940 (= *T. cruzi-*like?, see Deane, 1964*b*)
Carollia perspicillata	Cuba	Cartaya, 1910 (= *T. cruzi-*like?, see Marinkelle, 1968*b*)
Carollia perspicillata	Guarativana, Yaracuy, Venezuela	Dias and Pifano, 1941 (= *T. cruzi-*like?, see Marinkelle, 1968*b*)

TABLE 1.—*Continued.*

	Trypanosoma vespertilionis	
Carollia perspicillata, "*Lonchoglossa ecaudata*"	Rio de Janeiro, Brazil	Dias, 1940
Carollia perspicillata, *Choeroniscus minor,* *Glossophaga soricina,* "*Lonchoglossa ecaudata*"	Brazil	Dias *et al.*, 1942 (see Deane, 1964*a*)
Carollia perspicillata *Glossophaga soricina,* *Phyllostomus hastatus*	San José, Costa Rica	Zeledón and Vieto, 1957, 1958
Macrotus waterhousii	Coquimatlán, Colima, México	Mazzotti, 1946
Phyllostomus hastatus	Colombia	See Marinkelle, 1966*b*
	Trypanosoma spp.	
Carollia perspicillata	Limón, Costa Rica	Zeledón and Rosabal, 1969*b*
Lonchophylla mordax	Brazil	Romaña, 1940 (in Dias and Pifano, 1941)
"*Trachops elongatus*"	Brazil	Dias and Pifano, 1942
	OTHER SPECIES **Trypanosoma evansi**	
Artibeus jamaicensis*,* *Carollia perspicillata**,* *Glossophaga soricina**,* *Phyllostomus hastatus***	Panamá	Clark and Dunn, 1933
Desmodus rotundus*	Panamá	Dunn, 1932; Clark and Dunn, 1933; Johnson, 1936*a*, 1936*b*
Desmodus rotundus	Arauca and Cali, Colombia	Ayala and Wells, 1974
Desmodus rotundus	Valle de Cauca, Colombia	Ayala, 1972 (*in* Ayala and Wells, 1974)
	Trypanosoma equinum	
Desmodus rotundus*	Argentina	Acosta and Romaña, 1938; Hoare, 1965
	Trypanosoma rangeli-like	
Artibeus lituratus, *Glossophaga soricina*	Central and western Colombia	Marinkelle, 1966*b*; Tamsitt and Valdivieso, 1970
	"not **Trypanosoma cruzi**-like"	
Choeroniscus minor	Pará, Brazil	Garnham *et al.*, 1971

Trypanosoma (= Schizotrypanum) cruzi Chagas, 1909

Type host.—Panstrongylus megistus.

Site of infection.—In the intestine of the triatomid bug (originally), but also intercellularly in the blood (trypomastigote form) and intracellularly in the reticuloendothelial and other tissue cells (amastigote form) of vertebrate hosts.

Type locality.—Brazil.

Other records.—See Table 1.

Remarks.—Trypanosomes morphologically similar to *T. cruzi* have been recorded from more than 100 species of mammals (Deane, 1964a). Technically, forms identified as this species should be restricted to those which produce amastigote bodies in the organs of inoculated laboratory animals or in tissue cultures. In addition, the length of the trypomastigote blood form (approximately 20 microns), its nuclear index (approximately 1.4 to 1.6), its ability to develop in triatomid bugs, and whether or not the bat host(s) came from endemic areas of Chagas' disease should all be utilized as supportive evidence in such identifications (Deane, 1961). Only three reports (Table 1) use much of the above criteria to demonstrate conclusively the presence of *T. cruzi*, either naturally or experimentally, in American leaf-nosed bats.

Trypanosoma cruzi-like

Remarks.—Many of the bats in most of the countries of the Americas are hosts to trypanosomes structurally identical to *T. cruzi* (See Marinkelle, 1965). It is now generally accepted that these forms should be referred to as *T. cruzi*-like when only blood forms are studied or if they fail to produce amastigote bodies in living cells (Marinkelle, 1966b). However, Marinkelle (1968b) stated also that the majority of *T. cruzi*-like forms (*vespertilionis* group) are capable of forming amastigotes in cells of mammals. Deane (1964a), on the other hand, disagreed with this view and summarized well the difficulties encountered in working with bat trypanosomes: "The bat strains, however, remain a problem. At least some bats of the endemic area of Chagas' disease do harbour flagellates undistinguishable from *T. cruzi*, on the basis of morphology, biology and virulence and even immunologically. But most bats harbour strains which cannot, at present, be identified to the agent of Chagas' disease: they are of little or no virulence for laboratory animals and, besides, some strains do not seem to develop well in triatomid bugs and others show morphological differences that are said to be constant." Dias (1936a) offered somewhat of a compromise position by suggesting the trypanosomes of bats can, after repeated passage, change their virulence and lose the ability to infect other hosts. A translation of his original statements (p. 75, in Portuguese) follows: "One extremely interesting question that should be better investigated is that of the behavior of virulent *T. cruzi* in bats that are natural hosts to trypanosomes. Experiments done to date show that these mammals (at least some species) are very resistant, if not refractory, to infection by strains that are very pathogenic to other animals. One of our experiments demonstrated that before the trypanosomes are destroyed they experience an abrupt

and remarkable attenuation of virulence in bats. If, by means of repeated passages, one succeeds in obtaining infections that are more and more prolonged, finally adapting the trypanosome to the bat, it is possible that this adaptation will be made at the cost of the loss of infectiveness to other animals, because of a real effect which the organic environment of the mammal exercises on the flagellate. If this could be verified, *T. cruzi* will have been transformed into *T. vespertilionis*, just as *T. vespertilionis* can be identified as *T. cruzi* in those rare circumstances in which its inoculations into animals are positive."

Additional confusion in naming such forms stems from: the highly variable nature of structural dimensions during different phases of infection by a single strain of *T. cruzi*; the wide variation in nuclear indices reported for *T. cruzi* (from 0.95-1.63 by Baretto, 1965); and the possible influence of temperature on the morphology and pathology of various trypanosomes (Marinkelle, 1966*a*, 1968*b*). Such information points out the need for much additional work before the *T. cruzi*-like forms in bats can begin to be accurately separated.

Some of the first reports of *T. cruzi*-like parasites from bats in Latin America were by Dias and Pifano (1941, 1942) in Venezuela. However, Zeledón and Vieto (1958), based on their biometrical study of two lab strains of *T. cruzi* (from mice and triatomids) and of *T. vespertilionis* isolated from a *Glossophaga soricina* caught near San José, Costa Rica, considered the forms seen by Dias and Pifano (1942) to be different from *T. cruzi* and *T. vespertilionis*. Zeledón and Vieto (1958) and later Marinkelle (1968*b*), in a retrospective look at the literature, considered as *T. cruzi*-like the following phyllostomatid bat trypanosomes: those from *Carollia perspicillata* and described in Cuba by Cartaya (1910) as *T. phyllostomae*; the "phyllostomae" strain from *Carollia perspicillata* in Venezuela by Dias and Pifano (1941); the Brazilian strains from *C. perspicillata* and *Phyllostomus hastatus* studied by Deane (1964*a*); and the strains isolated from 11 species of phyllostomatids in Colombia (see Table 1) by Marinkelle (1966*b*, 1968*b*). Additional records to *T. cruzi*-like forms found in American phyllostomatids are listed in Table 1.

Trypanosoma equinum Voges, 1901

Type host.—*"Horses."*

Site of infection.—Extracellular blood parasite.

Type locality. "It originates in South America and occurs as far south as the Argentina provinces of St. Fe and Corrientes" (see Voges, 1901).

Other records.—See Table 1.

Remarks.—This species differs structurally from *T. evansi*, from which it probably arose, only in lacking a kinetoplast (Levine, 1973). *Trypanosoma equinum* infects cattle in an asymptomatic form, but produces a severe disease in horses called Mal de Caderas throughout much of South America, especially Brazil. It is unique (as is *T. evansi*) in that it has evolved to utilize the vampire bat, *Desmodus rotundus*, as a parallel host and as a vector of the disease (Hoare, 1965). In Argentina, it was demonstrated experimentally that vampire bats be-

come infected with *T. equinum* from horses and can transmit it by feeding on healthy horses (Acosta and Romaña, 1938).

Trypanosoma evansi (Steel, 1885)

Type host.—"Horses."
Site of infection.—Extracellular blood parasite.
Type locality.—Punjab, India.
Other records.—See Table 1.
Remarks.—*Trypanosoma evansi* (= *T. hippicum*) has a wide distribution in Latin America being prevalent in México, all of Central America, Venezuela, and Colombia, where it causes a disease called Murrina in horses (Hoare, 1965). Hoare (1957) stated that mechanical transmission of *T. evansi* (and of *T. equinum*) probably evolved as a secondary adaptation when it separated from its African ancestor *T. brucei* and lost its original intermediate host, the tsetse fly. After these two species became established in the New World, they acquired, in addition to blood sucking flies (Tabaniidae), a new type of vector, the vampire bat. Vampires are ideal vectors because their infection from cattle harboring small numbers of parasites is ensured by the large amount of blood taken during a meal (16 to 50 milliliters) (Hoare, 1965). The high rate of reproduction of the parasite within the vampire's body increases the chances of successful transmission to new hosts. Therefore, vampires play an important role in the spread of bovine Murrina among horses in Latin America.

Dunn (1932) first documented that the vampire bat *Desmodus rotundus* was a natural vector of *T. evansi* on the Isthmus of Panamá, and Clark and Dunn (1933) were able to transmit this trypanosome to other phyllostomatids (Table 1), but all specimens so infected, including the vampires, were highly susceptible to disease and died within a few weeks. Clark and Dunn apparently never found any phyllostomatids with "spontaneous" (= natural?) *T. evansi* infections, but felt that the vampire bat, inasmuch as it could be infected experimentally and fed with equal freedom on equine and bovine animals, might be an important vector in transmitting this parasite from reservoir cattle hosts to highly susceptible horses and mules. Johnson (1936a, 1936b) and Hoare (1957) also demonstrated that vampire bats acquire and transmit *T. evansi* under experimental conditions, but we found records of only 20 individual vampire bats with natural infections (Ayala and Wells, 1974; Clark, 1948; Johnson, 1936a, 1936b).

Trypanosoma lineatus Iturbe and Gonzalez, 1916

Type host.—*Vampyrops lineatus.*
Site of infection.—Extracellular blood parasite.
Type locality.—Venezuela.
Other records.—None to date.
Remarks.—Since this species was originally described, it has been mentioned on only three occasions in the literature. The first was a rather scathing review by one of the editors of Tropical Disease Bulletin (W. Y., 1917) and the other two times (Zeledón and Vieto, 1958; Marinkelle, 1968b) the authors considered

this form too *T. cruzi*-like to merit its own specific status. The validity of this species is, therefore, questionable. [*Vampyrops lineatus* is not known to occur in Venezuela, and the identification of the host is probably erroneous. Eds.]

Trypanosoma pessoai Deane and Sugay, 1963

In Venezuela, Dias and Pifano (1941) isolated a *megadermae*-type trypanosome (from *Myotis nigricans*) for the first time in the New World as these forms were previously known only from bats in Africa. Since then, several large unnamed trypanosomes of the *megadermae* group have been reported from phyllostomatids in the Western Hemisphere (Table 1), but only Deane and Sugay (1963), Esquival *et al.* (1967), and Marinkelle and Duarte (1968) described and pictured these parasites. Since its original description, this species has been reported in several species of phyllostomatids (Deane, 1964a; Esquival *et al.*, 1967). *Trypanosoma pessoai* differs from the *vespertilionis* group (particularly *T. cruzi*) not only in size, but also because xenodiagnosis, hemacultures, laboratory animals, and tissue sections and smears are always negative for other developmental stages (for example, amastigote forms) of the parasite.

Trypanosoma phyllostomae Cartaya, 1910

Type host.—*Carollia perspicillata.*
Site of infection.—Extracellular blood parasites.
Type locality.—Cuba
Other records.—See Table 1.
Remarks.—Most of those who work with bat trypanosomes believe this species to be too *T. cruzi*-like to distinguish it as a separate species (see Table 1).

Trypanosoma pifanoi Markinelle and Duarte, 1968

Type hosts.—*Artibeus lituratus* and *Phyllostomus hastatus.*
Site of infection.—Extracellular blood parasite.
Type localities.—Tibú and Tolima, Colombia.
Other records.—None to date.
Remarks.—This is only the second species of the *megadermae* group to be found in the Americas. Like *Trypanosoma pessoai*, developmental stages of this species could not be isolated in tissue sections of inoculated laboratory mice nor was multiplication observed in tissue cultures of mouse fibroblast cells or in the triatomid *Rhodnius prolixus* by xenodiagnosis (Marinkelle and Duarte, 1968). Attempted transmission of this species to *Carollia perspicillata* was unsuccessful, but blood forms isolated from a specimen of *Artibeus lituratus* were grown in NNN culture media and these culture forms closely resembled the blood and culture forms of *Trypanosoma cruzi*. Also, when 5000 NNN culture forms were inoculated intracoelomically into three species of triatomids, the parasite (when compared with control *T. cruzi*-inoculated bugs) proved highly fatal for the insects. Only three of 264 triatomids so inoculated lived for four weeks postinoculation (PI) and at 30 days PI their hemolymph had numerous, long, slender,

Trypanosoma rangeli-like epimastigote forms (Marinkelle and Duarte, 1968). This species differs from *T. pessoai* in size and by the absence of a twist of the posterior of the body.

Trypanosoma rangeli-like

Remarks.—Only Marinkelle (1966*b*) has reported what he called *T. rangeli*-like trypomastigote forms from American phyllostomatids. He found three bats (Table 1) harboring such parasites, and xenodiagnosis with the triatomids *R. prolixus* and *Cavernicola pilosa* showed abundant development of epimastigote stages of this parasite in the rectal ampulla of the bugs. Neither anterior station development nor signs of hemolymph infection took place and attempts to infect laboratory mice with these forms were unsuccessful.

Trypanosoma vespertilionis Battaglia, 1904

Type host.—*Pipistrellus* sp.
Site of infection.—Extracellular blood parasite.
Type locality.—Italy.
Other records.—See Table 1.
Remarks.—Since the original description of this parasite from vespertilionid bats in Europe, it has been observed on several occasions in bats of the Americas (for example, Deane, 1961), but few reports exist of its occurrence in phyllostomatids (Table 1). This species can easily be distinguished from others within the *vespertilionis* group by its small size (14 to 16 microns), its large nuclear index (2.6 to 2.7), and its apparent inability to infect laboratory animals or triatomid bugs.

Trypanosoma spp.

Remarks.—Unidentified forms of trypanosomes have been found in phyllostomatids on many occasions. In the majority of these records, the organisms seen were reported to belong to the *megadermae* group, but no illustrations of the parasite or structural data were provided (Table 1).

Phylum ACANTHOCEPHALA

Family Oligacanthorhynchidae

Neoncicola novellae (Parona, 1890)

Type host.—*Artibeus jamaicensis.*
Site of infection.—Small intestine.
Type locality.—Puerto Rico.
Other records.—None to date.
Remarks.—The acanthocephalan fauna of tropical American bats is restricted to a single species described from *A. jamaicensis* collected in Puerto Rico. It has apparently not been recorded since its original description. Schmidt (1972*a*) included seven species in the genus, all with 30 proboscis hooks. These parasites

have been reported in Carnivora, Chiroptera, and ducks (?) in South America, Malaysia, USSR, Puerto Rico, and Africa.

The life cycle of *N. novellae* is unknown. In a related genus, *Prosthenorchis*, species such as *P. elegans* and *P. spirula* are reported to use cockroaches (*Blatella germanica*, *Rhyparobis madarae*, and *Blabera fusca*) as well as beetles (*Lasioderma serricorne* and *Stegobium paniceum*) as intermediate hosts. Presumably similar insects serve as intermediate hosts for *N. novellae*. If this is true, the host bat becomes infected by eating a cockroach or beetle containing an infective larva, the cystacanth. It should be emphasized that intermediate hosts listed above represent experiments based on captive animals; the intermediate hosts in nature are not known.

Pathology due to acanthocephalans, in general, is influenced by numerous factors including the size, shape, and armature of the proboscis, number of parasites present, general health of the host prior to infection, and ability of the host to overcome secondary infection by pathogenic organisms (see Schmidt, 1972*b*). Inasmuch as the effect of *N. novellae* is unknown in *Artibeus*, a general discussion of pathology, diagnosis, treatment, and control of related species is not included here (see Schmidt, 1972*b*).

<div align="center">

Phylum PENTASTOMIDA

Family Porocephalidae

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Porocephalus crotali (Humboldt, 1808)

Type host.—*Crotalus durissus.*
Site of infection.—Body cavity.
Type locality.—Unable to locate.
Other records.—See below.

Remarks.—Members of the phylum Pentastomida, often referred to as tongue worms, are of uncertain systematic position, although evidence is accumulating that they are related to the brachiuran crustaceans. The genus *Porocephalus* is among the most highly evolved of the pentastomes. All species parasitize snakes as adults, and most may utilize a mammal in their development as does *P. crotali*, the only species recorded from bats (Self, 1969).

Porocephalus crotali occurs as an adult in various species of snakes, and has been reported as nymphs encysted in the liver of *Phyllostomus discolor* from Cumana, Venezuela, and Brazil (see Penn, 1942; Sambon, 1922; Shipley, 1898).

The life cycle of *P. crotali* has been studied intensively by Esslinger (1962*a*, 1962*b*, 1962*c*). Adult bats probably can be infected by ingesting eggs that contaminate food. From experiments with albino rats, it is known that the larvae hatch in the intestine and migrate through the wall into the viscera and mesentaries, leaving a trail of host neutrophils. After reaching the liver or other organs, they molt and eventually form sixth stage nymphs that show marked sexual differentiation. Development of the sixth stage nymph is completed in three months and it is then infective to the snake definitive host. Infection occurs by ingestion of the infected bat host, which may be a more common occurrence than previously suspected (Gillette and Kimbrough, 1970).

Pathology of pentastomes to their bat hosts probably is related directly to the development of the two pairs of hooks on the head. During metamorphosis to the sixth stage nymph, the adult hooks develop from papillae representing the atrophied appendages of the primary larvae. The median and lateral hooks project and have blades that extend above the surface of the head and serve to anchor the nymph to the tissue. As seen in Fig. 1, the lateral hooks project conspicuously from the surface and undoubtedly cause the primary destruction of host tissue. As the parasite develops in the liver, and in probable response to the hooks, a granulomatous lesion forms. At least four distinctive progressions of the disease can be determined: an initial macrophage proliferation with eosinophils, epithelioid, and giant cells accumulating in the area of the lesion lasting about three weeks; clonic development with involvement of fibroblastic tissue, plasma cells, and lymphocytes during the second and third months; reduction in inflammation during the fourth month; and production of a dense hyaline fibrous capsule by the sixth month. Again, it must be emphasized that the life cycle and pathology as determined by Esslinger (1962a, 1962b, 1962c) did not employ bats. *Porocephalus crotali* is also recorded in man (Stiles and Nolan, 1931).

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Phylum PLATYHELMINTHES

Class TREMATODA

Family Anenterotrematidae

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Anenterotrema auritum Stunkard, 1938

Type host.—*Micronycteris megalotis.*
Site of infection.—Small intestine.
Type locality.—Cueva de Xmahit Tekax, Xconsacab, Tizimin, Yucatán, México.

Anenterotrema eduardocaballeroi (Freitas, 1960)

Type host.—*Eumops glaucinus.*
Site of infection.—Small intestine.
Type locality.—São Paulo, Brazil.
Other records.—Travassos *et al.*, (1969) gave the following host records from Brazil: *Molussus rufus, M. major crassicaudatus,* and *Phyllostomus elongatus.*

Anenterotrema freitasi Caballero y Caballero, 1964

Type host.—*Micronycteris hirsuta.*
Site of infection.—Small intestine.
Type locality.—Costa Rica.

Anenterotrema liliputianum (Travassos, 1928)

Type host.—*Peropteryx canina.*
Site of infection.—Small intestine.
Type locality.—Angra dos Reis, Brazil.

FIG. 1.—Scanning electron photomicrograph of lateral hook on the head of *Porocephalus crotali* from the body cavity of *Eptesicus fuscus* collected at the Black Gap Wildlife Management Area, Brewster County, Texas. The above report is the first listing of *P. crotali* in North American bats. (×215)

Other records.—Travossos *et al.* (1969) gave the following host records from Brazil: "Molossidae sp.," *Molossus obscurus, M. major crassicaudatus,* and *Phyllostomus elongatus.* Teixera de Freitas and Dobbin (1963) also reported finding *A. liliputianum* in *Molossus obscurus.* [The name *Peropteryx canina* could refer either to *Peropteryx kappleri* or *P. macrotis.* Eds.]

Anenterotrema stunkardi Caballero y Caballero and Grocott, 1960

Type host.—*Phyllostomus hastatus.*
Site of infection.—Small intestine.
Type locality.—Panamá.
Remarks.—All known species of *Anenterotrema* have been found in the small intestine of their hosts. Members of this genus are unique because, unlike most digenetic trematodes, they lack a digestive tract. This evolutionary structural modification most certainly restricts their habitat selection in modern day hosts. Yamaguti (1969) examined histologically the parenchymal cells of *A. auritum* and later (1971) stated that the nuclei of these cells were involved in nutritional activity. No glandular-secretory cell types have ever been reported (Yamaguti, 1969).

Although five of the six species of *Anenterotrema* occur in phyllostomatid bats, they are not specific. *Anenterotrema freitasi* and *A. stunkardi* are both recorded from a single host species and are known only from the original descrip-

tions. It is probable that additional collections will indicate a general lack of host specificity.

The biology of this genus is completely unknown. Inasmuch as these trematodes are so unusual morphologically, additional studies are needed.

Family Dicrocoeliidae

Athesmia parkeri Perez-Vigueras, 1942

> *Type host.*—*Artibeus jamaicensis.*
> *Site of infection.*—Small intestine.
> *Type locality.*—Province Pinar del Río, Cuba.
> *Remarks.*—The species is recorded only from the type host in the original description. Teixera de Freitas (1962) considered this species conspecific with *A. heterolecithodes* (Braun, 1899) Looss, 1899, common in the bile duct of a variety of birds. The only other species in mammals, *A. foxi* Goldberger and Crane, 1911, occurs in primates. The ecology, pathology, and life cycle of *A. parkeri* are unknown.

Parametadelphis compactus Travassos, 1955

> *Type host.*—*Micronycteris behni.*
> *Site of infection.*—Bile duct and bladder.
> *Type locality.*—Cachimbo, Pará, Brazil.
> *Remarks.*—This trematode has been reported only in the original description. Nothing is known of its biology.

Family Lecithodendrium

Lecithodendrium pricei Perez-Vigueras, 1940

> *Type host.*—*Artibeus jamaicensis.*
> *Site of infection.*—Small intestine.
> *Type locality.*—Santa María del Rosario, Habana Province, Cuba.
> *Remarks.*—Although the pathology and ecology are not known, Koga (1954) reported briefly on the life cycle of *Lecithodendrium lageniforme* (Ogata, 1947). Virgulate cercariae develop in an aquatic snail, *Semisulcospira libertina*, and encyst in *Stenopsyche grissipennis*. Bats are infected by ingesting the metacercariae transmitted by the trichopteran second intermediate host. The genus *Lecithodendrium* contains numerous species occurring in bats and chameleons. At least 19 species occur in bats but all species except *L. pricei* are found in bats from Eurasia.

Limatulum aberrans Caballero y Caballero and Bravo Hollis, 1950

> *Type host.*—*Macrotus waterhousii.*
> *Site of infection.*—Intestine.
> *Type locality.*—Cuicatlán, Oaxaca, México.
> *Other records.*—NICARAGUA: *Phyllostomus discolor* (KU 97445) collected at Hacienda San Isidro, 10 km. S Chinandega, 10 m. (TEL 480).

Limatulum isthmicus Caballero y Caballero, 1964

> *Type host.*—*Micronycteris hirsuta.*
> *Site of infection.*—Small intestine.
> *Type locality.*—Costa Rica.

Limatulum oklahomense Macy, 1931

> *Type host.*—*Tadarida brasiliensis.*
> *Site of infection.*—Small intestine.
> *Type locality.*—Aetna, Kansas, and Freedom, Oklahoma.

Other records.—MEXICO: *Macrotus waterhousii*, Cuicatlán, Oaxaca; *Natalus mexicanus*, Acolman (Caballero y Caballero and Bravo Hollis, 1950); PARAGUAY: *Myotis nigricans*, Chaco, (Lent *et al.*, 1945); UNITED STATES OF AMERICA: *Myotis grisescens*, Kansas (Ubelaker, 1966).

Remarks.—*Limatulum aberrans* and *L. isthmicus* apparently are restricted to phyllostomatid bats. Additional records are needed, however, before specificity can be established. Seven species occur in the genus and all except *L. okabei* (Koga, 1954) Yamaguti, 1958, occur in New World bats. The ecology of this genus is unknown.

Family Urotrematidae

Urotrema scabridum Braun, 1900

> *Type host.*—*Molossus major crassicaudatus.*
> *Site of infection.*—Small intestine.
> *Type locality.*—Brazil.

Other hosts.—*Noctilio leporinus*, *N. labialis*, *Molossus ater*, *Promops centralis*, *Phyllostomus hastatus*, *Lasiurus intermedius*, *Myotis nigricans*, *Phyllostomus* sp.; also in numerous bats in North America as reviewed by Webster (1973) and Caballero y Caballero (1960). Webster (1971) reported that *Pteronotus macleayii* and *Tadarida brasiliensis* from Jamaica were also hosts to this parasite.

Remarks.—Caballero y Caballero (1942) reviewed the systematics of this genus and concluded that the following species are synonyms of *U. scabridum*: *U. lasiurense* Alicata, 1932 (see also Chandler, 1938), *U. minutum* Macy, 1933, and *U. shillingeri* Price, 1931. Keys to this complex of species were presented by Macy (1933). Caballero y Caballero (1942) further considered *Urotrematulum* Macy, 1933 synonymous with *U. scabridum* and Caballero y Caballero and Grocott, (1960) considered *U. aelleni* Baer, 1957, parasitic in *Pipistrellus nanus* Cote D'Ivoire as synonymous with *U. scabridum*. Inasmuch as body shape, a more posterior position of the ovary from the acetabulum, lobed testes, and vitellaria that begin posterior to the acetabulum are all specific characters, it is doubtful that *Urotrematulum* is distinct. It is more reasonable to consider this species as *Urotrema attenuatum* (Macy, 1933) Caballero y Caballero, 1942, and distinct from *U. scabridum*.

Class CESTODA

Family Anoplocephalidae

Oochoristica immatura Arandas Rego, 1963

Type host.—Glossophaga soricina.
*Site of infection.—*Small intestine.
*Type locality.—*Brazil.
Remarks.—Oochoristica immatura was assigned originally to the genus *Mathevotaenia* by Arandas Rego (1963). However, Della Santa's (1956) synonomy of this genus with *Oochoristica* appears valid (see Flores-Barreota *et al.*, 1958, and Prudhoe and Manger, 1969).

Other species of *Oochoristica* in bats include *O. antrozoi* Voge, 1954, from *Antrozous pallidus* in the United States, *O. nyctophili* Hickman, 1954, from *Nyctophilus geoffroyi* in Tasmania, and *O. kerivoulae* Prudhoe and Manger, 1969, from *Kerivoula* sp. and *Tylonycteris* sp. from Malaya.

Family Hymenolepididae

Vampirolepis elongatus Arandas Rego, 1962

Type hosts and localities.—Glossophaga soricina, Rio de Janeiro, state of Guanabara; *Phyllostomus hastatus,* Conceição da Barra, state of Expírito Santo; *Mollossus ater,* Tingua e São Goncalo, state of Rio de Janeiro, Brazil.
*Site of infection.—*Small intestine.
Other records.—Glossophaga soricina: MEXICO: Chiapas, Ruinas de Palenque, 300 m. (KU 102308); NICARAGUA: 3 km. N Sabana Grande, 50 m. (KU 97589); Daraili, 5 km. N, 14 km. E Condega, 940 m. (KU 97533).

Specimens of *Artibeus lituratus* from Cali, Colombia (collected by M. E. Thomas) contained several cestodes of this species. The specimens differ slightly in some measurements and at the present time they are provisionally considered as *Vampirolepis elongatus.* Specimens from this latter collection have been deposited in the United States National Museum Helminthological Collections, Beltsville, Maryland.

Remarks.—Vampirolepis elongatus belongs to the subfamily Hymenolepidinae Perrier, 1897, and represents one of 27 species in the subfamily recorded from bats. Five species of *Vampirolepis* are known from the Western Hemisphere: *V. chiropterophila* Perez-Vigueras, 1941, in *Molossus tropidorhynchus* from Cuba; *V. decipiens* (Diesing, 1850) in *Pteronotus rubiginosa,* and *Eumops perotis* from Brazil; *V. chistensoni* (Macy, 1931) in *Myotis lucifugus* and other bats in North America; *V. gertschi* (Macy, 1947) in *Myotis californicus* from North America and *V. roudabushi* (Macy and Rausch, 1946) in various bats in North America. An excellent review of host records of *Vampirolepis* spp. from North American bats is available (Webster, 1973).

Vampirolepis elongatus is most closely related to *V. chiropterophila* but differs principally in measurements of the rostellum and eggs. *Vampirolepis elongatus* is potentially dangerous to its hosts for the rostellum interrupts the integrity of the intestinal epithelium and may produce ulcerous conditions in infected animals.

FIG. 2.—Scanning electron photomicrograph of posterior proglottids of the strobila of *Vampirolepis elongatus* from the small intestine of *Glossophaga soricina* collected in Nicaragua. Note the decreasing dimensions of the proglottids and the opening of the excretory system (at arrow). (×700)

The surface of *Vampirolepis elongatus* is clearly similar to other hymenolepidiid cestodes in that it is cellular and covered with a dense microvillar surface that presumably aids in the absorption of available nutrients from the host (see Ubelaker *et al.*, 1973). Examination of the strobila by scanning electron microscopy reveals that even the terminal proglottids (filled with eggs) are covered by a dense absorptive surface (Fig. 2). As groups of proglottids become gravid, they detach and are passed out with the feces. Although intermediate hosts

of other hymenolepidiid cestodes involve various insects, the life cycles of all *Vampirolepis* are unknown. Kochseder (1969) suggested that *Hymenolepis grisea* (van Beneden, 1873) had a higher incidence in younger animals (*Myotis myotis, M. emarginatus, Rhinolophus ferrumequinum,* and *Barbastella barbastellus*) than older ones.

Phylum NEMATODA

Family Dipetalonematidae

Litomosoides artibei Esslinger, 1973

Type host.—*Artibeus cinereus.*
Site of infection.—Thoracic or abdominal cavity.
Type locality.—Vicinity of Buena Ventura, Valle, Colombia.

Litomosoides brasiliensis Lins de Almeida, 1936

Type host.—*Myotis* sp.
Site of infection.—Thoracic or abdominal cavity.
Type locality.—Brazil.
Synonymy.—Esslinger (1973) synonymized the following species with *L. brasiliensis: L. carolliae* Caballero y Caballero, 1944, and *L. caballeroi* Garcia-Rodrigo, 1954.
Other records.—The following are those listed by Esslinger, 1973: *Carollia perspicillata* in Brazil (Sandground, 1934), México and Panamá (Caballero y Caballero, 1944), Costa Rica (Jimenez-Quiros and Arroyo, 1960), Venezuela (Garcia-Rodrigo, 1959; Diaz-Ungria, 1963), and Colombia (Esslinger, 1973); "*Carollia subflavus*" in Colombia (Martin, 1969, personal communication); *Glossophaga* sp. in Brazil (Arandas Rego, 1961*a*); *Glossophaga soricina* in Brazil (Arandas Rego, 1961*a*); *Phyllostomus* sp. in Venezuela (Diaz-Ungria, 1963); and an unidentified phyllostomatid bat in Brazil (Arandas Rego, 1961*a*).
Remarks.—*Filaria spiculatum* was poorly described from specimens of "*Phyllostoma*" sp., *Carollia perspicillata,* and *Sturnira lilium* in Brazil (Molin, 1858). Although positive identification cannot be determined until the original specimens are reexamined, they are probably *Litomosoides brasiliensis.*

Litomosoides caliensis Esslinger, 1973

Type host.—*Sturnira lilium.*
Site of infection.—Unknown, microfilariae in blood.
Type locality.—Vicinity of Cali, Valle, Colombia.
Other records.—None to date.

Litomosoides chandleri Esslinger, 1973

Type host.—*Artibeus jamaicensis.*
Site of infection.—Thoracic or abdominal cavity.
Type locality.—Vicinity of Buena Ventura, Valle, Colombia.
Other records.—Vicinity of Cali, Valle, Colombia (Esslinger, 1973).

Litomosoides colombiensis Esslinger, 1973

Type host.—*Vampyrops dorsalis.*
Site of infection.—Unknown.
Type locality.—Vicinity of Buena Ventura, Valle, Colombia.
Other records.—*Artibeus jamaicensis* in the vicinity of the type locality also were found to be infected (Esslinger, 1973).

Litomosoides fosteri Caballero y Caballero, 1947

Type host.—*Glossophaga soricina.*
Site of infection.—Thoracic or abdominal cavity.
Type locality.—Panamá.
Other records.—None to date.

Litomosoides guiterasi (Perez-Vigueras, 1934)

Type host.—*Artibeus jamaicensis.*
Site of infection.—Body cavity.
Type locality.—Santa Clara and La Havana, Cuba.
Synonymy.—Esslinger (1973) listed the following synonymies: *Finlaynema guiterasi* Perez-Vigueras, 1934; *L. hamletti* Sandground, 1934; and *L. penai* Jimenez-Quiros and Arroyo, 1960.
Other records.—*Glossophaga soricina* in Brazil (Sandground, 1934), in México (Chitwood, 1938) and in Colombia (Esslinger, 1973); *Glossophaga* sp. in Brazil (Arandas Rego, 1961b); *Tadarida laticaudata* and *T. brasiliensis muscula* in Cuba (Baruš and del Valle, 1967); and *Pteronotus parnelli* in Jamaica (Webster, 1971). We recovered a single specimen of this species in *Glossophaga soricina* (KU 102354) from Las Margaritas, 1500 m., Chiapas, México (DLK 358, 23 July 1965).

Litomosoides leonilavazquezae Caballero y Caballero, 1939

Type host.—*Macrotus waterhousii.*
Site of infection.—Body cavity.
Type locality.—México.

Litomosoides teshi Esslinger, 1973

Type host.—*Carollia perspicillata.*
Site of infection.—Thoracic or abdominal cavity.
Type locality.—Vicinity of Buga, Valle, Colombia.
Remarks.—Filariid nematodes of the genus *Litomosoides* are common in leaf-nosed bats; of the 12 recognized species within this genus (Esslinger, 1973), nine are reported from phyllostomatids and the existing records seem to indicate that these parasites are relatively stenoxenous. Of the 10 species found in bats, seven are recorded from a single host species and another, *Litomosoides colombiensis*, is recorded from only two host genera, *Artibeus* and *Vampyrops*. Only two species, *Litomosoides brasiliensis* and *L. guiterasi*, have been recorded from

more than one family of bats. Although these adult filariids tend to be relatively host specific, a given bat may serve as the definitive host for several members of this genus, for example, *Artibeus jamaicensis* has been found to host *Litomosoides chandleri*, *L. colombiensis*, *L. guiterasi*, and *Litomosoides* sp. of Chitwood (1938).

The adult parasites occur in the body cavity of bats. Mature females give birth ovoviviparously to microfilariae, which migrate to the circulatory system and are picked up from the peripheral blood by mites that serve as the vector.

Unidentified microfilariae have been reported from numerous bats including *Carollia castanea*, *C. perspicillata*, *Glossophaga soricina*, *Phyllostomus* sp., and *P. hastatus*. Such microfilariae probably represent members of the genus *Litomosoides*, but no author prior to Esslinger (1973) has attempted to identify these nematodes on the basis of larval structures alone.

Family Trichostrongylidae

Biacantha desmoda Wolfgang, 1954

Type host.—*Desmodus rotundus.*
Site of infection.—Small intestine.
Type locality.—Trinidad, West Indies.
Other records.—We found this species in several *Desmodus rotundus* at La Pacifica, Costa Rica (DWD 166-LP-8, 168-LP-12, 169-LP-13, 170-LP-14, 176-LP-6, 12 July 1967), and it has also been reported from *D. rotundus* from Jalpa, Zacatecas, and San Bals, México (Wolfgang, 1956).

Remarks.—Specimens of this species are identified easily by the two asymmetrically placed cephalic hooks (Fig. 3) and a series of longitudinal ridges that extend the entire length of the body (Fig. 4).

Bidigiticauda vivipara Chitwood, 1938

Type host.—*Artibeus jamaicensis.*
Type locality.—Puz Cave, Oxkutzcab, Yucatán, México.
Site of infection.—Small intestine.
Other records.—*Artibeus jamaicensis:* COSTA RICA: La Pacifica (DWD 162-LP-48, 12 July 1967) and the Osa Peninsula (DWD 253-OP-42, 28 July 1967); MEXICO: (KU 102469) Chiapas, Finca San Salvador, 17 km. SE San Clemente, 1000 m. (JDS no. 927, 4 August 1965); NICARAGUA: (KU 9779) 2 km. N Sabana Grande, 50 m. (JKJ no. 4559, 15 July 1964); (KU 97726) San Antonio, 15 m. (JKJ, 6 July 1964); (KU 97773) 14 km. S Boaco, 200 m. (JKJ no. 4569); (KU 97804) 11 km. S, 3 km. E Rivas, 50 m. (TEL, 24 July 1964); (KU 97785) Moyogalpa, NW end Isla de Ometepe, 40 m. (JDS, 31 July 1964); (KU 977130) Finca Tepeyac, 10.5 km. N, 9 km. E Matagalpa, 960 m. (TEL no. 591, 7 August 1964).

Artibeus lituratus: MÉXICO: (KU 1025329) Chiapas, Ruinas de Palenque, 300 m. (JDS no. 721, 17 June 1965); (KU 192469) Chiapas, 4 km. NE Pichucalco, 100 m. (DLK no. 254, 30 June 1965).

Remarks.—The characteristic posterior extremity of this species is presented in Fig. 5, but the functional significance of the divided appendages is unknown.

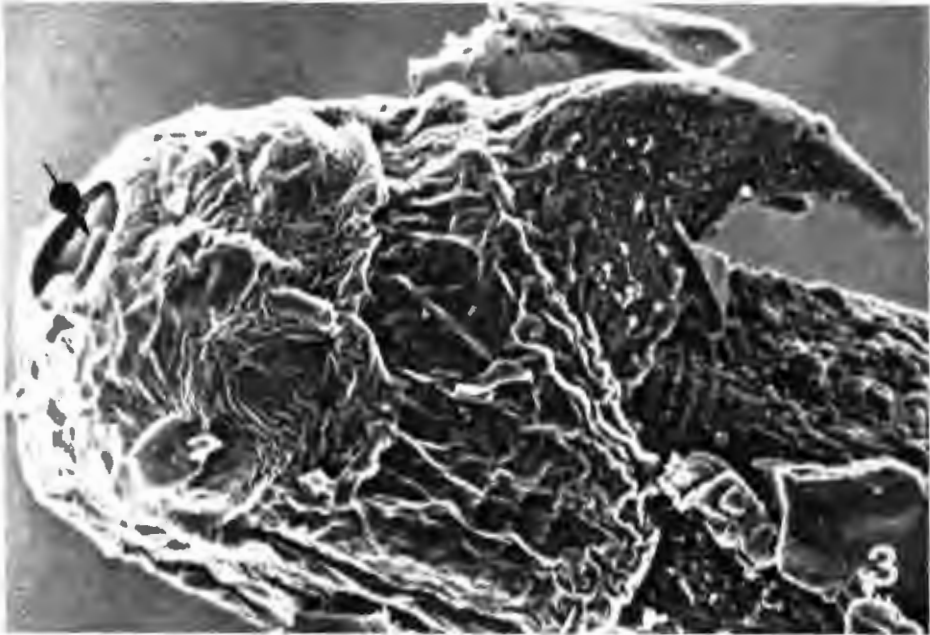FIG. 3.—Scanning electron photomicrograph of anterior end of *Biacantha desmoda* from small intestine of *Desmodus rotundus* collected at La Pacifica, Costa Rica. The irregular surface is an artifact resulting from alcohol fixation. Note platelike teeth in vestibule (arrow). (×765)

FIG. 4.—Scanning electron photomicrograph of body surface of *Biacantha desmoda*. Ridges (arrow) are raised above the general body surface. (×1175)
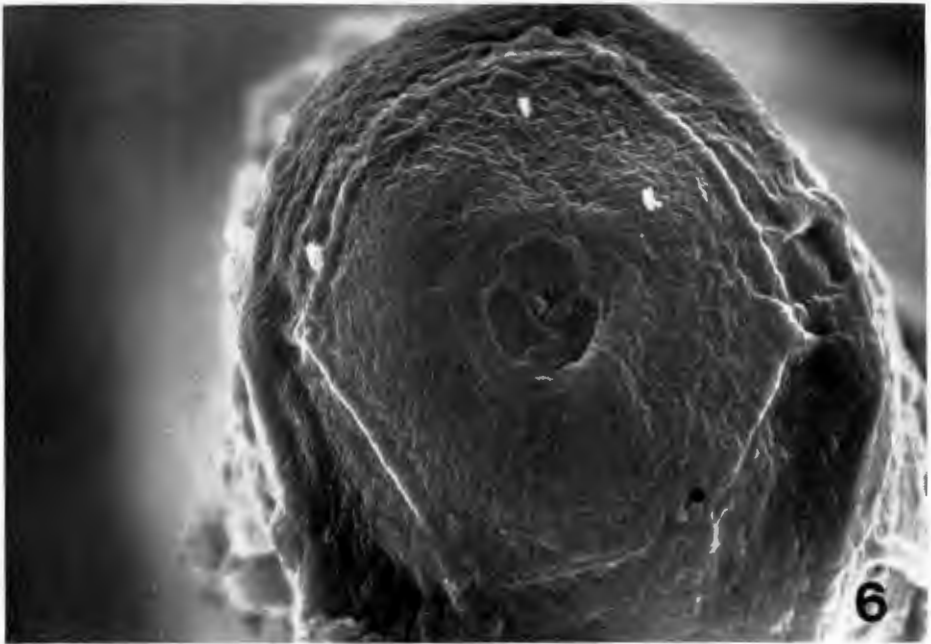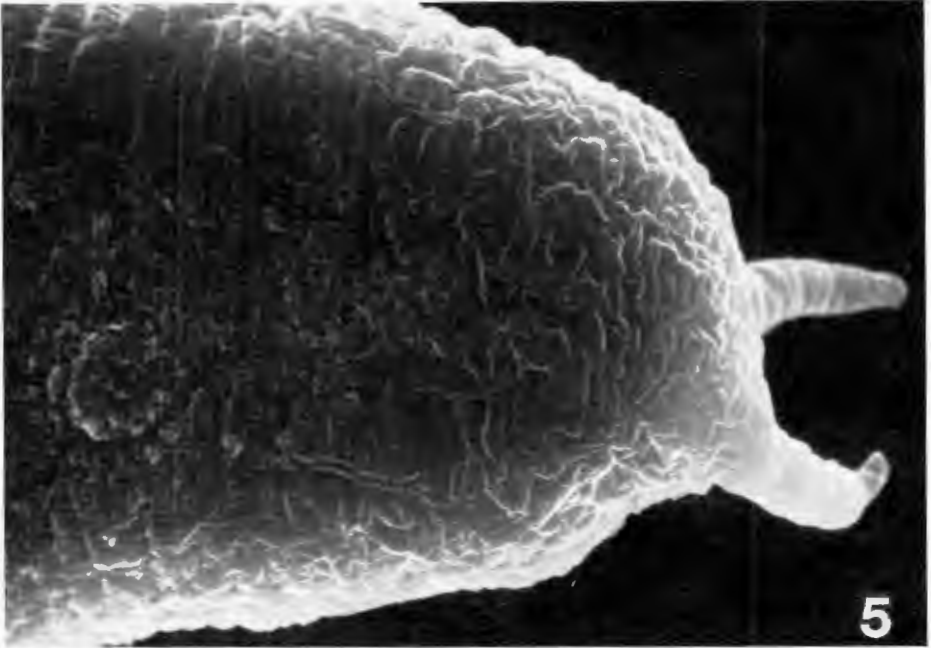
FIG. 5.—Scanning electron photomicrograph of posterior end of body of *Bidigiticauda vivipara.* (×675)

FIG. 6.—Scanning electron photomicrograph of head of *Bidigiticauda vivipara*. Papillae (arrow) and teeth in vestibule (clear arrow) are evident. (×2840)
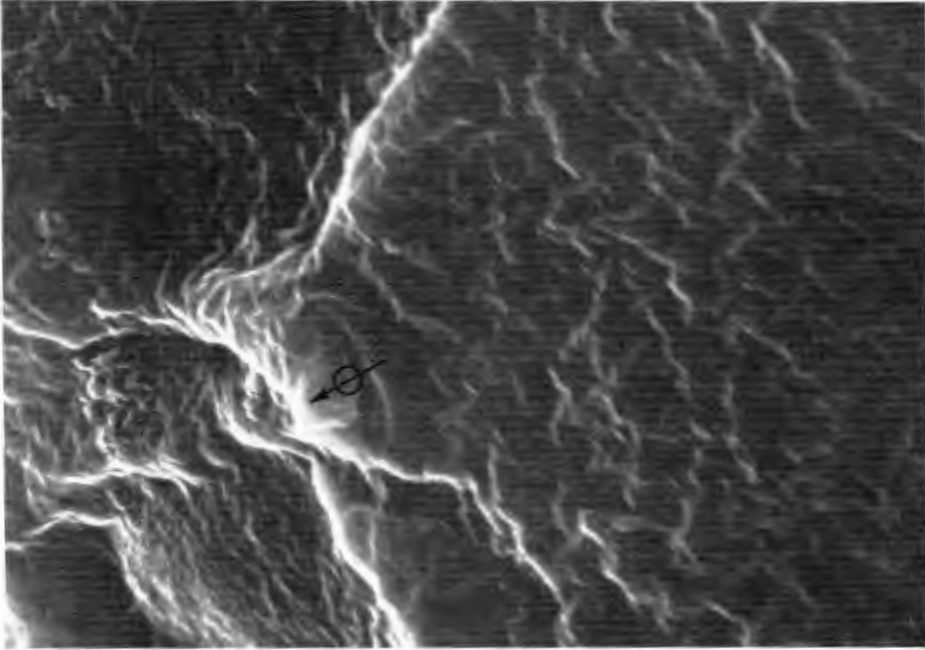
Fig. 7.—Scanning electron photomicrograph of cephalic papillae of *Bidigiticauda vivipara*. Papillae (at arrow) are raised above the cuticle. (×3600)

The cephalic characters, including the six cephalic papillae and the teeth in the vestibule, are also shown (Figs. 6, 7).

Cheiropteronema globocephala Sandground, 1929

Type host.—*Artibeus jamaicensis.*
Site of infection.—Stomach.
Type locality.—Yucatán, México.
Other records.—*Artibeus jamaicensis:* Costa Rica: Osa Peninsula, Costa Rica (DWD 253-OP-42, 28 July 1967); Mexico: Ebizt Cave, Oxkutzcab Yucatán (Chitwood, 1938); (KU 1024620) Chiapas, 12 km. W (Sabana de) San Quintin, 274 m. (JDS no. 849, 14 July 1965); (KU 102471) Chiapas, Finca San Salvador, 14 km. SE San Clemente, 1000 m. (JDS no. 979, 4 August 1965); Nicaragua: (KU 97700) 2 km. N Sabana Grande, 50 m. (TEL no. 488, 15 July 1964); (KU 97730) San Antonio, 15 m. (TEL no. 435, 6 July 1964); (KU 97718) Hacienda San Isidro, 10 km. S Chinandega, 10 m. (JDS no. 482, 11 July 1964); (KU 97772) 14 km. S Boaco, 220 m. (CER no. 19, 18 July 1964).

Artibeus lituratus: Mexico: (KU 1025310) Chiapas, Ruinas de Palenque, 300 m. (DLKJ no. 396, 17 June 1965); (KU1025690) Chiapas, 4 km. NE Pichucalco, 100 m. (JDS no. 783, 2 July 1965); Nicaragua: (KU 97816) Daraili, 5 km. N, 14 km. E Condega, 940 m. (TEL no. 361, 24 June 1964).

Artibeus phaeotis: COSTA RICA: Osa Peninsula (DWD 268-OP-48, 28 July 1967); MEXICO: (KU 102591) Chiapas, Ruinos de Palenque, 300 m. (JDS no. 740, 29 June 1965); NICARAGUA: (KU 97830) 11 km. S, 3 km. E Rivas, 50 m. (JKJ no. 457, 24 July 1964); (KU 97828) San Antonio, 15 m. (JKJ no. 4616, 7 July 1964).

Artibeus toltecus: MEXICO: (KU 102583) Chiapas, Finca San Salvador, 14 km. SE San Clemente, 1000 m (JDS no. 970, 7 August 1965).

Carollia perspicillata: COSTA RICA: Osa Peninsula (DWD 239-OP-01, 27 July 1967): NICARAGUA: (KU 976410) 6 km. E Moyagalpa, NW end Isla de Omotepe, 400 m. (TEL no. 612, 11 August 1964).

Remarks.—The original report of Chitwood (1938) is the only published record of this parasite. The records cited above represent new hosts and distributional records. There is no information on the biology or pathology of this species. The specimens found in *Artibeus jamaicensis* from Costa Rica (DWD 253-OP-42) were examined by scanning electron microscopy to confirm some aspects of the original description (Figs. 8, 9).

Glyptostrongylus collaris nomen nudum

Type host.—*Macrotus californicus.*
Site of infection.—Small intestine.
Type locality.—Southern California.
Remarks.—This parasite is listed by Voge (1956) as in the process of being described by Neiland. We can find no other published record.

Histiostrongylus coronatus Molin, 1861

Type host.—*Phyllostomus discolor.*
Site of infection.—Small intestine.
Type locality.—Mato Grosso region, Brazil.
Other reports.—*Phyllostomus discolor*: MEXICO: (KU 102293) Chiapas, Finca San Salvador, 15 km. SE San Clemente, 1000 m. (JDS 934, 5 August 1965); NICARAGUA: (KU 97478) 3 km. N Sabana Grande, 50 m. (TEL no. 346, 21 June 1964); (KU 97425) Hacienda San Isidoro, 10 km. S Chinandega, 10 m. (TEL no. 466, 11 July 1964); (KU 97463) 14 km. S Boaco, 220 m. (LMH no. 2575, 18 July 1964); (KU 97484) 11 km. S, 3 km. E Rivas, 50 m. (TEL, 24 July 1964).

Phyllostomus hastatus: NICARAGUA: (KU 97478) 3 km. N Sabana Grande, 50 m. (TEL no. 346, 21 June 1964); (KU 97416) Daraili, 5 km. N. 14 km. E Condega, 940 m. (JKJ no. 4463).

Phyllonycteris poeyi: CUBA: Jamaica, near Habana (Perez-Vigueras, 1941a); the cave of William Palmer, Guanajay, Pinar del Río (Baruš and del Valle, 1967).

This species also was reported from the stomach and small intestine of *Pteronotus fuliginosa torrei* taken at San José del Lago, Mayaijigua, Las Villas Province, Cuba (Baruš and del Valle, 1967).

Histiostrongylus octacantha Lent and Freitas, 1940
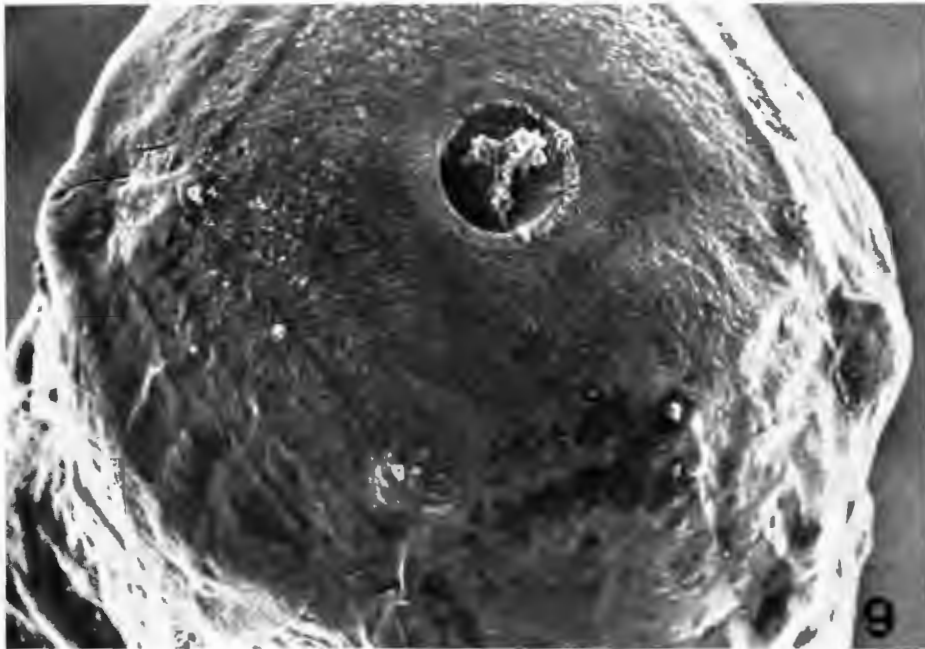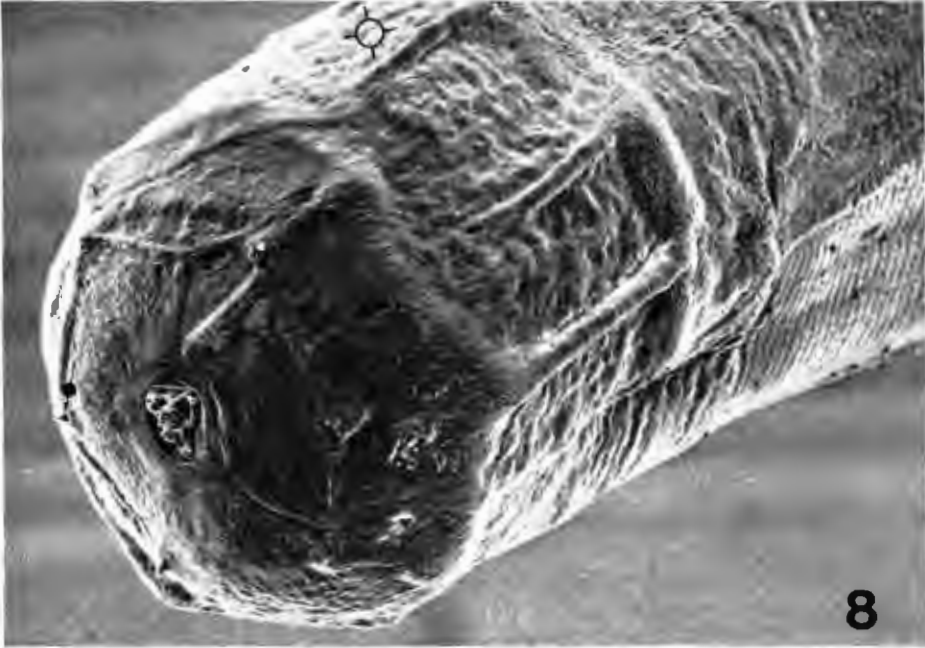
Type host.—*Phyllostomus hastatus.*

FIG. 8.—Scanning electron photomicrograph of *Cheiropteronema globocephala* from *Artibeus lituratus* from Nicaragua. Cephalic collar (clear circle) is collapsed. Lateral papillae (arrow) are prominent. (×2890)

FIG. 9.—Scanning electron photomicrograph of *Cheiropteronema globocephala*. Higher magnification of head showing mouth opening. (×2940)

Site of infection.—Small intestine.

Type locality.—Fazenda Bento, state of Rio de Janeiro and Campo Grande, Mato Grosso, Brazil.

Other records.—*Phyllostomus hastatus*: NICARAGUA: (KU 97418) Daraili, 5 km. N, 14 km. E Condega, 940 m. (TEL no. 396, 25 June 1964); (KU 97416) same location (JKJ no. 4463, 23 June 1964).

Artibeus jamaicensis: NICARAGUA: (KU 97800) 11 km. S, 3 km. E Rivas, 50 m. (CER no. 41, 24 July 1964).

Remarks.—Based primarily on the shape of the spicules, Perez-Vigueras (1941*a*) renamed *H. octacantha* as the type of a genus, *Parahistiostrongylus*. Yamaguti (1961) and Baruš and Rysavy (1971) did not accept the new genus based on spicule characteristics, and we consider it as a member of the genus *Histiostrongylus*.

Records obtained from the Index Catalogue of Medical and Veterinary Zoology at Beltsville, Maryland included a report of *H. paradoxus* Travassos, 1918, from *P. spiculatum* as referenced by Travassos, 1920. We have not verified this report.

Torrestrongylus torrei Perez-Vigueras

Type host.—*Macrotus waterhousii.*
Site of infection.—Small intestine.
Type locality.—Cueva del Rincon de Guanabo, Habana Province, Cuba.
Other records.—This species has also been reported by Baruš and del Valle (1967) in *Pteronotus macleayii* from Caba San José del Lago, Mayaijign, Las Villas Provence, Cuba.

Tricholeiperia leiperi Travassos, 1937

Type host.—*Trachops cirrhosus.*
Site of infection.—Small intestine.
Type locality.—Brazil.
Other reports.—Caballero y Caballero (1951) also reported this species in *T. cirrhosus* from México (in Index Catalogue, USDA, Beltsville, Maryland, not verified).

Unidentified strongylid nematodes

Host.—*Glossophaga soricina.*
Site of infection.—In embryo.
Type locality.—Arapuá in eastern Mato Grosso, Brazil.
Remarks.—Hamlett (1934) identified these nematodes only as being hookworms. These specimens undoubtedly belong to the family Trichostrongylidae, but without a reexamination of Hamlett's specimens, no further conclusions can be made.

Family Trichuridae

Capillaria sp.

Type host.—*Micronycteris megalotis.*
Site of infection.—Small intestine.
Type locality.—Yucatán, México.

Capillaria cubana Teixera de Freitas and Lent, 1937

Type host.—*Artibeus jamaicensis.*
Site of infection.—Stomach.
Type locality.—Santa Clara, Habana, Cuba.
Other reports.—Baruš and del Valle (1967) reported this species in *Molossus major tropidorhynchus* collected at Santiago, Cuba.

Capillaria phyllonycteris Baruš and del Valle, 1967

Type host.—*Phyllonycteris poeyi.*
Site of infection.—Intestine.
Type locality.—The cave of William Palmer, Guanajay, Cuba.

Capillaria pintoi Teixera de Freitas, 1934

Type host.—Unidentified bat.
Site of infection.—Intestine.
Type locality.—Brazil.
Other records.—This species may occur in phyllostomatid bats.

Capillaria pusilla Travassos, 1914

Type host.—*Sturnira lilium.*
Site of infection.—Intestine.
Type locality.—Manguinhos, Rio de Janeiro, Brazil.
Other records.—None to date, but Teixera de Freitas (1934) redescribed the species based on the type specimens from the Institute of Oswaldo Cruz, Brazil.

Capillaria viguerasi Teixera de Freitas and Lent, 1937

Type host.—*Macrotus waterhousii.*
Site of infection.—Small intestine.
Type locality.—Rincón de Guanabo, Cuba.
Other records.—None to date.
Remarks.—The capillariid complex is difficult to assess. Descriptions are frequently based on few specimens. Until more information is available on species variation, the above species in bats are considered valid.

DISCUSSION

The early studies of von Ihering (1891) on the specificity of a parasitic species, or complex of related species, in a particular taxa of hosts has suggested to many authors that parasites can possibly indicate phylogenetic relationships and geographic distribution of hosts. As much as concepts are often based only on collection records, the use of parasites as evolutionary tags should be used with appropriate caution. In this context the comments of Mayr (1957) are timely: "We are dealing here with something very basic, with the whole principle of phylogeny, with the principle of this study of parallel phylogeny, and we must be awfully sure of these tools we use, that we do not misuse them, and we must, at all times, allow for an occasional transfer of parasites, and we must allow for different rates of evolution, and we must realize that the comparative anatomy is something more reliable. Two kinds can exchange their parasites, nothing prevents this, but I have not yet seen two kinds exchanging their heads, their wings or their legs. These have come down from its ancestors and not from another kind that nested in a hole right next to it!"

In bats, ectoparasitic arthropods have received the greatest attention in examining phylogenetic information based on host-parasite relationships. In the phyllostomatid bats under consideration here, ecological factors are of paramount concern, especially when two or more host species come into close physical proximity either in roosting together or in occupying the same site at different times of the year (Wenzel and Tipton, 1966).

Among ectoparasitic arthropods, the wing mites of the family Spinturnicidae (Acarina, Mesostigmata) have attracted the most attention because most members show modified life cycles with reduced nymphal stages and the development of ovoviviparity (Baer, 1951; Rudnick, 1960). Although much has been written on this complex of mites, the works of Machado-Allison (1965, 1967), Radovsky (1967), and Dusbabek (1967, 1969a, 1969b) are important references concerning the parallel course of evolution of bats and their ectoparasites (also see Webb and Loomis, this volume).

Bat flies of the family Streblidae are reported to suggest interesting relationships, but these ectoparasites are not as host specific as are the spinturnicids (Wenzel et al., 1966).

Although Metcalf (1929) was among the earliest to point out the aid of protozoan parasites in problems of taxonomy, geographical distribution, and paleogeography of host species, protozoa have been studied little in bats. In particular, some species of *Eimeria* are so markedly host specific that Doran (1953) demonstrated that *E. mohavensis* was restricted to the kangaroo rat, *Dipodomys panamintinus,* but not found in *D. merriami* even though both rats occupied the same geographical area and presumably have similar feeding habits. Inasmuch as collections of coccidians are so easy to obtain under field conditions (oocysts are found in fecal material), it is surprising that only three species are recorded from bats in the Western Hemisphere.

The haemoflagellates of bats have been rather extensively investigated, though, perhaps, they are still not well understood. The study of blood sporozoans (for

example, malarial parasites) of phyllostomatids, however, is an area about which virtually nothing is known. Again, such organisms are also easy to obtain under field conditions.

Only a single adult acanthocephalan is recorded from phyllostomatid bats. Inasmuch as that parasite is known only from the original report, it is difficult to determine any degree of host specificity. The genus *Neoncicola* possesses species widely distributed in carnivores. Baruš (1973) reported an acanthella of *Pachisentis* sp. in the body cavity of *Taphozous nudiventris* and an acanthella of *Moniliformis* sp. in the body cavity of *Otonycteris hemprichi* from Egypt. Baruš suggested that bats exhibit reservoir parasitism of an active accumulating type. Whether or not this is true for acanthocephala cannot be ascertained until additional reports are available.

The remarks concerning the acanthocephala are also generally true for the pentastomids. If the few available reports are indicative, reservoir parasitism is involved here also.

The potential value of trematodes as indicators of host phylogeny or zoogeography has been suggested by Szidat (1955, 1956a, 1956b) and effectively demonstrated in some hosts by Kabata (1963), Margolis (1965), and a number of other workers (see reviews by Kabata, 1963, and Cameron, 1964). Although trematodes are reasonably common in phyllostomatid bats, they generally lack specificity in these hosts.

The genus *Anenterotrema* seems to be mainly associated with the leaf-nosed bats with some members occurring in the Molossidae. There are no life cycles available for any trematode species in phyllostomatid bats. Until studies involving allometric growth (Martin, 1969) and individual variation are made and additional distribution records are available, this parasitic fauna will be of little use in examining host phylogeny. Because the various members of *Anenterotrema* lack a digestive tract, the establishment of this parasite as a laboratory model would allow important advances in the biology of trematodes, especially in nutrition.

Only a single species of cestode, *Vampirolepis elongatus* is of interest in light of this discussion, for it appears to be restricted to the Phyllostomatidae except for a single report in *Molossus ater*. The numerous records from Brazil, Nicaragua, Colombia, and southern México, suggest this organism is the major tapeworm of leaf-nosed bats. Inasmuch as this organism is not rare in occurrence, studies on life cycle, pathology, and so forth may be feasible. In the only life cycle known of tapeworms in bats, Kochseder (1969) recovered cysticercoids within the intestinal mucosa suggesting auto-infection of *Hymenolepis grisea*, perhaps similar to that of *H. nana*.

Inglis (1965) examined patterns of evolution in nematodes. According to this author, generally, parasitic nematodes are not host specific but they tend to occur in animals with similar feeding and ecological habitats. Baruš and Rysavy (1971) evaluated morphological relationships, specificity, and geographical distribution of trichostrongylid nematodes in their respective bat hosts. Their results suggested to them that phylogenetical development of these parasites and hosts proceeded along parallel lines. Because more information is available concerning these nematodes they are reanalyzed here.

The first morphological group of nematodes listed by Baruš and Rysavy (1971) included the genera *Strongylacantha* and *Biacantha*; the former species occurring in Rhinolophidae, the latter species occurring in *Desmodus* and *Natalus*. We prefer to consider *Biacantha* as belonging to the second group for reasons presented below. Because of morphological features exhibited by *Strongylacantha*, this genus is the most primitive. Dougherty (1951) and Chaubaud (1965*a*, 1965*b*, 1965*c*, 1965*d*) present arguments that the trichostrongylids evolved from primitive strongylids and the placing of *Strongylacantha* in the Ancylostomatidae reflects this relationship. Both seem to have existed before the Paleocene (Patterson, 1957) and perhaps split as early as the Eocene. It is tempting to suggest that the origin of trichostrongylids of bats occurred in Eocene times in the Megachiroptera. Subsequently, and probably closely correlated with the origin and radiation of the Microchiroptera, these nematodes gave rise to the second group of nematodes described below.

The second group of nematodes according to Baruš and Rysavy (1971), included the genera *Spinostrongylus, Histiostrongylus, Neohistiostrongylus*, and provisionally *Cheiropteronema*. This complex (excluding *Cheiropteronema*) is characterized principally in having a reduced cephalic vesicle, sclerotized spine-like hooks on the head, and a general conical tail, usually with spines.

The genus *Biacantha* is known only from the Neotropical region with *B. desmoda* recorded from *Desmodus rotundus* from México, Costa Rica, and Trinidad. A second species, *B. silvai*, is recorded from *Natalus lepidus* from Cuba.

The distribution of species of *Histiostrongylus* from *Phyllostomus, Phyllonycteris*, and *Pteronotus* argues that the latter and its relatives should be reexamined as possible members of the phyllostomatid complex of bats. The other genera in the second group, *Neohistiostrongylus* and *Spinostrongylus*, occur in Old World bat hosts.

The remaining genera of bat nematodes show little specificity. Although several species are recorded from only a single host species, additional records are badly needed before confidence can be placed on the degree of host specificity.

At present, it is impossible to make definitive conclusions on the evolution of any bat species by examining endoparasites. Such work shows promise, however, particularly in the nematodes where certain genera show relationships with the hosts: *Cheiropteronema* and *Bidigiticauda* with *Artibeus*; *Histiostrongylus* and *Torrestrongylus* with vespertilionids. Based on such relationships (however tenuous) Baruš and Rysavy (1971) speculated that the phyllostomatids served as a stem host group for development of the trichostrongylids of New World bats.

Phyllostomatid bats are similar to other groups of Chiroptera in serving as intermediate, reservoir, or definitive hosts. Their role as intermediate hosts is minimal. Although *Porocephalus crotali* functions as a larval parasite in *Phyllostomus discolor* and is later transmitted to the snake definitive host, it has not been reported in bats in the last 50 years.

According to the classification suggested by Odening (1968), bats in general are "eureservoir, stationary hosts." This classification would hold true for phyllostomatid bats also. Most endoparasites use phyllostomatid bats as definitive

hosts and not as transitory bioreceptor hosts as suggested for other groups of bats by Rysavy and Baruš (1965), Baruš and Tenora (1967), or Shults and Davtyan (1955). Additional collections should clarify these relationships.

SUMMARY

The endoparasites of phyllostomatid bats are reviewed for the first time. A historical review emphasizes the lack of systematic collections of parasites from this group of bats. The major parasitic groups reviewed include the Protozoa, Acanthocephala, Pentastomida, Trematoda, Cestoda, and Nematoda.

New host and distributional records are as follows (a single asterisk indicates that a parasite was known previously from a given host; double asterisks, known previously from a given locality): TREMATODA: *Limatulum aberrans* in *Phyllostomus discolor* from Nicaragua. CESTODA: *Vampirolepis elongatus* in *Glossophaga soricina* from Nicaragua and México, and in *Artibeus lituratus* from Colombia. NEMATODA: *Biacantha desmoda* in *Desmodus rotundus** from Costa Rica; *Bidigiticauda vivipara* in *Artibeus jamaicensis** from Costa Rica, Nicaragua, and México, and in *Artibeus lituratus* from México; *Cheiropteronema globocephala* in *Artibeus lituratus* from México** and Nicaragua, *Carollia perspicillata* from Costa Rica and Nicaragua, *Artibeus jamaicensis** from Nicaragua and Costa Rica, *Artibeus phaeotis* from Nicaragua, Costa Rica, and México, and in *A. toltecus* from México; *Histiostrongylus coronatus* in *Phyllostomus discolor* from México and Nicaragua, and in *Phyllostomus hastatus* from Nicaragua; *H. octacantha* in *Phyllostomus hastatus* and in *Artibeus jamaicensis* from Nicaragua; *Litomomosides brasiliensis* in *Carollia subflavus* from Colombia; *Litomosoides guiterias* in *Glossophaga soricina* from México.

Scanning electron photomicrographs are presented for *Vampyrolepis elongatus, Cheiropteronema globocephala, Biacantha desmoda, Bidigiticauda vivipara,* and *Porocephalus crotali. Porocephalus crotali* is reported from *Eptesicus fuscus* for the first time.

ADDENDUM

After the present review was submitted, several articles have been published, and others brought to our attention, which should be mentioned here. Marinkelle (1976) reviewed the biology of all bat trypanosomes and listed four subgenera, including 20 species, as occurring in these mammals. His first subgenus, *Megatrypanum*, included the large, broad forms listed in the *megadermae* group of this review (*T. pessoai, T. pifanoi*). He divided the smaller forms of the classical *vespertilionis* group into two subgenera, *Schizotrypanum* (*T. cruzi, T. cruzi*-like, *T. phyllostomae, T. vespertilionis*) and *Herpetosoma* (*T. lineatus*). His fourth subgenus, *Trypanozoon*, included *T. evansi.* He emphasized, as did we, that the forms in the subgenus *Schizotrypanum* are difficult to separate into defined species.

An excellent review of cestodes in the genus *Hymenolepis* from bats in North America and Hawaii was written by Rausch (1975). This paper critically evaluated the taxonomic status of the hymenolepiid cestodes and added a new

species, *H. lasionycteridis*, from eight species of bats in North America and Hawaii. Rausch (1975) also discussed briefly the zoogeography of cestodes of bats.

Chabaud and Bain (1974) described a new genus and species of muspiceid nematode, *Lukonema lukoschusi*, from *Noctilio labialis*, *Tonatia carrikeri*, *Carollia perspicillata*, *Desmodus rotundus*, *Saccopteryx leptura*, and *Eptesicus melanopterus* collected in Surinam and French Guyana. The biology, host-parasite relationship, and life-history of *L. lukoschusi* also are discussed in this paper.

Other papers that merit attention include those by Caballero-Deloya (1971), Durette-Desset and Chabaud (1975), and Chabaud and Durette-Desset (1975). The first paper redescribed *Bidigiticauda vivipara* collected from *Artibeus lituratus palmarum* in Guerrero, México. The latter two papers reviewed nematodes from European bats, analyzed the trichostrongylid nematode fauna of bats, proposed a hypothesis for the origin of these nematodes, and indicated a possible phyletic relationship between the Tupaiidae and the Chiroptera.

Teixera de Freitas and Machado de Mendonca (1960, 1963) assigned several species of nematodes from bats to the genus *Parallintoschius*, but Durette-Desset and Chabaud (1975) considered *Parallintoschius* to be synonymous with *Allintoschius*. We have not been able to locate the original papers of Teixera de Freitas and Machado de Mendonca (1960, 1963) for confirmation.

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APPENDIX 1.—*Parasite-host records. Species are arranged in alphabetical order, and experimental infections are indicated by an asterisk.*

PROTOZOA

Babesiidae
"piroplasma" (see Renjifo *et al.*, 1952)
Phyllostomus hastatus
Plasmodiidae
Polychromophilus deanei
Glossophaga soricina
Toxoplasmatidae
Toxoplasma gondii
Artibeus lituratus
Trypanosomatidae
Trypanosoma cruzi
Artibeus jamaicensis
Artibeus lituratus
Carollia perspicillata
Desmodus rotundus
Glossophaga soricina
Phyllostomus discolor
Phyllostomus hastatus
Uroderma bilobatum
Trypanosoma cruzi-like
Artibeus cinereus
Artibeus jamaicensis
Artibeus lituratus
Carollia perspicillata
Choeroniscus minor
Desmodus rotundus
Glossophaga soricina
Lonchophylla mordax
Lonchophylla thomasi
Micronycteris megalotis
Mimon bennettii
Phyllostomus discolor
Phyllostomus elongatus
Phyllostomus hastatus
Uroderma bilobatum
Vampyrum spectrum
Trypanosoma equinum
*Desmodus rotundus**
Trypanosoma evansi
*Artibeus jamaicensis**
*Carollia perspicillata**
Desmodus rotundus
*Desmodus rotundus**
*Glossophaga soricina**
*Phyllostomus hastatus**
Trypanosoma lineatus
Vampyrops lineatus
Trypanosoma pessoai
Artibeus cinereus

Artibeus jamaicensis
Carollia perspicillata
Choeroniscus minor
Desmodus rotundus
Trypanosoma phyllostomae
Carollia perspicillata
Trypanosoma pifanoi
Artibeus lituratus
Phyllostomus hastatus
Trypanosoma rangeli-like
Artibeus lituratus
Glossophaga soricina
Trypanosoma vespertilionis
Anoura caudifer
Carollia perspicillata
Choeroniscus minor
Glossophaga soricina
Macrotus waterhousii
Phyllostomus hastatus
Trypanosoma sp. (*megadermae*-type)
Anoura caudifer
Carollia perspicillata
Choeroniscus minor
Desmodus rotundus
Glossophaga soricina
Trypanosoma sp. (*verpertilionis*-type)
Carollia perspicillata
Lonchophylla mordax
Trypanosoma sp. (not *T. cruzi*-like)
Choeroniscus minor

ACANTHOCEPHALA

Oligacanthorhynchidae
Neoncicula novellae
Artibeus jamaicensis

PENTASTOMIDA

Porocephalidae
Porocephalus crotali
Phyllostomus discolor

TREMATODA

Anenterotrematidae
Anenterotrema auritum
Micronycteris megalotis
Anenterotrema eduradocaballeroi
Phyllostomus elongatus
Anenterotrema freitasi
Micronycteris hirsuta

APPENDIX 1.—*Continued.*

Anenterotrema lilipatianum
  Phyllostomus elongatus
Anenterotrema stunkardi
  Phyllostomus hastatus
Dicrocoeliidae
  Athesmia parkeri
    Artibeus jamaicensis
  Parametadelphis compactus
    Micronycteris behni
Lecithodendriidae
  Lecithodendrium pricei
    Artibeus jamaicensis
  Limatulum aberrans
    Macrotus waterhousii
    Phyllostomus discolor
  Limatulum isthmicus
    Micronycteris hirsuta
  Limatulum oklahomensis
    Macrotus waterhousii
Urotrematidae
  Urotrema scabridum
    Phyllostomus sp.
    Phyllostomus hastatus

CESTODA

Anoplocephalidae
  Oochoristica immatura
    Glossophaga soricina
Hymenolepididae
  Vampirolepis elongatus
    Artibeus lituratus
    Glossophaga soricina
    Phyllostomus hastatus

NEMATODA

Dipetalonematidae
  Litomosoides sp.
    Artibeus jamaicensis
    Glossophaga soricina
  Litomosoides artibei
    Artibeus cinereus
  Litomosoides brasiliensis
    Carollia perspicillata
    Carollia subflavus
    Glossophaga sp.
    Glossophaga soricina
    Phyllostomus sp.
  Litomosoides caliensis
    Sturnira lilium
  Litomosoides chandleri
    Artibeus jamaicensis

Litomosoides colombiensis
  Artibeus jamaicensis
  Vampyrops dorsalis
Litomosoides fosteri
  Glossophaga soricina
Litomosoides guiterasi
  Artibeus jamaicensis
  Glossophaga sp.
  Glossophaga soricina
Litomosoides leonilavazquezae
  Macrotus waterhousii
Litomosoides teshi
  Carollia perspicillata
Filaridae
  Filaria serpiculum
    Carollia perspicillata
    Phyllostomus sp.
    Sturnira lilium
Trichostrongylidae
  Biacantha desmoda
    Desmodus rotundus
  Bidigiticauda vivipara
    Artibeus jamaicensis
    Artibeus lituratus
  Cheiropteronema globocephala
    Artibeus jamaicensis
    Artibeus lituratus
    Artibeus phaeotis
    Artibeus toltecus
    Carollia perspicillata
  Glyptostrongylus collaris
    Macrotus californicus
  Histiostrongylus sp.
    Phyllostomus hastatus
  Histiostrongylus cornatus
    Phyllonycteris poeyi
    Phyllostomus discolor
    Phyllostomus hastatus
  Histiostrongylus octacantha
    Artibeus jamaicensis
    Phyllostomus hastatus
  Torrestrongylus torrei
    Macrotus waterhousii
  Tricholeiperia leiperi
    Trachops cirrhosus
  Unidentified strongylid nematodes
    Glossophaga soricina
Trichuridae
  Capillaria sp.
    Micronycteris megalotis
  Capillaria cubana
    Artibeus jamaicensis

APPENDIX 1.—*Continued.*

Capillaria phyllonycteris	*Capillaria pusilla*
Phyllonycteris poeyi	*Sturnira lilium*
Capillaria pintoi	*Capillaria viguerasi*
Unidentified bat	*Macrotus waterhousii*

[1] [Possibly a *lapsus calami* for *Carollia subrufa*. Eds.]

APPENDIX 2.—*Host-parasite list. Taxa are arranged in alphabetical order, and experimental infections are indicated by an asterisk.*

Anoura caudifer
  Protozoa
    Trypanosoma vespertilionis
    Trypanosoma sp. (*megadermae*-type)
Artibeus cinereus
  Nematoda
    Litomosoides artibei
  Protozoa
    Trypanosoma cruzi-like
    Trypanosoma pessoai
Artibeus jamaicensis
  Acanthocephala
    Neoncicula novellae
  Nematoda
    Bidigiticauda vivipara
    Capillaria cubana
    Cheiropteronema globocephala
    Histiostrongylus octacantha
    Litomosoides sp.
    Litomosoides chandleri
    Litomosoides colombiensis
    Litomosoides guiterasi
  Protozoa
    Trypanosoma cruzi
    Trypanosoma cruzi-like
    Trypanosoma pessoai
    Trypanosoma evansi
  Trematoda
    Athesmia parkeri
    Lecithodendrium pricei
Artibeus lituratus
  Cestoda
    Vampirolepis elongatus
  Nematoda
    Bidigiticauda vivipara
  Protozoa
    Toxoplasma gondii
    Trypanosoma cruzi
    Trypanosoma cruzi-like
    Trypanosoma pifanoi
    Trypanosoma rangeli-like
Artibeus phaeotis
  Nematoda
    Cheiropteronema globocephala
Artibeus toltecus
  Nematoda
    Cheiropteronema globocephala
Carollia perspicillata
  Nematoda
    Cheiropteronema globocephala
    Filaria serpiculum
    Litomosoides brasiliensis

    Litomosoides teshi
  Protozoa
    Trypanosoma cruzi
    *Trypanosoma cruzi**
    Trypanosoma cruzi-like
    Trypanosoma evansi
    Trypanosoma pessoai
    Trypanosoma phyllostomae
    Trypanosoma vespertilionis
    Trypanosoma sp. (*megadermae*-type)
    Trypanosoma sp. (*vespertilionis*-type)
"*Carollia subflavus*"[1]
  Nematoda
    Litomosoides brasiliensis
Choeroniscus minor
  Protozoa
    Trypanosoma cruzi-like
    Trypanosoma pessoai
    Trypanosoma vespertilionis
    Trypanosoma sp. (*megadermae*-type)
    Trypanosoma sp. (not *T. cruzi*-like)
Desmodus rotundus
  Nematoda
    Biacantha desmoda
  Protozoa
    Trypanosoma cruzi
    Trypanosoma cruzi-like
    Trypanosoma evansi
    *Trypanosoma evansi**
    *Trypanosoma equinum**
    Trypanosoma pessoai
    Trypanosoma sp. (*megadermae*-type)
Glossophaga sp.
  Nematoda
    Litomosoides brasiliensis
    Litomosoides guiterasi
Glossophaga soricina
  Cestoda
    Oochoristica immatura
    Vampirolepis elongatus
  Nematoda
    Litomosoides sp.
    Litomosoides brasiliensis
    Litomosoides fosteri
    Litomosoides guiterasi
  Protozoa
    Polychromophilus deanei
    Trypanosoma cruzi
    Trypanosoma cruzi-like
    Trypanosoma evansi
    Trypanosoma rangeli-like
    Trypanosoma sp. (*megadermae*-type)

APPENDIX 2.—*Continued.*

Trypanosoma vespertilionis
Lonchophylla mordax
  Protozoa
    Trypanosoma cruzi-like
    Trypanosoma sp. (*vespertilionis*-type)
Lonchophylla thomasi
  Protozoa
    Trypanosoma cruzi-like
Macrotus californicus
  Nematoda
    Glyptostrongylus collaris
Macrotus waterhousii
  Nematoda
    Capillaria viguerasi
    Litomosoides leonilavazguezae
    Torrestrongylus torrei
  Protozoa
    Trypanosoma vespertilionis
  Trematoda
    Limatulum aberrans
    Limatulum oklahomensis
Micronycteris behni
  Trematoda
    Parametadelphis compactus
Micronycteris megalotis
  Protozoa
    T. cruzi-like
  Nematoda
    Capillaria sp.
  Trematoda
    Anenterotrema auritum
Micronycteris hirsuta
  Trematoda
    Anenterotrema freitasi
    Limatulum isthmicus
Mimon bennettii
  Protozoa
    Trypanosoma cruzi-like
Phyllonycteris poeyi
  Nematoda
    Capillaria phyllonycteris
    Histiostrongylus cornatus
Phyllostomus sp.
  Nematoda
    Filaria serpiculum
    Litomosoides brasiliensis
  Trematoda
    Urotrema scabridum
Phyllostomus discolor
  Nematoda
    Histiostrongylus cornatus
  Pentastomida
    Porocephalus crotali

Protozoa
  Trypanosoma cruzi
  Trypanosoma cruzi-like
Trematoda
  Limatulum aberrans
Phyllostomus elongatus
  Protozoa
    Trypanosoma cruzi-like
  Trematoda
    Anenterotrema eduardocaballeroi
    Anenterotrema liliputianum
Phyllostomus hastatus
  Cestoda
    Vampirolepis elongatus
  Nematoda
    Histiostrongylus cornatus
    Histiostrongylus octacantha
    Histiostrongylus sp.
  Protozoa
    "piroplasma"
    Trypanosoma cruzi
    Trypanxoma cruzi-like
    *Trypanosoma evansi**
    Trypanosoma pifanoi
    Trypanosoma vespertilionis
  Trematoda
    Anenterotrema stunkardi
    Urotrema scabridum
Sturnira lilium
  Nematoda
    Capillaria pusilla
    Filaria serpiculum
    Litomosoides caliensis
Trachops cirrhosus
  Nematoda
    Tricholeiperia leiperi
"*Trachops elongatus*"
  Protozoa
    Trypanosoma sp. (*vespertilionis*-type)
Uroderma bilobatum
  Protozoa
    Trypanosoma cruzi
    Trypanosoma cruzi-like
Vampyrops dorsalis
  Nematoda
    Litomosoides colombiensis
Vampyrops lineatus
  Protozoa
    Trypanosoma lineatus
Vampyrum spectrum
  Protozoa
    Trypanosoma cruzi-like

[1] [Possibly a *lapsus calami* for *Carollia subrufa.* Eds.]

ECTOPARASITES

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Phyllostomatid bats harbor an assemblage of ectoparasites numbering more than 230 species that represent 15 families of acarines and two families of dipteran insects. Among all chiropteran families, only the vespertilionids, with 18 acarine and six insect families, have more parasites. Streblids account for the greatest number of species of any of the phyllostomatid-infesting groups, having 83, comprising 20 genera. The nycteribiids are represented by 13 species in the genus *Basilia*. The remainder consists of 150 species of mites and ticks presently recognized in 49 genera. We found no substantiated literature records of siphonapterans, anoplurans, cimicids, or polyctenids regularly associated with phyllostomatids, although fleas were listed as questionable parasites of Venezuelan phyllostomatids (Tipton and Machado-Allison, 1972), two species of *Hesperoctenes* (polyctenids) were mentioned (Hoffmann, 1972) from *Glossophaga* and *Artibeus* species, and *H. fumarius* (Westwood) was reported (Maa, 1961) from Venezuelan *Phyllostomus hastatus*. In addition, Gerberg and Goble (1941) recorded two species of mallophagan lice from leaf-nosed bats, including *Physconelloides* (near *galapogensis*) recovered from a Panamanian *Carollia perspicillata* and thought by the authors to represent a possible bird-bat association. *Geomydoecus geomydis*, which normally infest pocket gophers, was also mentioned from a Mexican *Leptonycteris nivalis*. Other insects, for example culicids, psychodids, and ceratopogonids, which may be associated with bats were not included in this review.

A comprehensive worldwide list of bats and their acarine parasites, including phyllostomatid-associated mites and ticks, was compiled by Anciaux de Faveaux (1971). Additional recent citations are listed under each family.

MACRONYSSIDAE Oudemans, 1936

Sixteen species of macronyssid mites comprising six genera have been described from phyllostomatid bats. *Radfordiella* Fonseca, *Parichoronyssus* Radovsky, *Macronyssoides* Radovsky, and *Chiroecetes* Herrin and Radovsky are in the *Macronyssus*- group and are considered by Radovsky (1967) and Herrin and Radovsky (1974) to be the more primitive and closely aligned with the laelapine stock, whereas the *Streatonyssus*- group has more highly specialized representatives. *Nycteronyssus desmodus* Saunders and Yunker (1973), based on a single female from a *Diaemus youngii*, was considered by its authors as possibly of another dermanyssoid family.

Radovsky (1967:59) suggested that the macronyssids evolved from progenitors that closely resembled extant laelapids because certain features are common to *Neolaelaps* Hirst and *Notolaelpas* Womersley in the Laelapinae and to *Bewsiella* Domrow, *Ichoronyssus* Kolenati, and *Parichoronyssus* in the Macronyssidae. This relationship between the laelapines and macronyssids seems to suggest a relatively recent association with bats.

Parasitic development by an invading organism on a new host is one of diversification. *Parichoronyssus* and the others of this group apparently are now in the early phases of this process. A number of the *Radfordiella* species have adapted, as depicted by the protonymphal stage, to a higher level of specialization. *Radfordiella monophylli*, *R. oricola*, and *R. anourae*, all described by Radovsky *et al.* (1971), are known only from protonymphs found in the soft palate tissue of several phyllostomatid species. Each of these species may cause dental and peridontal destruction in bats (Phillips, 1971; Phillips *et al.*, 1969; Radovsky *et al.*, 1971) and at least one bat, *Leptonycteris sanborni*, may have evolved certain tongue modifications that prohibit the establishment of mites in their mouths (Greenbaum and Phillips, 1974). In most other species, the protonymphs and adults feed on skin tissues or blood while situated in the fur, rarely on the naked wing or patagial membranes. When compared with species of either *Macronyssoides* or *Parichoronyssus*, the occupation of the intraoral niche by three species of *Radfordiella* suggests a longer affiliation with phyllostomatids. Blood feeding may occur in *Macronyssoides* (Radovsky, 1967: 12), possibly accounting for its large number of host species as seen in *M. kochi*. Once adapted to hematophagy, the procurement of new hosts seems less difficult than in the case of adaptation to dermal histophagy, which involves exposure to a greater variation in nutritional and other components.

Chiroecetes is represented by *C. lonchophylla* and is known from a single female specimen. Herrin and Radovsky (1974) included this species with subgroup C of the *Macronyssus*-group based on chaetological criteria. Other stages of the life cycle are unknown.

Although *Steatonyssus joaquimi* (Fonseca) has been recorded from *Glossophaga soricina*, it probably is more commonly found on vespertilionids as demonstrated by its occurrence on *Myotis albescens* from Paraguay (Radovsky, 1967) and numerous other records of *Steatonyssus* species from vespertilionids (Anciaux de Faveaux, 1971).

Bat macronyssids are probably in or near the bat roosts when not on the host. Mating, however, most likely occurs on the host. Only unembryonated eggs have been found (Radovsky, 1967:13) in most species of *Macronyssus*, *Macronyssoides*, and *Radfordiella*; however, Radovsky (1967) postulated that ovoviviparity may occur in some species of *Macronyssus*. Aside from morphological correlations and overlap of features of egg development, relationships may be drawn between hosts and geographic ranges of *Macronyssus* species and the phyllostomatid-parasitizing macronyssid genera. *Macronyssus* has a cosmopolitan distribution as do its primary vespertilionid hosts. One line probably provided the common origin of *Radfordiella*, *Chiroecetes*, *Parichoronyssus*, *Macronyssoides*, and *Macronyssus*. Evidence for the rise of these genera from a *Macronyssus*-like progenitor may be seen in the relationship found today between Old World species of *Macronyssus* and Old World vespertilionid, rhinolophid, and hipposiderid bats. *Macronyssus granulosus* (Kolenati), *M. longimanus* (Kolenati), *M. rhinolophi* (Oudemans), and *M. coreanus* (Ah) all are found on vespertilionids and on rhinolophids or hipposiderids, or both. In the New World, remnants of *Macronyssus*-vespertilionid associations may still be found in the numerous reports of *M.*

crosbyi (Ewing and Stover) on vespertilionids, especially species of *Myotis*. *Macronyssus jonesi* (White) is known from North American vespertilionids as is *M. unidens* Radovsky, which also has been recorded (Radovsky, 1967) from the phyllostomatid *Leptonycteris nivalis*.

Host specificity coupled with the adaptive strategies of certain macronyssids, for example, species of *Radfordiella.*, on phyllostomatids suggests a long host association and a New World origin, possibly on vespertilionids.

Spinturnicidae Oudemans, 1902

Sixteen species of wing mites in one genus, *Periglischrus* Benoit, presently are recognized as parasites of phyllostomatids and are numerous and widespread from México and the Antilles to Paraguay.

Cameronieta was established as morphologically distinct from *Periglischrus* by Machado-Allison (1965) and its apparent host specificity on species of *Pteronotus* and *Mormoops* prompted Machado-Allison (1967) to suggest separate familial status for the mormoopids. Later, Smith (1972) separated mormoopids from phyllostomatids on the basis of various morphological criteria and referred to Machado-Allison's (1967) statements about parasite-host relationships for additional support. An apparent parallel to the *Periglischrus-Cameronieta* divergence in the New World may be seen in two Old World genera. *Eyndhovenia* Rudnick (1960) monotypic with *E. euryalis* (Canestrini), is found principally on rhinolophids, whereas *Paraperiglischrus* Rudnick (1960) is known both from rhinolophids and hipposiderids.

Spinturnicids on both phyllostomatids and Old World rhinolophids and hipposiderids probably arose from a line common with that of *Spinturnix* Von Heyden. *Spinturnix* is nearly cosmopolitan, primarily on vespertilionids, especially species of *Myotis* and *Eptesicus*, genera common to both the Old and New World. Although not recorded from Neotropical leaf-nosed bats, at least two species of *Spinturnix* have been recorded from rhinolophids (Anciaux de Faveaux, 1971). An Old World origin for the spinturnicids seems to be suggested by the diversification of taxa and by the geographic and taxonomic ranges of their hosts. Dispersal of wing mites to the New World probably occurred on vespertilionids with subsequent infestation of phyllostomatids.

Additional information regarding the new taxa and parasite records from phyllostomatids may be found in Dusbabek, 1970; Dusbabek and Lukoschus, 1971*b*; Hoffmann *et al.*, 1972; Kingston *et al.*, 1971; Machado-Allison and Antequera, 1971; Tamsitt and Fox, 1970*b*; Whitaker and Easterla, 1975; and Whitaker and Wilson, 1974.

Spelaeorhynchidae Oudemans, 1902

Originally described as a tick, *Spelaeorhynchus praecursor* Neumann served shortly thereafter as the type genus for the family Spelaeorhynchidae. The original specimens have been searched for and are presumed lost (Fain *et al.*, 1967). Considered for some time to be closely related to ixodids, later workers (Baker

and Wharton, 1952; Fain *et al.*, 1967) have placed this group in the Mesostigmata. Two of the three known species are found only on phyllostomatids.

Spelaeorhynchus praecursor has been reported (Anciaux de Faveaux, 1971; Dusbabek, 1970; Hoffmann and de Barrera, 1970; Tamsitt and Fox, 1970*b*) from leaf-nosed species taken in Puerto Rico, Cuba, México, Dominican Republic, Colombia, and Venezuela. *Monophyllus redmani* from Puerto Rico (Tamsitt and Fox, 1970*b*; Tamsitt and Valdivieso, 1970) is the only known host for *S. monophylli* Fain *et al.* The species *S. chilonycteris* Fain *et al.* is based on a single female from *Pteronotus rubiginosus*, a mormoopid, taken in Guatemala (Fain *et al.*, 1967). Two female specimens of *Spelaeorhynchus* species *incertae sedis* also were mentioned by Fain *et al.*, (1967) from Brazilian *Carollia brevicauda*.

Both *S. praecursor* and *S. monophylli* have been removed from the lower portion of the ear, often from the tragus, and usually embedded deep in the skin.

Only female spelaeorhynchids have been collected although larvae have been dissected from gravid females. Fain *et al.* (1967) postulated that the males of these mites are free-living nidicoles, although parthenogenesis also may be a possibility.

The origin of Spelaeorhynchidae may be from the laelapoids and the highly specialized features that make it distinguishable from extant relatives are described as fixation to its hosts (Fain *et al.*, 1967). This restriction to the hosts may reflect an inability to adapt to new hosts and may account for the small numbers of spelaeorhynchids encountered today.

Ixodidae Murray, 1877

Two genera and two species of ixodid ticks have been reported from leaf-nosed bats in the New World.

Amblyomma longirostre (Koch) is known from a single nymphal record recovered from a Venezuelan *Artibeus lituratus* and also was listed (Jones *et al.*, 1972) from a number of prehensile-tailed porcupines and a squirrel, *Sciurus granatensis* from Venezuela. In addition, Cooley and Kohls (1944) reported *A. longirostre* (as *A. avecolens* Cooley and Kohls) as occurring on birds from Texas, Belize (formerly British Honduras), and Panamá.

A single larva of *Ixodes downsi* (Kohls, 1957) was listed from *Anoura geoffroyi* and a male, female, and three nymphs were found crawling on a cave wall in Trinidad. As mentioned further by Kohls, this larval tick represented the first bat record for the genus *Ixodes* from the New World, but it is unknown whether *I. downsi* regularly parasitizes bats. Jones *et al.* (1972) subsequently have recorded a number of cases of *Ixodes* species from *Artibeus jamaicensis* and two species of *Sturnira* from Venezuela.

Species of *Amblyomma* and *Ixodes* are generally not bat affiliates and the records from phyllostomatids probably represent accidental associations, although three species of *Ixodes* apparently are usual parasites of Old World leaf-nosed and vespertilionid species (Anciaux de Faveaux, 1971).

ARGASIDAE Canestrini, 1890

Nine species of *Ornithodoros* Koch and two species of *Antricola* Cooley and Kohls are the soft ticks presently known from phyllostomatid hosts. *Ornithodoros viguerasi* Cooley and Kohls has been placed in the subgenus *Subparmatus* Clifford, Kohls, and Sonenshine; six species belong to the subgenus *Alectorobius* Pocock; and two species, *O. mimon* Kohls, Clifford, and Jones (1969) and *O. peruvianus* Kohls, Clifford, and Jones are unassigned to subgenus. Only a single larva of *O. mimon* has been recovered from a phyllostomatid, *Mimon crenulatum* from Bolivia, whereas 38 specimens were removed from a number of Uruguayan *Eptesicus brasiliensis*. The larvae of *O. peruvianus* have been reported by Kohls *et al.* (1969) to resemble superficially *O. (Alectorobius) kellyi* Cooley and Kohls. The species *O. (A.) puertoricensis* Fox has been recovered from lizards, various mammals, including burrow dwellers, and a number of emballonurid, molossid, mormoopid, and noctilionid bats, and there is a questionable record (Jones *et al.*, 1972) from a Venezuelan *Artibeus lituratus*.

Looking at host-parasite relationships, indications are that the members of the subgenus *Alectorobius* may have arisen from a line closely related to the Old World *Pavlovskyella*, as each subgenus parasitizes a wide variety of hosts such as reptiles, birds, and burrowing and nonburrowing mammals. The mode of distribution from the Old to the New World, where *Alectorobius* may have originated and radiated, is unclear, but avian or rodent hosts, or both, are suspect transporters. However, because members of both subgenera are found on birds, *O. (A.) capensis* Neumann, taken from marine birds that live in tropical and temperate regions world-wide, and *O. (A) denmarki* Kohls, Sonenshine, and Clifford, also from marine birds living on islands in Pacific and Caribbean waters, are of particular note. The possibility of the original migration of *Alectorobius* progenitors via a bat carrier common to both the Old and New Worlds seems remote, at least relative to present day distributional patterns of *Ornithodoros* species. Even though specimens of *Alectorobius* have been collected from vespertilionid, emballonurid, and molossid bats of the New World, only one record of this subgenus has been recorded (Anciaux de Faveaux, 1971) from any Old World representatives of these bat families.

Already adapted to feeding on a wide variety of mammalian hosts, invading species of the *Alectorobius* line adjusted to using bats, especially phyllostomatids, as hosts. A number of mainland ticks developed as species limited to the phyllostomatid host type, then apparently spread to adjacent Caribbean islands, and then from island to island in the Antillean chain. An example of this is provided by *O. (A.) azteci* Matheson, which has been reported from México, Panamá, Venezuela, and from the islands of Trinidad, Jamaica, and Cuba (Kohls *et al.*, 1965; Anciaux de Faveaux, 1971; Jones *et al.*, 1972).

Ornithodoros (Subparmatus) viguerasi differs greatly from the other species of *Ornithodoros* (Clifford *et al.*, 1964). However, its affinity for certain bats suggests an origin from the Antillean *Alectorobius* line, as *O. viguerasi* parasitizes Cuban *Phyllonycteris poeyi* and *Brachyphylla nana*, and Puerto Rican *Erophylla bombifrons* (Tamsitt and Fox, 1970b), all phyllostomatids. A strong

association with mormoopids is indicated by the records of *O. viguerasi* on *Pteronotus* from Cuba and Jamaica, and on *Pteronotus* and *Mormoops* from Trinidad. Furthermore, *Pteronotus parnellii* has yielded a number of these ticks in Panamá (Fairchild *et al.*, 1966), as have *Mormoops megalophylla* and species of *Pteronotus* from Venezuela (Jones *et al.*, 1972).

The species of *Antricola* seem to exhibit the same host and general distributional patterns of *O. viguerasi* on the mainland and Caribbean islands. Two of these, *A. marginatus* (Banks) and *A. silvai* Cerný, have been taken from *Phyllonycteris poeyi*, endemic to Cuba (Hall and Kelson, 1959), but are also known from Cuban mormoopid species (Anciaux de Faveaux, 1971), and *A. silvai* was recorded by Jones *et al.* (1972) from Venezuelan *Mormoops megalophylla* and *Pteronotus*. Mainland phyllostomatids have not yielded *Antricola*, which may suggest that *Antricola* arose from island-inhabiting *Ornithodoros* types on phyllostomatids or on mormoopids. Island-hopping mormoopids may have brought the ticks to the mainland where *A. mexicanus* seems specific to mormoopid species such as Mexican and Panamanian *Pteronotus* in addition to being found in bat caves in Guatemala and México (Fairchild *et al.*, 1966). *Antricola coprophilus* (McIntosh), although never recorded from a chiropteran host, is known from caves and mines in Arizona and Texas inhabited by vespertilionid bats (Cooley and Kohls, 1944), and numerous *A. granasi* de la Cruz (1973) were recorded from a cave in Cuba.

The overall trend of development of species and distributional patterns seems to indicate an origin of a line of phyllostomatid-infesting *Ornithodoros* (*Alectorobius*) species in southern Central America or northeastern South America. Radiation has occurred northward into México and the southwestern United States, eastward onto the Caribbean islands, and southward into other parts of South America. The northern and southern distributional patterns appear to be reflections of one another with adaptations by these ticks to more temperate-ranging bat species such as certain vespertilionids and molossids. In the north, *O. (A.) yumatensis* and *O. (A.) rossi*, both parasitic on tropical and subtropical phyllostomatids, parasitize vespertilionid bat species as far north as Arizona (Cooley and Kohls, 1944; Kohls *et al.*, 1965; Jones *et al.*, 1972). Southward, the species *O. (A.) boliviensis*, for instance, has been recovered from Bolivian *Myotis nigricans* and *Molossus major* (Kohls and Clifford, 1964), and *O. eptesicus* is known (Kohls *et al.*, 1969) from Venezuelan *Eptesicus furinalis*.

 EREYNETIDAE Oudemans, 1931

Five species of speleognathine ereynetids all of the genus *Speleochir* Fain are known to infest the nasal passages of phyllostomatid bats: *Speleochir aitkeni* Fain (1966) from *Anoura geoffroyi* taken in Trinidad; *S. brasiliensis* Fain and Aitken (1969) from *Vampyrodes caraccioloi* and *Artibeus jamaicensis*; *S. barbulata* Fain and Aitken (1970) from *Mimon crenulatum* of Brazil; *S. phyllostomi* (Clark, 1967) from *Phyllostomus hastatus* of Colombia; and *S. carolliae* Fain and Lukoschus (1971) taken from *Carollia perspicillata* in Surinam.

Some ereynetids are free-living predators, but most are adapted to a mucosal environment and the origins of the Ereynetidae seem to lie with a ground or plant-living ancestor that adapted to mucosal secretions or mucosal secreting environs. Rodents are the most numerous and widely represented mammalian hosts although many bird species also harbor speleognathines. A common, relatively recent, ancestral history seems to be suggested for both mammalian and avian ereynetids as both types are well represented and included together in the Speleognathinae.

Comparisons of rodent and bat host records have revealed certain related patterns. For instance, species of *Paraspeleognathopsis* Fain are known from Africa, Europe, Korea, and Australia from different species of murid rodents; species of *Speleorodens* Fain have been reported from Africa, Europe, the United States, and Panamá from sciurid rodents, and from Australia and Panamá from murid rodents; and cricetid rodent records are cited from Panamá, Trinidad, Brazil, and Holland (Fain, 1970*b*). A similar Old and New World distributional pattern for species of the same genus is exhibited by *Neospeleognathopsis* on vespertilionid bats from Europe (Belgium) and from the United States. All but one of the species of *Speleochir* are known from Neotropical phyllostomatids; *S. duboisi* (Fain) is from an African *Nycteris*.

Interpretation of these patterns leads to the assumption that two possible routes of dispersal may have been involved. The Old World murid rodents apparently provided a possible dispersion mechanism as they spread worldwide, with speleorognathines secondarily infesting sciurids, cricetids, and other mammals. The other possible route centers with the vespertilionid bats, which may have transported speleognathines to the Neotropics where the leaf-nosed bats became hosts and sites of development for these mites.

The genus *Speleochir* appears to have originated in the New World on phyllostomatid bats, from Old World progenitors carried to the Neotropics by one form or another. The occurrence of congeneric species in two widely separated regions—*S. duboisi* in Africa and the five Neotropical *Speleochir* species—may suggest a greater distribution for nycterid bats in the geological past or that the generic position of *S. duboisi* is in need of reevaluation.

MYOBIIDAE Megnin, 1877

More than 50 species of myobiid fur mites are recorded from chiropteran hosts. *Eudusbabekia* Jameson contains nine of these species that are known exclusively from leaf-nosed species. Five species of *Eudusbabekia* have been found on Cuba or Isla de Pinos (Dusbabek, 1967), a small island near Cuba: *E. cernyi* (Dusbabek) from *Brachyphylla nana*, *E. danieli* from *Phyllonycteris poeyi*, *E. samsinaki* from *Macrotus waterhousii*, and *E. viguerasi* from *Artibeus jamaicensis*. Jameson (1971) subsequently named two species, *E. lepidoseta* from *Sturnira lilium* and *E. phyllostomi* from *Phyllostomus discolor* taken in Nicaragua. Later, Vomero (1972) described *E. arganoi* from *Desmodus rotundus* taken is San Luis Potosí, México, and Fain (1972) described *E. urodermae* from a single Brazilian *Uroderma magnirostrum*. Two other, *E. jimenezi* (Dusbabek)

and *E. saguei* (Dusbabek) are found on species of Cuban *Pteronotus*, a mormoopid genus. The genus *Ioannela* (Dusbabek and Lukoschus, 1973) contains *I. martae* (known from seven females and three tritonymphs) from a Surinam *Mimon crenulatum*.

Each of these myobiids has been taken in association with an individual phyllostomatid bat species. The recent recovery of a female *E. viguerasi* (identified by Dr. E. W. Jameson, Jr.) from *Artibeus jamaicensis* from Veracruz, México, suggests a recent connection between the mainland *A. jamaicensis* and insular *A. jamaicensis* on Cuba.

A cheyletoid ancestry for the Myobiidae was proposed by Dusbabek (1969) who also suggested a close phylogenetic affinity among *Eudusbabekia*, *Ewingana*, and *Ugandobia*, all found on bats. Species of *Ewingana* are parasites principally of molossids found in the Old and New Worlds. *Ewingana molossi* Dusbabek from *Molossus molossus* and *E. yaguajayensis* Dusbabek from *Tadarida laticaudata*, both from Cuba, may indicate a host link between the Old and New Worlds.

Evidence for a vespertilionid transport system may be seen in the relationship between Old World *Neomyobia* Radford and species of vespertilionid and leaf-nosed bats. *Neomyobia chiropteralis* (Michael) has been found on *Pipistrellus pipistrellus*, *Eptesicus nilssonii*, and *Rhinolophus hipposideros* in Europe and several other *Neomyobia* species are reported from European, African, and Asian *Rhinolophus* species. These associations may parallel those between vespertilionids and phyllostomatids in the Neotropics. Additionally, several species of *Pteracarus* are known from the Old and New Worlds from vespertilionids and one, *P. chalinolobus* (Womersley), is known from Australia, North America, and Czechoslovakia (Anciaux de Faveaux, 1971).

A New World origin is suggested for species of *Eudusbabekia* specifically, but the bat-infesting myobiids in general probably arose in the Old World, as there is seemingly less taxonomic differentiation and host specificity exhibited by the myobiids on New World chiropterans when compared to their Old World counterparts.

DEMODICIDAE Nicolet, 1855

Three species of demodicid mites (*Demodex*), all from Surinam, are known from *Phyllostomus hastatus* (*D. phyllostomatis* Leydig, 1859) and *Carollia perspicillata* (*D. carolliae* Desch *et al.*, 1971 and *D. longissimus* Desch *et al.*, 1972). It seems likely that many other chiropterans harbor *Demodex* mites, as only these three phyllostomatids, six vespertilionids, and a molossid are recorded hosts (Anciaux de Faveaux, 1971; Desch *et al.*, 1972; Fain, 1960; Lukoschus *et al.*, 1972).

A commensalistic cheyletoid ancestor was hypothesized (Nutting, 1964, 1965) for demodicid mites, the intermediate, less specialized forms of which are exemplified today by species of *Stomatodex* Fain and *Rhinodex baeri* Fain. Both *Stomatodex galagoensis* Fain and *R. baeri* occupy intraoral and nasal cavities of *Galago senegalensis*, a lorisid primate, whereas the other three *Stomatodex* species inhabit the same microhabitat of a pteropodid, a nycterid, and several

vespertilionid bat species. Because they are only slightly modified morphological-ly, it seems that these mites invaded the relatively stable nasal and oral cavities early in demodicid phylogeny and have changed little since. The association of more primitive *Stomatodex* species with five bat species that range from Central Africa to Europe suggests a comparatively long affiliation by demodicids with chiropterans. The origins then of *Demodex* may have been with bat hosts in the Old World.

Vespertilionids are the most numerous and widespread host bats of *Demodex* species and are recorded from the Old and New Worlds (Anciaux de Faveaux, 1971). The tumors or small papules on the skin from which the phyllostomatid-infesting *Demodex* were recovered may be tissue reactions, suggesting a recent incorporation of leaf-nosed bats as hosts, perhaps by demodicids previously associated with vespertilionid bats. Nutting (1964:443) has expressed doubts about recent interspecific transfer. He further stated that phylogenetic patterns and species specificity are indeterminable.

PSORERGATIDAE Dubinin, 1955

Three of the 11 species of *Psorergatoides* Fain are presently known (Luko-schus *et al.*, 1973) to infest phyllostomatids—*P. lonchorhinae* from *Lonchorhina aurita* from Venezuela, and *P. glossophagae* from *Glossophaga soricina* and *P. artibei* from *Artibeus lituratus*, both from Surinam. In the Old World, the species of this genus occur on rhinolophid and hipposiderid bats throughout Europe and into Africa, one species is found on vespertilionids in Africa and another species was taken from molossids in Surinam, which may indicate some evidence for a vespertilionid or molossid host link between the Old and New Worlds.

The *Psorergatoides* species are intradermal inhabitants of the ears and wings of their hosts, apparently feeding on dermal tissues. Host tissue reaction has been observed and discussed (Lukoschus *et al.*, 1973), and is especially pro-nounced in the phyllostomatid hosts of *P. glossophagae* and *P. artibei*, and in *P. molossi* (found on *Molossus molossus*), perhaps suggestive of a relatively recent invasion of these hosts. This possibility and the fact that *P. rhinolophi* Fain has adapted to nasal membranes, wings, and ears, and is widespread on eight species of rhinolophid bats in Europe and Africa may suggest an Old World origin for the group.

Nutting (1965) noted the possibility that psorergatids arose from a cheyletoid ancestor common with the basal stock that produced the demodicids, myobiids, and several other families parasitic on vertebrates. The *Psorergatoides* group shows close affinities with the species of *Psorergates* Tyrrell, which are restrict-ed to nonchiropteran mammals. Movement of *Psorergates*-like species onto bats from rodents or other small mammals may account for the seemingly strong similarities between species of the two mite genera. It is also feasible that the *Psorergatoides* taxa evolved along with the chiropterans from insectivore-para-sitizing ancestors as there are many species of *Psorergates* known from extant species of insectivores. However, this seems unlikely as one would expect to find

the psorergatids more widely distributed on bat hosts and greater differences between species of *Psorergates* and *Psorergatoides*.

TROMBICULIDAE Ewing, 1944

Trombiculid mites (including Leeuwenhoekiinae) are parasitic on many kinds of vertebrates, including bats. More than 1500 species are known from temperate and tropical regions of the world. The larval stage, commonly called a chigger, is a frequent ectoparasite and occasionally an endoparasite of phyllostomatids.

Most of the trombiculid literature concerning bats can be found in Anciaux de Faveaux (1971). Several regional papers include those on México (Loomis, 1969), Panamá (Brennen and Yunker, 1966), Surinam (Brennen and Lukoschus, 1971; Brennan and van Bronswijk, 1975), Trinidad (Brennan and Jones, 1960), and Venezuela (Brennan and Reed, 1973, 1974, 1975; Reed and Brennen, 1975). Major taxonomic papers deal with the genera *Beamerella*, *Hooperella*, and *Tecomatlana* (Vercammen-Grandjean, 1967), *Chiroptella* and *Leptotrombidium* (Vercammen-Grandjean and Langston, 1971), *Loomisia* (Brennan and Reed, 1972), *Microtrombicula* (Webb and Loomis, 1971), *Nycterinastes* (Brennan and Reed, 1973), *Parasecia* (Brennan, 1969*a*), and *Perissopalla* (Brennan, 1969*b*, 1970). The generic status of certain taxa has been questioned by Vercammen-Grandjean *et al.* (1973); however, they are recognized as subgenera.

There are 51 species, belonging to 22 genera of two subfamilies (Trombiculinae and Leeuwenhoekiinae) known from phyllostomatids. Records of three species seem to be based on accidentals or errors in handling—*Blankaartia sinnamaryi* normally parasitizes birds, *Pseudoschoengastia bulbifera* is abundant on small mammals, especially rodents, and *Trombicula dunni* is known from a variety of terrestrial mammals (Brennan and Yunker, 1966). Occasional and possibly accidental records include seven species of the abundant and widespread genus *Eutrombicula* (Brennan and Reed, 1974), and *Leptotrombidium hamaxiaium* known to regularly infest rodents and rabbits. *Xenodontacarus serratus* Loomis and Goff (1973) was described from a single larva taken from a Mexican *Artibeus lituratus*, the only record of a *Xenodontacarus* from a bat.

The remaining 40 trombiculids regularly infest bats of the Americas and are documented from phyllostomatids. These consist of species in the genera *Alexfainia* (one of two known species), *Beamerella* (two of three), *Chiroptella* (one of three American species), *Hooperella* (three of four), *Loomisia* (five of six), *Microtrombicula* (three of about 20 American species), *Nasicola* (one species), *Nycterinastes* (two species), *Parascoschoengastia* (two of five), *Parasecia* (three of 12), *Perates* (one of two), *Perissopalla* (six of 12), *Speleocola* (two of five), *Tecomatlana* (two), *Wagenaaria* (one), *Whartonia* (four of eight American species), and *Xenodontacarus* (one of four).

The usual life cycle consists of the egg, deutovum, a parasitic larva (which attaches to the host, feeds on lymph and histolyzed tissue, and then leaves the host after engorgement), inactive protonymph, active and predaceous

deutonymph, inactive tritonymph, and the figure-eight-shaped predaceous adult, either male or female. The parasitic larval stage is relatively brief, whereas the free-living nymphs and adults must have the proper substrate and prey. A good host will pick up the larva, provide a favorable parasitope and nourishment, and deliver it after engorgement to a suitable drop-off site, frequently the original or a similar microhabitat in which the larva was picked up.

The larvae usually attach singly or in clusters on or in the ears (*Microtrombicula, Speleocola, Tecomatlana*, and *Xenodontacarus*), wings and tail membranes (*Beamerella, Chiroptella, Hooperella, Loomisia, Perissopalla, Perates, Parasecia, Whartonia*, and some *Tecomatlana* and *Parascoschoengastia*), toes (*Perates*), and nasal passages (*Alexfainia* and *Nasicola*). Chiggers are occasionally found on the head, lips, body area, and the genitalia. The enlarged larva is oval in shape, rarely larger than one millimeter in length, and may be red (*Beamerella, Hooperella, Tecomatlana, Whartonia*), orange (*Perissopalla, Loomisia*), yellow (*Chiroptella, Nasicola, Parasecia, Perates*), to whitish (*Speleocola, Parasecia*).

Emergence of the unfed larvae of most temperate and many tropical chiggers is seasonal, either correlated with temperature in alternately hot and cool regions, or synchronized with wet or dry periods.

Modifications in larval morphology that seem correlated with chiropteran hosts include greater sclerotization of legs and palpi, projections on certain leg and palpal segments (Vercammen-Grandjean, 1967), and enlarged and serrated cheliceral blades on those that attach externally (but usually there is a moderate blade on those that attach within ears and small blades on intranasal species). The oval-shaped larvae may be red or orange in larger ectoparasites and yellow or nearly white in those that normally attach deep in the ears or are free in the nasal passage.

Virtually all of the seven most frequently parasitized phyllostomatids (*Artibeus, Carollia, Desmodus, Glossophaga, Macrotus, Micronycteris*, and *Phyllostomus*), as well as other heavily infested tropical American bats, such as *Balantiopteryx plicata, Mormoops*, and *Pteronotus parnellii*, are regular or wholly inhabitants of caves and rock crevices. The remaining host phyllostomatids normally roost in hollow trees. In addition, nearly all of these hosts usually roost in clusters or large colonies.

Although most free-living stages of these and similar genera are known only from laboratory-reared material, most if not all of those listed probably inhabit cracks in rocks or decaying wood (frass). Closely related species in the genera *Parasecia* and *Microtrombicula* are known to inhabit decaying logs, stumps, and dead standing trees. Other *Microtrombicula* and *Whartonia* are associated closely with rock crevices in cliffs and caves. Bats taken in caves and mines were infested heavily with larvae of the genera *Beamerella, Hooperella, Loomisia, Microtrombicula, Perissopalla, Speleocola, Tecomatlana*, and *Whartonia*.

Bats recovered from bridges, houses, and other artificial structures rarely possess trombiculids, nor are they found on bats that usually or always roost among leaves on living branches of trees.

None of the well known genera and few of the species have been recorded only from phyllostomatids, although most of them are known only from bats, including emballonurids, molossids, mormoopids, and vespertilionids. Genera associated with bats and of probable Neotropical origin consist of *Nasicola* and *Speleocola* (members of a world-wide group including *Microtrombicula*), *Loomisia* (a distinct group), *Perissopalla* (possibly related to Old World genera including *Riedlinia* and *Trisetica*, according to Vercammen-Grandjean *et al.*, 1973), and the distinct American trombiculine taxa consisting of *Beamerella*, *Hooperella*, *Tecomatlana*, *Alexfainia*, *Nycterinastes*, and *Perates*. Leeuwenhoekiine genera consist of *Wagenaaria* (closely resembling the genus *Sasacarus*, which is abundant on desert and tropical American terrestrial mammals); *Xenodontacarus serratus*, one of four known species in a group regularly on small terrestrial mammals; and *Whartonia*, which is world-wide in distribution and found on many different kinds of bats. *Whartonia nudosetosa* and *W. pachywhartoni* represent typical species and are restricted to the New World tropics, whereas *Whartonia glenni* and *W. guerrerensis* are mostly northern Neotropical. These *Whartonia* also have been found on a wide variety of American bats including emballonurids, molossids, and mormoopids, and all American genera of leeuwenhoekiines seem to be northern in origin and mostly northern Neotropical in distribution.

Bats, including a number of phyllostomatids, are common hosts of *Parascoschoengastia* and *Parasecia*, which seem to be acquired by hosts in hollow trees and other roosting sites associated with decaying wood. *Parascoschoengastia aemulata* and *P. megastyrax* are recorded only from bats, as is *Parasecia soucouyanti*; however, *Parasecia longicalcar* and *P. manueli* also are known from a number of other small mammals and birds (Brennan, 1969*a*).

ROSENSTEINIIDAE Cooreman, 1954

The subfamily Nycteriglyphinae Fain consists of two genera and 13 species (Anciaux de Faveaux, 1971) associated with bats or bat roosts. Only one of these, *Nycteriglyphus sturnirae* Fain (1963), based on a single tritonymph, has been found in association with a phyllostomatid (a Brazilian *Sturnira lilium*). Dusbabek (1967*b*) subsequently reported a male and female *N. sturnirae* from *Molossus molossus* taken on Isla de Pinos, Cuba.

LABIDOCARPIDAE Gunther, 1942

The family Labidocarpidae consists of eight genera previously placed in the families Listrophoridae or Chirodiscidae. Species of four genera have been reported from phyllostomatids. *Alabidocarpus furmani* was listed from Trinidad (Pinichpongse, 1963*a*) from *Anoura geoffroyi* and also from *A. geoffroyi* and *Glossophaga soricina* taken in Nicaragua (McDaniel, 1970). Other Nicaraguan species include *A. nicaraguae* from *Uroderma bilobatum* and *A. jonesi* from *Vampyrops helleri*. Three species of *Paralabidocarpus* Pinichpongse have been recorded exclusively from phyllostomatids. *Paralabidocarpus artibei* Pinichpongse (1963*b*) was originally described from mites on *Artibeus lituratus*

from Trinidad and later reported (Tamsitt and Fox, 1970*a*) on *A. lituratus* and *Stenoderma rufum* taken in Puerto Rico. Subsequently, de la Cruz *et al.* (1974) described *P. stenodermi* from *S. rufum* and *P. foxi* from *Artibeus jamaicensis*, both from Puerto Rico. *Lawrenceocarpus micropilus* Dusbabek and de la Cruz was originally described from specimens obtained from the mormoopid *Pteronotus fuliginosus* taken in Havana Province of Cuba (McDaniel, 1970). A later record of *L. micropilus* was noted by Tamsitt and Fox (1970*a*) from *Brachyphylla cavernarum* collected in Puerto Rico, which were also the host and locality records for the species *L. puertoricensis* de la Cruz, Tamsitt, and Valdivieso (1974). Fain (1970*b*) has reported some recent records from Surinam phyllostomatids and McDaniel (1972) reported numerous labidocarpids from Venezuelan leaf-nosed species.

Labidocarpids have anterior appendages specialized for clasping individual hairs in the fur of their mammalian hosts. Food habits have not been noted, but, as with other listrophoroids, they probably feed on dermal tissues and secretions at the base of the hair.

The life cycle includes a hexapod larval stage, which after parturition may molt either into a nymphal male or female. The nymphal male molts again to become an adult, whereas the nymphal female undergoes another molt in which the ecdysium remains around her, thus forming a puparium or chrysalis. During mating, the male clasps a hair while a female is attached to his posterior end *in copulo* with the anterior end of each facing in opposite directions. How the male and copulatory female initially unite is unclear as the legs of the puparium have no apparent morphological adaptive quality for holding fast to hair or skin and, before pupal formation, were of little locomotive value to the nymph because of their diminutive size. Furthermore, the fate of the copulatory female after disengagement from the male is questionable for the same reasons. The "three-legged," fully chitinized stage with the next stage developing inside as seen by Lawrence (1952:137) was possibly a representative of a separate species in which the short or nearly absent legs of the nymphal female are characteristic of that taxon. Ovoviviparity is seen in these mites for fully formed larvae have been observed inside normal females (McDaniel, 1970) and mature females give birth shortly after shedding the pupal skin.

The genera *Labidocarpus*, *Alabidocarpus*, and *Olabidocarpus*, which parasitize phyllostomatids, have both New and Old World species. All three also have representatives on vespertilionid bats either in the New World (*Labidocarpus*) or in both the New and Old Worlds (the other two genera). The relatively greater differences among the seven genera in México, Central America, or South America suggest the site of origin was in the New World. Only a single monotypic genus is known from the Old World. Furthermore, phyllostomatids harbor the greatest number of labidocarpid species, suggesting a relatively long association.

Additional evidence for the initial establishment of labidocarpids on phyllostomatids may be implied in the Old and New World distribution of the mite species. If they had invaded the Old World rhinolophids or hipposiderids or

vespertilionids of either realm in the beginning, we would expect to see a much broader range of these host species, something that is not in evidence. If originally on New World molossids, then why are they not found on Old World free-tailed bats? The accumulated evidence seems to indicate a New World origin for labidocarpid mites on phyllostomatid bats with radiation to the molossids, noctilionids, and vespertilionids followed by dissemination to the Old World rhinolophids and hipposiderids via the cosmopolitan vespertilionid species.

CHIRORHYNCHOBIIDAE Fain, 1967

This sarcoptiform family consists of two species known only from phyllostomatids. *Chirorhynchobia urodermae* Fain (1967) was based on a single female from a Panamanian *Uroderma bilobatum*, and the seven females of *C. matsoni* Yunker (1970) were attached by their mouthparts to the trailing edge of the wing membrane of a single *Anoura geoffroyi* netted in Zulia, Venezuela.

SARCOPTIDAE Trouessart, 1892

One genus of sarcoptid mite is known from phyllostomatid bats. *Chirnyssoides* was proposed by Fain (1959) to include *C. caparti* recovered from *Artibeus jamaicensis*, *C. amazonae* from *Carollia perspicillata*, *C. brasiliensis* from *Sturnira lilium* (all from Brazil), and *C. venezuelae* from a Venezuelan *Tonatia venezuelae*. Fain (1962) later described *C. carolliae* from Panamanian *Carollia perspicillata* and *C. castanea*. Only phyllostomatids were known to be the hosts for *Chirnyssoides* until Fain and Lukoschus (1971b) transferred *Notoedres noctilionis* to *Chirnyssoides* and erected a new subgenus (*Noctiliocoptes*) for it. *Chirnyssoides noctilionis* is known from Cuba and Surinam from noctilionid bats. Two other species, *C. surinamensis* and *C. zanderyensis* both taken from Surinam *Carollia perspicillata* were placed in a separate subgenus, *Carollicoptes*.

Known parasitopes for *Chirnyssoides* species are the skin of the leading or trailing edges of wings or ears.

The *Chirnyssoides* species group may have arisen from stock common to that including the species of *Notoedres*. Certain evidence suggests an Old World origin for the *Notoedres* group, possibly from an ancestral line that includes the genera *Chirnyssus* and *Nycteridocoptes*. Support for this idea seems to be implied by several things. There are many more species of *Notoedres* in the Old World and they are found on a greater variety of bat hosts. A number of species of *Nycteridocoptes* and *Chirnyssus* are inhabitants of the bucal cavity in some bats, a condition that may be seen with other groups of acarines that have long associations with their hosts. *Nycteridocoptes* and *Notoedres* have representatives on pteropodids, rhinolophids, hipposiderids, molossids, and vespertilionids in the Old World and numerous species are known from vespertilionids in the New World. The developmental sequence in the phylogeny of these mites seems to indicate an early establishment on pteropodids followed by a movement onto rhinolophids and then to vespertilionids, which carried them to the New World to phyllostomatids.

GASTRONYSSIDAE Fain, 1956

Phyllostomonyssus conradyunkeri Fain (1970c) of the subfamily Rodhainyssinae Fain, is the only gastronyssid reported from phyllostomatids. It has been found in the nasal passages of Venezuelan *Artibeus lituratus* and *Uroderma bilobatum, Vampyrops helleri,* and *A. lituratus* from Surinam (Fain and Lukoschus, 1972). Leaf-nosed bats may have acquired this mite from associations with vespertilionids. The few additional reports of rodhainyssines from the New World include the vespertilionid *Histiotus velatus* from Brazil and Chile, the molossid *Eumops abrasus* from Surinam, and the emballonurid *Balantiopteryx plicata* from México (Anciaux de Faveaux, 1971). All were infested with species of *Rodhainyssus* Fain, a genus also known from Europe and Africa.

From the description and discussion by Fain (1956, 1970c) *Phyllostomonyssus conradyunkeri* appears to be more specialized than any species of *Rodhainyssus.* The loss of the apical tarsal seta, the reduction in length of the post-ventral opisthosomal setae, and development of large clawlike extensions of tarsi III and IV, all seem to parallel the specializations of *Gastronyssus bakeri* Fain, a parasite of the gastric and intestinal mucosa of pteropodid bats.

NYCTERIBIIDAE Samouelle, 1819

Nycteribiids are wingless, spiderlike, and obligately hematophagous, parasitic flies of bats. Little is known about the biology of nycteribiid batflies except that all species are larviparous and pupation immediately follows larvipostion (Guimarães, 1968). Two genera, *Basilia* Ribeiro and *Hershkovitzia* Guimarães and D'Andretta are found in the American Neotropics, but only *Basilia* has representatives (12 species) on phyllostomatids. New World species principally parasitize vespertilionid bats (Guimarães, 1968) and it is assumed that nycteribiids entered North America on members of that family. Theodor (1957) noted that the closest relatives of *Basilia* belong to an Old World group that, except for one species, is totally tropical. Thus, the evidence suggests an Old World tropical origin for nycteribiids where adaptation and radiation has led to a nearly cosmopolitan occupation of chiropteran hosts. Apparently, the success of streblid batflies in the New World has affected the ability of nycteribiids to invade niches provided by Neotropical bats.

Additional literature regarding nycteribiids are generally of a taxonomic nature and include Ferris (1924), Guimarães (1946, 1966, 1972), Guimarães and D'Andretta (1956), Peterson and Maa (1970), and Whitaker and Easterla (1975).

STREBLIDAE Kolenati, 1863

Streblid batflies are hematophagous, pupiparous, and obligate parasites of bats found in both the Old and New World tropics. In the Americas, Wenzel (1970) recognized a total of 94 batfly species in 23 genera. The present account lists 83 species in 20 genera from New World leaf-nosed bats.

Wenzel *et al.* (1966:636-649) have provided an extensive discussion of host-parasite relationships, including host specificity, parasite faunules, and ecology

of parasitism. They concluded that streblid distribution in habitats and on hosts was due, to a degree, to ecological factors; few have been found on bats commonly restricted to forest habitats for example, whereas cave dwelling bats generally harbored more streblids in species and in number. Bats in long established roosts also tended to have more streblids. It was further suggested that within the host's preferred habitat, however, host specificity was great even though the same streblid species may be found on a number of other species of bats. Earlier, Ross (1961) stated the same situation for several Nearctic phyllostomatid and two vespertilionid species. His observation of the apparent noninfestation of molossids cohabiting with infested vespertilionid and leaf-nosed bats may be due to recent streblid dispersal to these temperate regions as a number of molossids serve as hosts for batflies in the tropics (Jobling, 1949; Wenzel, 1970; Wenzel *et al.*, 1966).

Although Jobling (1949) stated that streblids probably arose from an ancestor that was not blood sucking, it seems more likely that they originated from hematophagous, calypterate, muscoid flies as Theodor (1957) has postulated, and that the adaptation was originally to bats.

Theodor (1957) further stated that because of a complete lack of streblid fossils no conclusions about the evolution and phylogeny could be drawn regarding batflies and their hosts. Certain observations may be made, however. For instance, the greatest differentiation of species (94) and genera (23) has occurred in the New World as compared to 62 species and 4 genera of the Old World (Wenzel, 1970). Indicative of this great taxonomic range is the spectrum of morphological features of New World streblids from the generalized calypterate taxa to the small-winged and flightless flies (certain species of *Strebla*, for example) and to the wingless species of *Paradyschiria*. Further reflections of adaptations by Neotropical batflies may be seen in the polyctenoid appearance of *Strebla* and other species and in the siphonapteroid *Nycterophilia*. These diversifications seem to indicate a New World origin for streblid batflies. The endoparasitic mode of *Ascodipteron* on Old World bats may merely reflect an adaptation to competitive factors with other ectoparasites, such as nycteribiids.

Additional evidence for New World origins may be seen in the hyperparasitic relationship between certain streblids and the trombidiid mite, *Monunguis streblida*, first noted by Wharton (1938) as an ectoparasite on streblids—*Megistopoda aranea* (Coquillett) and *Trichobius dugesii* Townsend—from caves in Yucatán, México. From other material obtained from California State University, Long Beach, more specimens of *M. streblida* have been recovered from *Nycterophilia* (identified by Dr. B. V. Peterson) taken from *Macrotus waterhousii* from Sinaloa, México.

We assume the streblid-bat association occurred before the mite-fly relationship, and *M. streblida* probably encountered the streblids on the cave floor where the parasitic flies emerged from the puparia. It would seem probable that the mite is a relatively recent parasite on streblids as it does not exhibit host specificity or selectivity. It is probably also more closely associated with a suitable cave environment, large colonies of bats, and adequate populations of suitable streblids.

Other published papers regarding streblids include those of Guimarães (1944), Peterson and Hůrka (1974), Peterson and Ross (1972), Reddell (1970), Starrett and de la Torre (1964), and Whitaker and Esterla (1975).

DISCUSSION

Ectoparasites are recorded from 39 of 49 genera (89 of 136 species) of phyllostomatids. There are two general host-parasite categories: either the parasite remains on the host throughout the entire life cycle (for example, demodicids, myobiids, and spinturnicids), or it spends part of the cycle off the host in the bat roost (for example, argasids, ixodids, macronyssids, and trombiculids) and may parasitize a variety of bats and even other vertebrates that trespass into its territory. *Nycteriglyphus sturnirae*, a rosensteiniid mite, is a commensal with two species of leaf-nosed bats.

For part-time ectoparasites, the host is visited at least once, and sometimes two to three times. This type moves onto the available host, attaches to some part of the body, and commences feeding. The feeding site is termed the parasitope (Fain and Vercammen-Grandjean, 1953; Wrenn and Loomis, 1967) and seems to be selected by the parasite although it may be influenced by grooming or scratching behavior of the host.

The microbiotope refers to the area of normal activity of each parasite, which may be on the entire surface of the host for batflies, or in a single dermal pore by demodicid mites. Others, such as soft ticks and macronyssids, also must survive in microhabitats off the host.

The parasitope and microbiotope may be virtually the same for endophilic demodicid, sarcoptid, and psorergatid mites. Myobiids and labidocarpids have microbiotopes where they clasp individual hairs, and their feeding parasitope is visited periodically at the base of the hairs. Spinturnicid mites and the batflies have extensive microbiotopes. Wing mites usually are found on the wing and leg membranes and rarely invade the fur, whereas batflies move over much of the body surface. Argasids and most trombiculids find and climb onto the host and move quickly to feeding sites, so the parasitope and biotope are essentially the same. They remain at these feeding sites and on the host for relatively brief periods. Gastronyssids, ereynetids, and some trombiculids occupy the respiratory passages, and certain macronyssids (*Radfordiella*) are found in peridontal tissues. The females of chirorhynchobiids have been recovered from wing membranes and spelaeorhynchids were embedded in the skin of the ear.

Three feeding categories are suggested for these ectoparasites: hematophagy, histophagy, and mucophagy. The hematophagous soft and hard ticks, the two families of batflies, spinturnicids, and some macronyssids derive most if not all of their nourishment from blood meals. The remaining parasites, except for intranasal and intraoral taxa, feed on dermal tissues, fluids, or skin secretions. Those inhabiting oral and respiratory cavities apparently feed on mucus, although histophagy also has been suggested. Protonymphs of several species of *Radfordiella* feed on tissues surrounding teeth, resulting in extensive damage in some instances.

The highest degree of niche and host specialization occurs in ectoparasites of birds and bats and is attributed to their relative ecologic and geographic isolation (Wenzel and Tipton, 1966). Furthermore, the degree of host specificity is correlated with the extent to which a parasite is host limited. Examples of familial specificity of ectoparasites include Streblidae, Nycteribiidae, Polyctenidae, and Spinturnicidae and certain trombiculid species exhibit host-species restriction. However, most literature on phyllostomatid ectoparasites does not contain carefully documented information about host-parasite relationships. An approach to bypass the shortcomings of a host-parasite list is to find two or more separate studies listing a particular parasite from a specific bat species or other taxa. On this basis, it appears that few phyllostomatid infestors are monoxenous. Examples of monoxeny, however, include *Periglischrus herrerai* taken only from *Desmodus rotundus* and *Speleochir phyllostomi* recovered solely from *Phyllostomus hastatus*, both of which corroborate Wenzel and Tipton's (1966) idea of higher host specificity in host-limited taxa. The usual hosts for several streblids appear to be *Artibeus jamaicensis* for *Megistopoda aranea*, *Glossophaga soricina* for *Trichobius dugesii*, *Carollia perspicillata* for *T. joblingi*, *Phyllostomus hastatus* for *T. longipes* and *P. discolor* for *Strebla hertigi*. *Macronyssoides kochi* noted from *A. jamaicensis* and *Desmodus rotundus* with single records from *A. toltec*, *A. aztecus*, *A. lituratus*, *Brachyphylla nana*, *Glossophaga soricina*, and *Phyllonycteris poeyi* is oligoxenous and apparently agrees with the development of polyhaematophagy in ectoparasites that are not host-limited. The phyllostomatid-limited spinturnicids of the genus *Periglischrus* are seemingly in conflict with this latter idea, however, as they exhibit extensive polyhaematophagy, and are highly host-limited. Thus, selection for polyhaematophagy is not always restricted to ectoparasites that are not host-limited and in this case the parasites are not typically oligoxenous but rather exhibit subfamilial specificity (see Table 1) and are, therefore, stenoxenous. This host specificity is consistent with the subfamilial status of the vampire bats and other groups. Taxa of four other ectoparasitic families, Streblidae, Labidocarpidae, Sarcoptidae, and Gastronyssidae, also seem to show subfamilial specificity (see Table 1) and all are highly host limited.

New World leaf-nosed bats roost in caves, cliff crevices, trees, hollow tree trunks, or burrows, or in artificial structures such as culverts, buildings, or bridges (Humphrey and Bonaccorso, this volume). In general, fewer ectoparasites are found on those bats residing in man-made structures than on bats found in natural habitats, especially for species of habitat-dependent trombiculids, macronyssids, streblids, and nycteribiids.

Most phyllostomatids roost singly or in small clusters although there are exceptions such as the colonial species of *Phyllostomus*, *Desmodus*, *Brachyphylla*, *Phyllonycteris*, and *Erophylla*. A correlation may possibly be drawn between the large number of diverse ectoparasites and the more gregarious bats, especially *Desmodus rotundus*, *Phyllostomus discolor*, and *P. hastatus*, which host a wide range and number of ectoparasites. *Artibeus jamaicensis*, *Carollia perspicillata*, and *Glossophaga soricina* also are colonial and also harbor large numbers of

TABLE 1.—*Phyllostomatid subfamilies and number of ectoparasitic species exhibiting apparent subfamilial specificity.*

Parasite	Phyllostomatinae	Glossophaginae	Carolliinae	Stenoderminae	Phyllonycterinae	Desmodontinae
Gastronyssidae						
Phyllostomonyssus conradyunkeri				4		
Labidocarpidae						
Paralabidocarpus artibei				3		
Paralabidocarpus foxi				2		
Sarcoptidae						
Chirnyssoides caparti				7		1*
Spinturnicidae						
Periglischrus acutisternus	3			1*		
Periglischrus caligus		4				
Periglischrus cubanus					3	
Periglischrus delfinadoae	1					
Periglischrus dusbabeki	1					
Periglischrus gameroi	1					
Periglischrus herrerai						1
Periglischrus iheringi				18		
Periglischrus micronycteridis	2					
Periglischrus ojasti				2		
Periglischrus parvus	2					
Periglischrus ramirezi			1			
Periglischrus torrealbai	2					
Streblidae						
Anastrebla mattadeni		4				
Mastoptera minuta	3					
Neotrichobius delicatus	1*			4		
Paratrichobius longicrus			1*	4		

*Questionable or accidental occurrence

ectoparasites, most of them not host-limited. The extensive infestation of these bats may be explained by their colonial habits and their practice of cohabiting with other species of bats, sometimes, as with *C. perspicillata*, actually mixed with colonies of other bat species or in the same roost with other cavity-inhabiting bats (Pine, 1972). *Carollia perspicillata* may be the focus of infestation for these and other bat species through cohabitation as it is probably the most widespread and abundant species of colonial fruit-eating bat in the Neotropics. Fifty-eight species of ectoparasites are recorded form *C. perspicillata*, 18 of which are shared entirely or partially with *A. jamaicensis*, *G. soricina*, and *D. rotundus*. Although colonial, *Leptonycteris* and *Choeronycteris* harbor few ectoparasites, probably because of their migratory habits as they are flower feeders and migrate to stay in the "dry season" (Humphrey and Bonaccorso, this volume), extending into temperate regions where there are fewer parasitic arthropods.

Most of the phyllostomatid-infesting families of ectoparasites seemingly originated in the Old World; many probably were transported by vespertilionid bats to the New World where transfer to phyllostomatids and other bats occurred. Evidence for this mode of exchange may be seen in the macronyssids, spinturnicids, myobiids, sarcoptids, gastronyssids, and nycteribiids. Molossids may have been important for dissemination of the psorergatids from the Old World although vespertilionids once again are inferred strongly as the transport mechanism. Vespertilionids are likewise the major possible means of early dispersal to the New World for demodicids and ereynetids even though rodents, especially murids in the case of the ereynetids, may also have been significant transporters. Either rodent or avian hosts, or both, provided the ways and means for movement of the argasids to the New World. Emballonurids seem to have been important in older parasite transfer between the Old and New Worlds, particularly in the temperate climates and especially with the trombiculids and gastronyssids. The families Streblidae, Labidocarpidae, Spelaeorhynchidae, and probably Chirorhynchobiidae apparently arose in the New World. See Table 2.

Present day geographic distribution of certain ectoparasites possibly may be explained by the effects of continental proximity during early geologic times (Traub, 1972). Generally, however, today's geographic placement of nearly all families of phyllostomatid ectoparasites may be explained by Palaearctic migrational patterns of vespertilionid bats in late Cenozoic times or by over-water migration on birds of long-distance flight. Continental drift separated the land masses of Laurasia, Africa, and South America between 70 and 105 million years ago during the Cretaceous (Cracraft, 1974), forming water barriers to chiropteran and other vertebrate migrations in later periods. The earliest bat fossil from the early Eocene of Wyoming (Jepsen, 1966) is similar to extant microchiropterans. Even if bats had existed as early as the Paleocene (Vaughan, 1972), the oceanic gaps between continents still would have been a restrictive boundary to bats as most species generally do not traverse even small expanses of salt water.

Movement of tropical lowland mammal hosts, especially of rodents, and their parasites between South and Middle America apparently has been without great obstacles (Wenzel, 1972). Ectoparasites reflect the extensive range of a number of leaf-nosed species, several recorded from México to Peru and Brazil, and a free exchange between Mexican and South American tropical species may be seen with several examples: the streblid *Megistopoda aranea* found on *Artibeus jamaicensis* collected from México, Central America, and northern South America; the spinturnicid *Periglischrus iheringi* from *A. jamaicensis* from México, several Caribbean islands, and Venezuela; and the trombiculid *Loomisia desmodus* from *Glossophaga soricina* recovered from México, Nicaragua, Panamá, and northeastern South America. Others show an interchange between Central and South America, for example, *Trichobius joblingi* (streblid) from five Central American countries, Trinidad, Tobago, and northern South America. Because phyllostomatids are principally tropical species, the adjacent temperate climates represent barriers to them and their ectoparasites. The

TABLE 2.—*New World bat families and their ectoparasites. A single asterisk indicates a probable accidental record; a double asterisk indicates a commensal group; and a triple asterisk indicates a single record only.*

Parasitic group[1]	Emballonuridae	Noctilionidae	Phyllostomatidae	Mormoopidae	Natalidae	Furipteridae	Thyropteridae	Vespertilionidae	Molossidae
Acaridae								X	X
Anoetidae								X	
Argasidae	X	X	X	X	X			X	X
Chirorhynchobiidae			X						
Demodicidae			X					X	X[2]
Ereynetidae			X					X	
Gastronyssidae	X		X					X	X
Glycyphagidae								X	
Ixodidae		X***	X*					X***	
Labidocarpidae	X[3]	X[3, 4]	X	X				X	X
Laelapidae								X	
Macronyssidae	X		X	X	X			X	X
Myobiidae	X[5]		X	X				X	X
Psorergatidae	X		X					X[6]	X[6]
Pyroglyphidae								X	
Rosensteiniidae**			X					X	X
Sarcoptidae	X	X[7]	X					X	X
Spelaeorhynchidae			X	X					
Spinturnicidae		X	X	X	X			X	X
Trombiculidae	X	X[8]	X	X	X[8]			X	X
Nycteribiidae[9, 10]			X				X[10]	X	X
Streblidae[11]	X	X	X	X	X	X		X	X
Cimicidae[12]		X						X	X
Polyctenidae[13]				X					X
Siphonaptera[14, 15]								X	X

1, Records are from Anciaux de Faveaux, 1971, unless otherwise indicated; 2, Desch *et al.*, 1972; 3, Fain, 1970c; 4, McDaniel, 1970, 1972; 5, Dusbabek and Lukoschus, 1971a; 6, Lukoschus *et al.*, 1973; 7, Fain and Lukoschus, 1971b; 8, unpublished records of Loomis; 9, Guimarães, 1946; 10, Guimarães and D'Andretta, 1956; 11, Wenzel *et al.*, 1966; 12, Usinger, 1966; 13, Ueshima, 1972; 14, Tipton and Mendez, 1966; 15, Tipton and Machado-Allison, 1972.

temperate ectoparasitic fauna on bats, such as on species of the *Myotis nigricans* complex, shows little restriction to the temperate areas in the tropics in contrast to the rodent parasites (Wenzel, 1972), which is to be expected because of the volant nature of their hosts.

The distribution and numbers of the ectoparasitic taxa on phyllostomatid species may give some information regarding the relative duration of host-parasite associations. For instance, if one or two genera comprising only a few species of parasites are generally widespread on leaf-nosed bats, as in the case of the demodicids and psorergatids, then it may be assumed that the phyllostomatid-parasite relationship is a relatively recent one. In those with many species and genera, for example, macronyssids and labidocarpids, a longer period of as-

sociation is suggested. If the ectoparasites are represented by only a few genera containing numerous species, they probably have been affiliated for an intermediate period of time. Based on this interpretation, it appears that the streblid batflies with 20 genera and 82 species have had the longest association with phyllostomatid bats.

Fleas, polyctenids, and cimicids do not appear to be normal parasites of phyllostomatids, nor are they found regularly on Neotropical species of furipterids, emballonurids, mormoopids, natalids, noctilionids, or thyropterids. However, polyctenids are found almost exclusively on molossids and there are a few species of fleas and cimicids on the Neotropical members of the Molossidae and Vespertilionidae. These associations may suggest a recent arrival of these parasites from the Old World on members of these two advanced and widespread groups.

PARASITE-HOST LIST

Ectoparasites, and hosts for each, are listed alphabetically by genus and species. A single asterisck indicates an unpublished record from the Chigger Laboratory, California State University, Long Beach; two asterisks indicate an unpublished record from The Museum, Texas Tech University, Lubbock. Geographic origin of records is given if known. Since this list was prepared, four publications (Brennan and van Bronswijk, 1975; Brennan and Reed, 1975; Herrin and Yunker, 1975; Reed and Brennan, 1975) have appeared that should be consulted for additional records.

Alabidocarpus furmani Pinichpongse (LABIDOCARPIDAE)
    Anoura caudifer, Venezuela
    Anoura geoffroyi, Nicaragua and Trinidad
    Carollia brevicauda, Venezuela
    Carollia perspicillata, Venezuela
    Glossophaga longirostris, Venezuela
    Glossophaga soricina, Nicaragua
    Vampyrops helleri, Venezuela
Alabidocarpus guyanensis Fain
    Artibeus cinereus, Surinam
Alabidocarpus jonesi McDaniel
    Vampyrops helleri, Nicaragua and Venezuela
Alabidocarpus nicaraguae McDaniel
    Uroderma bilobatum, Nicaragua
    Uroderma magnirostrum, Venezuela
Alabidocarpus phyllostomi Fain
    Phyllostomus hastatus, Surinam
Alexfainia chilonycteris Yunker and Jones (TROMBICULIDAE)
    Carollia perspicillata, Panamá
Amblyomma sp. (IXODIDAE)
    Artibeus jamaicensis, Venezuela
    Artibeus lituratus, Venezuela
    Carollia brevicauda, Venezuela
    Carollia perspicillata, Venezuela
    Chiroderma villosum, Venezuela
    Choeroniscus monor, Venezuela
    Glossophaga longirostris, Venezuela

Glossophaga soricina, Venezuela
Sturnira tildae, Venezuela
Uroderma bilobatum, Venezuela
Vampyrops helleri, Venezuela
Amblyomma longirostre (Koch)
Artibeus lituratus, Venezuela
Anastrebla mattadeni Wenzel (STREBLIDAE)
Anoura sp., Venezuela
Anoura caudifer, Colombia
Anoura cultrata, Panamá
Anoura geoffroyi, Panama and Venezuela
Anastrebla modestini Wenzel
Anoura geoffroyi, Guatemala, México, Panamá, and Trinidad
Anastrebla nycteridis Wenzel
Lonchophylla robusta, Panamá
Anatrichobius scorzai Wenzel (STREBLIDAE)
Lonchophylla robusta, Panamá
Antricola sp. (ARGASIDAE)
Leptonycteris curasoae, Venezuela
Antricola marginatus (Banks)
Phyllonycteris poeyi, Cuba
Antricola silvai Cerný
Phyllonycteris poeyi, Cuba
Aspidoptera buscki Coquillett (STREBLIDAE)
Artibeus sp., Puerto Rico
Artibeus jamaicensis, Colombia, Cuba, Guatemala, México, and Panamá
Artibeus lituratus, Panamá
Carollia perspicillata, Panamá
Chiroderma villosum, Panamá
Phyllostomus discolor, Panamá
Vampyressa nymphaea, Panamá
Aspidoptera delatorrei Wenzel
Carollia perspicillata, Panamá
Sturnira lilium, Guatemala and Panamá
Aspidoptera phyllostomatis (Perty)
Anoura geoffroyi, Trinidad?
Artibeus sp.
Artibeus lituratus
Phyllostomus sp., Brazil
Sturnira lilium, Paraguay
Basilia sp. (NYCTERIBIIDAE)
Centurio senex
Basilia antrozoi (Townsend)
Leptonycteris sanborni
Basilia astochia Peterson and Maa
Vampyrops helleri, Colombia
Basilia bellardii Rondani
Phyllostomus sp., Brazil
Artibeus jamaicensis, Brazil
Basilia bequaerti Guimarães and D'Andretta
Micronycteris megalotis
Basilia constricta Guimarães and D'Andretta
Macrophyllum macrophyllum
Tonatia sylvicola
Uroderma bilobatum

Basilia corynorhini (Ferris)
   Leptonycteris nivalis, Texas
Basilia ferrisi Schuurmans-Stekhoven
   Desmodus rotundus, Venezuela
Basilia hughscotti Guimarães
   Chrotopterus auritus, Brazil
Basilia myotis Curran
   Uroderma bilobatum
Basilia rondanii Guimarães and D'Andretta
   Artibeus jamaicensis
   Hylonycteris underwoodi
Basilia speiseri (M. Ribeiro)
   Anoura geoffroyi
   Carollia perspicillata, Brazil
   Phyllostomus sp.
Basilia tiptoni Guimarães
   Mimon crenulatum, Panamá and Venezuela
Basilia wenzeli Guimarães and D'Andretta
   Artibeus jamaicensis, Panamá
   Lonchorhina aurita, Venezuela
Beamerella acutascuta Brennan (TROMBICULIDAE)
   Carollia sp., Costa Rica*
   Carollia perspicillata, Nicaragua*, Panamá, and Trinidad
   Glossophaga soricina, México*
   Lonchophylla concava, Costa Rica*
   Micronycteris hirsuta, Panamá and Trinidad
   Micronycteris megalotis, Panama
   Phyllostomus discolor, Nicaragua*
Beamerella subacutascuta Vercammen-Grandjean
   Micronycteris hirsuta, Trinidad
Blankaartia sinnamaryi Floch and Fauran (TROMBICULIDAE)
   Phyllostomus hastatus, Panamá
Chirnyssoides sp. (SARCOPTIDAE)
   Carollia perspicillata, Brazil
Chirnyssoides amazonae Fain
   Carollia perspicillata, Brazil
Chirnyssoides brasiliensis Fain
   Sturnira lilium, Brazil
Chirnyssoides caparti Fain
   Artibeus cinereus, Panamá
   Artibeus jamaicensis, Brazil, México**, and Panamá
   Artibeus toltecus, México** and Panamá
   Chiroderma salvini, Panamá
   Desmodus rotundus, Panamá
   Vampyressa pusilla, Panamá
   Vampyrodes caraccioloi, Panamá
   Vampyrops vittatus, Panamá
Chirnyssoides carolliae Fain
   Carollia sp., Panamá
   Carollia perspicillata, Panamá and Surinam
   Carollia subrufa, Panamá
   Glossophaga soricina, Surinam
   Micronycteris megalotis, Surinam
Chirnyssoides surinamensis Fain and Lukoschus
   Carollia perspicillata, Surinam

Chirnyssoides venezuelae Fain
  Tonatia venezuelae, Venezuela
Chirnyssoides zanderyensis Fain and Lukoschus
  Carollia perspicillata, Surinam
Chiroecetes lonchophylla Herrin and Radovsky (MACRONYSSIDAE)
  Lonchophylla robusta, Venezuela
Chiroptella myops Vitzthum (TROMBICULIDAE)
  Artibeus jamaicensis, México
Chirorhynchobia matsoni Yunker (CHIRORHYNCHOBIIDAE)
  Anoura geoffroyi, Venezuela
Chirnyssoides urodermae Fain
  Uroderma bilobatum, Panamá
Demodex carolliae Desch, Lebel, Nutting, and Lukoschus (DEMODICIDAE)
  Carollia perspicillata, Surinam
Demodex longissimus Desch, Nutting, and Lukoschus
  Carollia perspicillata, Surinam
Demodex phyllostomatis Leydig
  Phyllostomus hastatus, Surinam
Eldunnia breviceps Curran (STREBLIDAE)
  Lonchophylla robusta, Panamá
Eudusbabekia arganoi (Vomero) (MYOBIIDAE)
  Desmodus rotundus, México
Eudusbabekia cernyi (Dusbabek)
  Brachyphylla nana, Cuba
Eudusbabekia danieli (Dusbabek)
  Phyllonycteris poeyi, Cuba
Eudusbabekia lepidoseta Jameson
  Sturnira lilium, Nicaragua
Eudusbabekia phyllostomi Jameson
  Phyllostomus discolor, Nicaragua
Eudusbabekia rosickyi (Dusbabek)
  Monophyllus cubanus, Cuba
Eudusbabekia samsinaki (Dusbabek)
  Macrotus waterhousii, Cuba (Isla de Pinos)
Eudusbabekia urodermae Fain
  Uroderma magnirostrum, Brazil
Eudusbabekia viguerasi (Dusbabek)
  Artibeus jamaicensis, Cuba (Isla de Pinos) and México**
Eutrombicula alfreddugesi (Oudemans) (TROMBICULIDAE)
  Artibeus aztecus, México*
  Artibeus jamaicensis, Costa Rica*
Eutrombicula batatas (Linnaeus)
  Micronycteris megalotis, Venezuela
  Uroderma bilobatum, Trinidad
Eutrombicula goeldii (Oudemans)
  Artibeus cinereus, Trinidad
  Carollia brevicauda, Venezuela
  Glossophaga longirostris, Venezuela
  Phyllostomus discolor, Venezuela
  Phyllostomus hastatus, Venezuela
  Sturnira lilium, Venezuela
Eutrombicula nadchatrami Brennan and Reed
  Vampyrops helleri, Venezuela
Eutrombicula pacae (Floch and Fauran)
  Carollia brevicauda, Venezuela

Eutrombicula variabilis Brennan and Reed
Macrophyllum macrophyllum, Venezuela
Eutrombicula webbi Brennan and Reed
Artibeus jamaicensis, Venezuela
Exastinion clovisi (Pessôa and Guimarães) (STREBLIDAE)
Anoura sp., Venezuela
Anoura cultrata, Panamá
Anoura geoffroyi, Brazil, Colombia, Panamá, Trinidad, and Venezuela
Sturnira lilium
Hooperella saccopteryx Brennan and Jones (TROMBICULIDAE)
Artibeus jamaicensis, Costa Rica*
Desmodus rotundus, Trinidad
Glossophaga soricina, Costa Rica*
Glossophaga commissarisi, México*
Hooperella spinirostra Vercammen-Grandjean
Micronycteris megalotis, Brazil
Hooperella vesperuginis (Brennan and Jones)
Artibeus jamaicensis, México, Nicaragua*, and Trinidad
Artibeus lituratus, México*
Carollia sp., Panamá
Carollia castanea, Nicaragua*
Carollia perspicillata, Nicaragua*, Surinam, and Trinidad
Carollia subrufa, México* and Nicaragua*
Chrotopterus auritus, Nicaragua*
Desmodus rotundus, Nicaragua* and Trinidad
Glossophaga alticola, México* and Nicaragua*
Glossophaga commissarisi, Nicaragua*
Glossophaga soricina, México*, Nicaragua*, Panamá, and Surinam
Micronycteris hirsuta, Trinidad
Micronycteris megalotis, Trinidad
Phyllostomus discolor, Nicaragua*
Sturnira lilium, Nicaragua*
Vampyrum spectrum, Panamá and Trinidad
Ioannela martae Dusbabek and Lukoschus (MYOBIIDAE)
Mimon crenulatum, Venezuela
Ixodes sp. (IXODIDAE)
Artibeus jamaicensis, Venezuela
Sturnira lilium, Venezuela
Sturnira ludovici, Venezuela
Ixodes downsi Kohls
Anoura geoffroyi, Trinidad
Labidocarpus lukoschi Fain (LABIDOCARPIDAE)
Micronycteris megalotis, Surinam
Lawrenceocarpus lobus McDaniel (LABIDOCARPIDAE)
Carollia perspicillata, Nicaragua
Lawrenceocarpus micropilus Dusbabek and de la Cruz
Brachyphylla cavernarum, Puerto Rico
Lawrenceocarpus phyllostomus McDaniel
Micronycteris hirsuta, Venezuela
Phyllostomus elongatus, Venezuela
Lawrenceocarpus puertoricensis de la Cruz, Tamsitt, and Valdivieso
Brachyphylla cavernarum, Puerto Rico
Leptotrombidium hamaxiaium (Brennan and Dalmat) (TROMBICULIDAE)
Artibeus jamaicensis, Costa Rica*
Artibeus toltecus, Panamá

Loomisia alcithoae Brennan and Reed (TROMBICULIDAE)
>   *Carollia* sp., Venezuela

Loomisia desmodus (Brennan and Dalmat)
>   *Anoura geoffroyi*, Venezuela
>   *Artibeus toltecus*, Costa Rica* and Nicaragua*
>   *Carollia* sp., Venezuela
>   *Carollia castanea*, Costa Rica*
>   *Carollia perspicillata*, Colombia, Nicaragua*, Surinam, Trinidad and Venezuela
>   *Carollia subrufa*, Nicaragua*, Panamá, and Venezuela
>   *Desmodus rotundus*, Guatemala, Nicaragua*, and Venezuela
>   *Erophylla sezekorni*, Bahamas
>   *Glossophaga longirostris*, Venezuela
>   *Glossophaga soricina*, México, Nicaragua*, Panamá, Surinam, and Venezuela
>   *Lonchophylla robusta*, Costa Rica* and Venezuela
>   *Micronycteris megalotis*, Panamá and Trinidad
>   *Mimon cozumelae*, México
>   *Sturnira lilium*, Venezuela
>   *Trachops cirrhosus*, México*
>   *Vampyrops vittatus*, Costa Rica*

Loomisia sprocssi (Brennan)
>   *Carollia castanea*, Nicaragua*
>   *Glossophaga soricina*, México
>   *Lonchophylla concava*, Costa Rica*
>   *Macrotus californicus*, California

Loomisia univari (Brennan)
>   *Glossophaga soricina*, México*

Loomisia yunkeri Brennan and Reed
>   *Carollia* sp., Venezuela

Macronyssoides sp. (MACRONYSSIDAE)
>   *Enchisthenes hartii*, Panamá
>   *Uroderma bilobatum*, Panamá
>   *Vampyressa pusilla*, Panamá

Macronyssoides conciliatus Radovsky
>   *Vampyrops vittatus*, Panamá

Macronyssoides kochi (Fonseca)
>   *Artibeus aztecus*, Panamá
>   *Artibeus jamaicensis*, Cuba, Panamá, and Trinidad
>   *Artibeus lituratus*, Brazil, Colombia, and Trinidad
>   *Artibeus toltecus*, Panamá
>   *Brachyphylla nana*, Cuba
>   *Desmodus rotundus*, Brazil and Trinidad
>   *Glossophaga soricina*, Trinidad
>   *Phyllonycteris poeyi*, Cuba

Macronyssus unidens Radovsky (MACRONYSSIDAE)
>   *Leptonycteris sanborni*, Arizona

Mastoptera guimaraesi Wenzel (STREBLIDAE)
>   *Carollia perspicillata*, Panamá
>   *Phyllostomus* sp., Panamá
>   *Phyllostomus hastatus*, Colombia and Panamá

Mastoptera minuta (Costa Lima)
>   *Phyllostomus hastatus*, Colombia
>   *Tonatia* sp., Bolivia, Colombia, Ecuador, Perú, and Surinam
>   *Tonatia nicaraguae*, Panamá
>   *Tonatia sylvicola*, Brazil and Panamá

Megistopoda sp (STREBLIDAE)
  Artibeus cinereus, Trinidad
Megistopoda aranea (Coquillett)
  Artibeus jamaicensis, Brazil, Costa Rica, Colombia, Cuba, El Salvador,
      Guatemala, México, Panamá, Puerto Rico, Surinam, Trinidad, and Venezuela
  Artibeus lituratus, Colombia, Panamá, and Trinidad
  Carollia perspicillata, Panamá
  Desmodus rotundus, Panamá
  Phyllostomus sp., Brazil and Cuba
  Phyllostomus discolor, Panamá
Megistopoda pilatei Macquart
  Vampyrops lineatus, Brazil, Cuba, México, and U.S.A.
Megistopoda proxima (Séguy)
  Sturnira lilium, Colombia and Panamá
  Sturnira ludovici, Costa Rica
Megistopoda theodori Wenzel
  Sturnira ludovici, Panamá
Metelasmus pseudopterus Coquillett (STREBLIDAE)
  Artibeus jamaicensis, Panamá
  Artibeus lituratus, Panamá and Paraguay
  Carollia perspicillata, Panamá
  Vampyressa nymphaea, Panamá
Microtrombicula boneti (Hoffmann) (TROMBICULIDAE)
  Artibeus toltecus, México*
  Desmodus rotundus, México*
  Erophylla sezekorni, Bahamas
  Glossophaga soricina, México*
  Micronycteris megalotis, Curaçao
  Phyllostomus hastatus, Panamá
Microtrombicula carmenae (Brennan and Jones)
  Artibeus jamaicensis, Panamá
  Phyllostomus discolor, Costa Rica, Nicaragua, and Trinidad
  Phyllostomus hastatus, Panamá
  Sturnira ludovici, Costa Rica and Panamá
  Sturnira mordax, Costa Rica
Microtrombicula sturnirae Webb and Loomis
  Sturnira lilium, México and Nicaragua
  Sturnira ludovici, Costa Rica and Panamá
  Sturnira mordax, Costa Rica
Nasicola annereauxi Brennan and Yunker (TROMBICULIDAE)
  Phyllostomus hastatus, Venezuela
Neotrichobius delicatus (Machado-Allison) (STREBLIDAE)
  Artibeus cinereus, Panamá and Trinidad
  Artibeus jamaicensis, Panamá
  Phyllostomus hastatus, Surinam
  Uroderma bilobatum, Panamá
  Vampyressa pusilla, Panamá and Venezuela
Nycteriglyphus sturnirae Fain (ROSENSTEINIIDAE)
  Sturnira lilium, Brazil
Nycterinastes primus Brennan and Reed (TROMBICULIDAE)
  Anoura sp., Venezuela
  Anoura geoffroyi, Venezuela
  Carollia perspicillata, Venezuela
  Desmodus rotundus, Venezuela

    Glossophaga soricina, Venezuela
    Lionycteris spurrelli, Venezuela
    Lonchorhina aurita, Venezuela
Nycterinastes secundus Brennan and Reed
    Anoura geoffroyi, Costa Rica* and Venezuela
    Lonchophylla robusta, Costa Rica*
Nycteronyssus desmodus Herrin and Radovsky (MACRONYSSIDAE)
    Diaemus youngii, Venezuela
Nycterophilia sp. (STREBLIDAE)
    Macrotus waterhousii, México*
Nycterophilia coxata Ferris
    Artibeus jamaicensis
    Brachyphylla cavernarum, British West Indies
    Macrotus californicus, Arizona and California
    Macrotus waterhousii, México
Nycterophilia parnelli Wenzel
    Carollia perspicillata, Panamá
    Macrotus waterhousii, Cuba
Ornithodoros sp. (ARGASIDAE)
    Leptonycteris curasoae, Venezuela
    Lonchorhina orinocensis, Venezuela
    Macrotus californicus, Arizona
    Mimon crenulatum, Venezuela
    Sturnira lilium, Venezuela
    Trachops cirrhosus, Venezuela
Ornithodoros azteci Matheson
    Artibeus jamaicensis, Cuba, México, and Venezuela
    Brachyphylla nana, Cuba
    Carollia sp., Venezuela
    Desmodus rotundus, México, Panamá, Trinidad
    Glossophaga longirostris, Venezuela
    Glossophaga soricina, Venezuela
    Lonchorhina aurita, Cuba, Jamaica, Trinidad, and Venezuela
    Macrophyllum macrophyllum, Venezuela
    Macrotus waterhousii, Cuba
    Phyllostomus hastatus, Venezuela
    Trachops cirrhosus, Venezuela
Ornithodoros brodyi Matheson
    Artibeus jamaicensis, México
    Carollia sp., Venezuela
    Carollia perspicillata, Panamá and Venezuela
    Chrotopterus auritus, México
    Lonchorhina aurita, Venezuela
    Trachops cirrhosus, Panamá
Ornithodoros dusbabeki Cerný
    Artibeus jamaicensis, Cuba (Isla de Pinos)
Ornithodoros hasei (Schulze)
    Artibeus jamaicensis, Venezuela
    Artibeus lituratus, Costa Rica
    Brachyphylla cavernarum, Guadeloupe* and Martinique
    Carollia sp., Venezuela
    Carollia perspicillata, Venezuela
    Chiroderma salvini, Venezuela
    Glossophaga longirostris, Venezuela

Lonchorhina aurita, Venezuela
Lonchorhina orinocensis, Venezuela
Macrotus waterhousii, Jamaica**
Mimon crenulatum, Venezuela
Phyllonycteris aphylla, Jamaica**
Phyllostomus hastatus, Venezuela
Sturnira lilium, Venezuela
Sturnira ludovici, Venezuela
Tonatia sylvicola, Panamá
Uroderma bilobatum, Panamá
Uroderma magnirostrum, Venezuela
Vampyrops helleri, Panamá
Ornithodoros mimon Kohls, Clifford, and Jones
Mimon crenulatum, Bolivia
Ornithodoros peruvianus Kohls, Clifford, and Jones
Desmodus rotundus, Perú
Glossophaga sp., Perú
Ornithodoros rossi Kohls, Sonenshine, and Clifford
Glossophaga longirostris, Venezuela
Leptonycteris nivalis, Arizona
Lonchorhina orinocensis, Venezuela
Macrotus californicus, México
Ornithodoros viguerasi Cooley and Kohls
Brachyphylla nana, Cuba
Erophylla bombifrons, Puerto Rico
Phylloncyteris poeyi, Cuba and Haiti**
Ornithodoros yumatensis Cooley and Kohls
Artibeus aztecus, México
Artibeus lituratus, México
Carollia perspicillata, Venezuela
Desmodus rotundus, México
Paradyschiria parvuloides Wenzel (STREBLIDAE)
Anoura geoffroyi
Glossophaga soricina
Paraeuctenodes longipes Pessôa and Guimarães (STREBLIDAE)
Anoura caudifer, Brazil
Anoura geoffroyi
Phyllostomus hastatus, Brazil
Parakosa maxima McDaniel (LABIDOCARPIDAE)
Enchisthenes hartii, Venezuela
Glossophaga longirostris, Venezuela
Parakosa tadarida McDaniel and Lawrence
Carollia brevicauda, Venezuela
Glossophaga longirostris, Venezuela
Sturnira lilium, Venezuela
Paralabidocarpus artibei Pinichpongse (LABIDOCARPIDAE)
Artibeus lituratus, Trinidad
Stenoderma rufum, Puerto Rico
Sturnira lilium, Nicaragua
Paralabidocarpus carolliae Fain
Carollia perspicillata, Surinam
Paralabidocarpus desmodus Fain
Desmodus rotundus, Surinam
Paralabidocarpus foxi de la Cruz, Tamsitt, and Valdivieso
Artibeus jamaicensis, Puerto Rico
Stenoderma rufum, Puerto Rico

Paralabidocarpus macrophyllum Fain
  Macrophyllum macrophyllum, Surinam
Paralabidocarpus stenodermi de la Cruz, Tamsitt, and Valdivieso
  Stenoderma rufum, Puerto Rico
Paralabidocarpus tonatiae Fain
  Tonatia venezuelae, Venezuela
Paralabidocarpus trachops Fain
  Trachops cirrhosus, Surinam
Parascoschoengastia aemulata (Brennan and Jones) (TROMBICULIDAE)
  Anoura caudifer, Venezuela
  Sturnira lilium, México*
Parascoschoengastia megastyrax (Brennan and Jones)
  Carollia perspicillata, Panamá
Parasecia longicalcar (Brennan and Jones) (TROMBICULIDAE)
  Desmodus rotundus, Trinidad
  Vampyrum spectrum, Panamá
Parasecia manueli (Brennan and Yunker)
  Uroderma bilobatum; Costa Rica*
Parasecia soucouyanti (Brennan and Yunker)
  Sturnira ludovici, Panamá
Parastrebla handleyi Wenzel (STREBLIDAE)
  Micronycteris nicefori, Panamá
Paratrichobius sp. (STREBLIDAE)
  Artibeus aztecus, Panamá
  Artibeus lituratus, Colombia and Panamá
  Artibeus toltecus, Panamá
  Chiroderma villosum, Panamá
  Vampyrops helleri, Panamá
  Vampyrops vittatus, Panamá
Paratrichobius americanus Peterson and Ross
  Choeronycteris mexicana, Arizona
Paratrichobius dunni (Curran)
  Artibeus jamaicensis
  Uroderma bilobatum, Panamá
Paratrichobius longicrus (M. Ribeiro)
  Artibeus jamaicensis, Brazil, Colombia, and Panamá
  Artibeus lituratus, El Salvador and Trinidad
  Carollia perspicillata
  Uroderma bilobatum
  Vampyrops lineatus
Paratrichobius lowei Wenzel
  Artibeus watsoni, Panamá
Paratrichobius salvini Wenzel
  Chiroderma salvini, Panamá
Paratrichobius sanchezi Wenzel
  Enchisthenes hartii, Panamá and Venezuela
Parichoronyssus sp. (MACRONYSSIDAE)
  Artibeus aztecus, Panamá
  Artibeus toltecus, Panamá
  Vampyrodes caraccioloi, Panamá
Parichoronyssus crassipes Radovsky
  Carollia perspicillata, Panamá
Parichoronyssus euthysternum Radovsky
  Sturnira ludovici, Panamá

Parichoronyssus sclerus Radovsky

> *Glossophaga soricina*, Panamá
> *Phyllostomus* sp., Costa Rica

Perates anophthalma (Hoffmann) (Trombiculidae)

> *Artibeus aztecus*, México*
> *Carollia perspicillata*, Trinidad
> *Desmodus rotundus*, México and Panamá
> *Erophylla sezekorni*, Bahamas
> *Micronycteris megalotis*, Colombia and Perú

Periglischrus sp. (Spinturnicidae)

> *Carollia perspicillata*, Panamá
> *Lonchophylla robusta*, Panamá
> *Macrophyllum macrophyllum*, Panamá

Periglischrus acutisternus Machado-Allison

> *Artibeus concolor*, Venezuela
> *Phyllostomus discolor*, Trinidad and Venezuela
> *Phyllostomus elongatus*, Trinidad and Venezuela
> *Phyllostomus hastatus*, Colombia, Panamá, Trinidad, and Venezuela

Periglischrus caligus Kolenati

> *Anoura caudifer*, Venezuela
> *Anoura cultrata*, Venezuela
> *Glossophaga* sp., México and Panamá
> *Glossophaga longirostris*, Venezuela
> *Glossophaga soricina*, Brazil, Panamá, Surinam, Trinidad, and Venezuela

Periglischrus cubanus Dusbabek

> *Brachyphylla nana*, Cuba
> *Erophylla sezekorni*, Cuba
> *Phyllonycteris poeyi*, Cuba

Periglischrus delfinadoae Dusbabek

> *Macrotus waterhousii*, Cuba

Periglischrus dusbabeki Machado-Allison and Antequera

> *Mimon crenulatum*, Venezuela

Periglischrus gameroi Machado-Allison and Antequera

> *Lonchorhina aurita*, Venezuela

Periglischrus herrerai Machado-Allison

> *Desmodus rotundus*, Panamá, Trinidad, and Venezuela

Periglischrus hopkinsi Machado-Allison

> *Lionycteris spurrelli*, Venezuela
> *Rhinophylla pumilio*, Brazil and Venezuela

Periglischrus iheringi Oudemans

> *Artibeus* sp., Panamá
> *Artibeus aztecus*, México, Panamá, and Venezuela
> *Artibeus cinereus*, Panamá, Paraguay, and Venezuela
> *Artibeus toltecus*, Panamá and Venezuela
> *Artibeus concolor*, Venezuela
> *Artibeus jamaicensis*, Cuba, México, Panamá, Puerto Rico, Venezuela, and Virgin Islands
> *Artibeus lituratus*, Brazil, Colombia, Guatemala, Honduras, Panamá, Paraguay, Surinam, Trinidad, and Venezuela
> *Chiroderma* sp., Venezuela
> *Chiroderma salvini*, Panamá and Venezuela
> *Desmodus rotundus*, México and Panamá
> *Enchisthenes hartii*, Panamá and Venezuela
> *Stenoderma rufum*, Puerto Rico

  Sturnira lilium, México
  Sturnira ludovici, Colombia and Venezuela
  Uroderma bilobatum, Guatemala, Panamá, Paraguay, and Venezuela
  Vampyressa pusilla, Panamá
  Vampyrodes caraccioloi, Panamá
  Vampyrops sp., Paraguay
  Vampyrops dorsalis, Venezuela
  Vampyrops helleri, México and Panamá
  Vampyrops lineatus, Brazil
  Vampyrops vittatus, Panamá, Paraguay, and Venezuela
Periglischrus micronycteridis Furman
  Micronycteris megalotis, Panamá and Trinidad
  Micronycteris minuta, Panamá
Periglischrus ojasti Machado-Allison
  Artibeus toltecus, México**
  Sturnira lilium, Panamá, Trinidad, and Venezuela
  Sturnira ludovici, Panamá
Periglischrus paracutisternus Machado-Allison
  Anoura geoffroyi, Venezuela
  Trachops cirrhosus, Venezuela
Periglischrus parvus Machado-Allison
  Micronycteris sp., Venezuela
  Micronycteris megalotis, Panamá and Trinidad
  Micronycteris minuta, Panamá
Periglischrus ramirezi Machado-Allison and Antequera
  Rhinophylla pumilio, Brazil and Venezuela
Periglischrus torrealbai Machado-Allison
  Phyllostomus discolor, Venezuela
  Phyllostomus hastatus, Panamá, Trinidad, and Venezuela
Periglischrus vargasi Hoffmann
  Anoura sp., Guatemala
  Anoura caudifer, Venezuela
  Anoura cultrata, Panamá and Venezuela
  Anoura geoffroyi, Colombia, Guatemala, México, Panamá, and Venezuela
  Artibeus jamaicensis, Cuba and Puerto Rico
  Leptonycteris nivalis, México and Texas
  Leptonycteris sanborni, México
  Macrotus californicus, México
  Macrotus waterhousii, México
  Monophyllus cubanus, Cuba
  Sturnira lilium, México
  Trachops cirrhosus, Panamá
Perissopalla barticonycteris Brennan (Trombiculidae)
  Carollia perspicillata, Surinam
  Micronycteris daviesi, Brazil
Perissopalla beltrani (Hoffmann)
  Artibeus aztecus, México*
  Artibeus hirsutus, México*
  Glossophaga soricina, México*
  Macrotus californicus, Arizona*, California*, and México*
Perissopalla deopertus (Brennan)
  Micronycteris megalotis, Perú
Perissopalla exhumatus (Brennan)
  Carollia perspicillata, Perú and Trinidad

   Desmodus rotundus, Trinidad
   Diaemus youngii, Trinidad
   Glossophaga soricina, Trinidad
   Micronycteris megalotis, Perú
Perissopalla ipeani Brennan
   Carollia perspicillata, Brazil and Surinam
Perissopalla precaria (Brennan and Dalmat)
   Desmodus rotundus, Trinidad
   Glossophaga soricina, México
   Micronycteris megalotis, Panamá
Phyllostomonyssus conradyunkeri Fain (GASTRONYSSIDAE)
   Artibeus jamaicensis, Venezuela
   Artibeus lituratus, Surinam and Venezuela
   Uroderma bilobatum, Surinam
   Vampyrops helleri, Surinam
Pseudoalabidocarpus secus McDaniel (LABIDOCARPIDAE)
   Phyllostomus discolor, Venezuela
   Phyllostomus elongatus, Venezuela
Pseudoschoengastia bulbifera Brennan (TROMBICULIDAE)
   Sturnira ludovici, Panamá
Pseudostrebla greenwelli Wenzel (STREBLIDAE)
   Tonatia nicaraguae, Panamá
Pseudostrebla ribeiroi Costa Lima
   Tonatia sylvicola, Brazil and Panamá
Psorergatoides artibei Lukoschus, Rosmalen, and Fain (PSORERGATIDAE)
   Artibeus lituratus, Surinam
Psorergatoides glossophagae Lukoschus, Rosmalen, and Fain
   Glossophaga soricina, Surinam
Psorergatoides lonchorhinae Fain
   Lonchorhina aurita, Venezuela
Radfordiella anourae Radovsky, Jones, and Phillips (MACRONYSSIDAE)
   Anoura geoffroyi, México
Radfordiella carolliae Radovsky
   Carollia castanea, Panamá
   Carollia perspicillata, Panamá (Canal Zone)
Radfordiella desmodi Radovsky
   Carollia perspicillata, Trinidad
   Desmodus rotundus, Panamá and Trinidad
Radfordiella monophylli Radovsky, Jones, and Phillips
   Monophyllus redmani, Cuba
Radfordiella oricola Radovsky, Jones, and Phillips
   Anoura geoffroyi, México
   Leptonycteris nivalis, México
Radfordiella oudemansi Fonseca
   Brachyphylla cavernarum, Puerto Rico
   Desmodus rotundus, Brazil
   Diaemus youngii, Trinidad
Speiseria ambigua Kessel (STREBLIDAE)
   Anoura geoffroyi, Trinidad
   Carollia castanea, Panamá
   Carollia perspicillata, Colombia, Panamá, and Trinidad
   Carollia subrufa, Panamá
   Desmodus rotundus, Panamá
   Glossophaga soricina, Trinidad
   Lonchophylla robusta, Panamá

    Lonchorhina aurita, Panamá
    Micronycteris brachyotis, Trinidad
    Phyllostomus hastatus, Panamá
    Tonatia bidens
    Trachops cirrhosus, Panamá
    Vampyrops vittatus, Panamá
Spelaeorhynchus sp. (SPELAEORHYNCHIDAE)
    Carollia perspicillata, Brazil
Spelaeorhynchus monophylli Fain, Anastos, Camin, and Johnston
    Monophyllus redmani, Puerto Rico
Spelaeorhynchus praecursor Neumann
    Artibeus sp., México
    Artibeus jamaicensis, Cuba, Dominican Republic, Mexico**, and Puerto Rico
    Carollia castanea, México
    Carollia perspicillata, Brazil, Colombia, México, and Venezuela
    Glossophaga soricina, Amazon(?)
Speleochir aitkeni Fain (EREYNETIDAE)
    Anoura geoffroyi, Trinidad
Speleochir barbulata Fain and Aitken
    Mimon crenulatum, Brazil
Speleochir brasiliensis Fain and Aitken
    Artibeus jamaicensis, Brazil
    Vampyrodes caraccioloi, Brazil
Speleochir carolliae Fain and Lukoschus
    Carollia perspicillata, Surinam
Speleochir phyllostomi (Clark)
    Phyllostomus hastatus, Colombia
Speleocola davisi Webb and Loomis (TROMBICULIDAE)
    Desmodus rotundus, México
    Glossophaga soricina, México
    Leptonycteris sanborni, México
Speleocola secunda Brennan and Jones
    Carollia castanea, Nicaragua*
    Carollia perspicillata, Surinam
    Carollia subrufa, Nicaragua*
    Desmodus rotundus, Trinidad
    Glossophaga commissarisi, Nicaragua*
    Glossophaga soricina, Nicaragua
    Micronycteris hirsuta, Trinidad
    Micronycteris megalotis, Trinidad
Steatonyssus joaquimi (Fonseca) (MACRONYSSIDAE)
    Glossophaga soricina, Brazil
Stizostrebla longirostris Jobling (STREBLIDAE)
    Tonatia sp., Brazil and Colombia
Strebla sp. (STREBLIDAE)
    Diaemus youngii, Trinidad
Strebla altmani Wenzel
    Carollia perspicillata, Panamá
    Lonchorhina aurita, Panamá and Venezuela
    Macrophyllum macrophyllum, Panamá
    Trachops cirrhosus, Panamá
Strebla alvarezi Wenzel
    Micronycteris megalotis, Panamá
    Micronycteris nicefori, Panamá
    Micronycteris sylvestris, Panamá

Strebla carolliae Wenzel
  Artibeus jamaicensis, Panamá
  Carollia sp., Surinam
  Carollia castanea, Panamá
  Carollia perspicillata, Brazil, Colombia, Panamá, Trinidad, and Venezuela
  Carollia subrufa, Panamá
  Desmodus rotundus, Panamá
  Glossophaga soricina, El Salvador, Panamá, and Venezuela
  Lonchophylla robusta, Panamá
  Lonchorhina aurita, Panamá
  Macrophyllum macrophyllum, Panamá
  Phyllostomus hastatus, Panamá
  Trachops cirrhosus, Panamá
Strebla christinae Wenzel
  Phylloderma stenops, Panamá
Strebla consocius Wenzel
  Carollia perspicillata, Trinidad
  Phyllostomus sp., Perú and Surinam
  Phyllostomus discolor, Colombia
  Phyllostomus hastatus, Surinam, Trinidad, and Venezuela
  Trachops sp., Perú
Strebla diaemi Wenzel
  Diaemus youngii, Colombia and Panamá
Strebla diphyllae Wenzel
  Desmodus rotundus, Guatemala
  Diphylla ecaudata, Guatemala and México
  Trachops cirrhosus, Guatemala
Streble galindoi Wenzel
  Tonatia sp., Trinidad
  Tonatia bidens, Panamá
Strebla hertigi Wenzel
  Artibeus jamaicensis, Panamá
  Desmodus rotundus, El Salvador and Panamá
  Phyllostomus discolor, Colombia, Costa Rica, El Salvador, México
      Nicaragua, Panamá, Surinam, Trinidad, and Venezuela
  Phyllostomus hastatus, Costa Rica, Nicaragua, and Panamá
Strebla hoogstraali Wenzel
  Tonatia nicaraguae, Panamá
Strebla kohlsi Wenzel
  Tonatia sylvicola, Colombia and Panamá
Strebla machadoi Wenzel
  Micronycteris minuta, Venezuela
Strebla mirabilis (Waterhouse)
  Carollia perspicillata, Brazil, Panamá, and Trinidad
  Desmodus rotundus, Perú and Trinidad
  Diphylla ecaudata
  Glossophaga soricina, Trinidad
  Phyllostomus sp., Brazil, Panamá, and Perú
  Phyllostomus discolor, Trinidad
  Phyllostomus elongatus
  Phyllostomus hastatus, Colombia, Panamá, Perú, and Trinidad
  Tonatia sp., Colombia
  Tonatia bidens
Strebla tonatiae (Kessel)
  Tonatia bidens
  Tonatia brasiliense, Ecuador and Panamá

Strebla wiedemanni Kolenati
    Anoura caudifer, Brazil
    Anoura geoffroyi
    Artibeus jamaicensis, Panamá
    Chrotopterus auritus, Brazil
    Desmodus rotundus, Colombia, Ecuador, El Salvador, Guatemala,
    Desmodus rotundus, Colombia, Ecuador, El Salvador, Guatemala, Honduras,
        México, Panamá, Perú, Surinam, Trinidad, and Venezuela
    Vampyrops lineatus, Brazil
Tecomatlana sandovali Hoffmann (TROMBICULIDAE)
    Artibeus phaeotis, México*
    Desmodus rotundus, México*
    Macrotus californicus, Arizona
Tecomatlana watkinsi Vercammen-Grandjean
    Macrotus californicus, Arizona*, California, and México*
Trichobioides perspicillatus (Pessôa and Galvão) (STREBLIDAE)
    Carollia perspicillata, Brazil, México, and Perú
    Desmodus rotundus, Panamá and Trinidad
    Phyllostomus discolor, Colombia, Panamá, and Trinidad
    Phyllostomus elongatus, Colombia
    Phyllostomus hastatus, Surinam
    Sturnira lilium, Panamá
Trichobius adamsi Augustson (STREBLIDAE)
    Macrotus californicus, Arizona, California, and México
Trichobius bequaerti Wenzel
    Tonatia bidens, Panamá
Trichobius brennani Wenzel
    Sturnira ludovici, Panamá
Trichobius cernyi Peterson and Hůrka
    Artibeus jamaicensis, Cuba
    Monophyllus redmani, Cuba
    Phyllonycteris poeyi, Cuba
Trichobius costalimai Guimarães
    Artibeus lituratus, Panamá
    Carollia perspicillata, Panamá
    Desmodus rotundus, Panamá
    Phyllostomus discolor, Colombia, El Salvador, Guatemala, Panamá, Perú,
        Puerto Rico, Trinidad, and Venezuela
    Uroderma bilobatum, Panama
Trichobius diphyllae Wenzel
    Diphylla ecaudata, Guatemala, México, and Venezuela
Trichobius dominicanus Peterson and Hůrka
    Monophyllus sp., Dominican Republic
Trichobius dugesii Townsend
    Anoura geoffroyi, Trinidad
    Artibeus jamaicensis, Cuba and Panamá
    Carollia perspicillata, Costa Rica, Nicaragua, Panamá, and
        Trinidad
    Desmodus rotundus, Trinidad
    Diaemus youngii, Trinidad
    Enchisthenes hartii, Trinidad
    Glossophaga soricina, Colombia, El Salvador, Guatemala, México,
        Panamá, Perú, and Trinidad
    Micronycteris brachyotis, Trinidad
    Phyllostomus hastatus, Trinidad
    Trachops cirrhosus, Panamá

Trichobius dugesioides Wenzel
  Carollia perspicillata, Panamá
  Chrotopterus auritus, Panamá
  Lonchorhina aurita, Panamá
  Trachops cirrhosus, Panamá
Trichobius dybasi Wenzel
  Tonatia sylvicola, Panamá
Trichobius frequens Peterson and Hůrka
  Artibeus jamaicensis, Cuba and Dominican Republic
  Brachyphylla nana, Cuba
  Brachyphylla pumila, Dominican Republic
  Erophylla sezekorni, Cuba
  Monophyllus redmani, Cuba
  Phyllonycteris poeyi, Cuba and Dominican Republic
Trichobius furmani Wenzel
  Desmodus rotundus, Perú
  Diphylla ecaudata, Colombia
  Glossophaga soricina, Paraguay
Trichobius intermedius Peterson and Hůrka
  Artibeus sp., Guatemala and El Salvador
  Artibeus hirsutus, México
  Artibeus jamaicensis, Bahamas, Cuba, Dominican Republic, Jamaica,
      México, Puerto Rico, and Virgin Islands
  Artibeus lituratus, México
  Erophylla sezekorni, Cuba
  Macrotus waterhousii, Jamaica
  Monophyllus redmani, Dominican Republic
  Phyllonycteris poeyi, Cuba and Dominican Republic
Trichobius joblingi Wenzel
  Artibeus jamaicensis, Panamá
  Artibeus lituratus, Panamá
  Carollia castanea, Panamá
  Carollia perspicillata, Brazil, Belize, Colombia, Costa Rica, El
      Salvador, Guatemala, Panamá, Perú, Surinam,
      Tobago, Trinidad, and Venezuela
  Carollia subrufa, Panamá
  Chiroderma villosum, Panamá
  Desmodus rotundus, Panamá and Trinidad
  Glossophaga soricina, Panamá and Trinidad
  Lonchophylla robusta, Panamá
  Lonchorhina aurita, Panamá
  Macrophyllum macrophyllum, Panamá
  Micronycteris brachyotis, Trinidad
  Micronycteris nicefori, Panamá
  Phyllostomus hastatus, Panamá and Trinidad
  Tonatia sylvicola, Panamá
  Trachops cirrhosus, Panamá
  Uroderma bilobatum, Panamá
Trichobius johnsonae Wenzel
  Carollia perspicillata, Panamá
  Lonchophylla robusta, Panamá
Trichobius keenani Wenzel
  Micronycteris megalotis, Panamá
  Micronycteris nicefori, Panamá
  Uroderma bilobatum, Panamá

Trichobius lionycteridis Wenzel
    Lionycteris spurrelli, Panamá and Perú
Trichobius lonchophyllae Wenzel
    Artibeus lituratus, Panamá
    Lonchophylla robusta, Panamá
Trichobius longipes (Rudow)
    Anoura geoffroyi, Trinidad
    Artibeus jamaicensis, Cuba and Panamá
    Carollia perspicillata, Panamá
    Choeronycteris mexicana, Arizona
    Phyllostomus sp., Panamá
    Phyllostomus discolor, Trinidad
    Phyllostomus hastatus, Bolivia, Costa Rica, Colombia, Guatemala, Panamá,
        Perú, Surinam, Trinidad, and Venezuela
Trichobius macrophylli Wenzel
    Carollia perspicillata, Panamá
    Lonchorhina aurita, Panamá
    Macrophyllum macrophyllum, Panamá
Trichobius macroti Peterson and Hůrka
    Macrotus waterhousii, Bahamas and Cuba
Trichobius mendezi Wenzel
    Tonatia nicaraguae, Panamá
Trichobius neotropicus Peterson and Hůrka
    Macrotus waterhousii, Dominican Republic
Trichobius parasiticus Gervais
    Carollia perspicillata, Trinidad
    Desmodus rotundus, Brazil, Colombia, Costa Rica, El Salvador,
        Guatemala, México, Panamá, Perú, Surinam,
        Trinidad, and Venezuela
    Diaemus youngii, Panamá
    Diphylla ecaudata, México
    Glossophaga soricina
    Monophyllus redmani, Jamaica
    Phyllonycteris poeyi
    Phyllostomus hastatus, Panamá
    Tonatia sylvicola, Brazil
    Vampyrum spectrum
Trichobius phyllostomae Kessel
    Phyllostomus sp., Brazil
    Phyllostomus hastatus
Trichobius pseudotruncatus Jobling
    Artibeus jamaicensis
Trichobius robynae Peterson and Hůrka
    Artibeus jamaicensis, Puerto Rico
    Erophylla sezekorni, Puerto Rico
    Monophyllus redmani, Puerto Rico
Trichobius sparsus Kessel
    Carollia perspicillata, Panamá
Trichobius sphaeronotus Jobling
    Leptonycteris nivalis, Texas
    Leptonycteris sanborni, Arizona, México, and New Mexico
Trichobius truncatus Kessel
    Artibeus jamaicensis
    Brachyphylla cavernarum, Puerto Rico
    Erophylla bombifrons, Puerto Rico

    Macrotus waterhousii, Cuba

    Monophyllus redmani, Puerto Rico

    Phyllonycteris poeyi

Trichobius uniformis Curran

    Artibeus jamaicensis, Panamá

    Desmodus rotundus, Panamá

    Glossophaga soricina, Costa Rica, Guatemala, Guyana, México,
        Panamá, Perú, and Venezuela

    Lonchophylla robusta, Panamá

Trichobius urodermae Wenzel

    Uroderma bilobatum, Panamá and Venezuela

Trichobius vampyropis Wenzel

    Artibeus lituratus, Panamá

    Vampyrops vittatus, Panamá and Venezuela

Trichobius yunkeri Wenzel

    Artibeus lituratus, Panamá

    Carollia perspicillata, Panamá

    Lonchorhina aurita, Panamá

    Sturnira ludovici, Panamá

Trombicula dunni Ewing (Trombiculidae)

    Vampyressa pusilla, Panamá

Wagenaaria similis Brennan (Trombiculidae)

    Glossophaga soricina, México*

Whartonia glenni californica Vercammen-Grandjean, Watkins,
    and Beck (Trombiculidae)

    Choeronycteris mexicana, México*

    Macrotus californicus, Arizona*, California, and México*

Whartonia guerrerensis Hoffmann

    Erophylla sezekorni, Bahamas

Whartonia nudosetosa (Warton)

    Artibeus jamaicensis, México

    Carollia sp., Costa Rica*

    Carollia perspicillata, Costa Rica*, Guatemala, México, Nicaragua*, and
        Trinidad

    Carollia subrufa, México*

    Desmodus rotundus, México and Trinidad

    Glossophaga soricina, México and Nicaragua*

    Macrotus sp., Jamaica

    Mimon cozumelae, México

Whartonia pachywhartoni Vercammen-Grandjean

    Micronycteris megalotis, Brazil

Xenodontacarus serratus Loomis and Goff (Trombiculidae)

    Artibeus lituratus, México

Host-Parasite List

Ectoparasites known from each host species are listed alphabetically. A single asterisk indicates an unpublished record from the Chigger Laboratory, California State University, Long Beach; two asterisks indicate an unpublished record from The Museum, Texas Tech University, Lubbock. Geographic origin of records is given if known. Since this list was prepared, four publications (Brennan and Bronswijk, 1975; Brennan and Reed, 1975; Herrin and Yunker, 1975; Reed and Brennan, 1975) have appeared that should be consulted for additional records.

Anoura sp.
    Anastrebla mattadeni (Streblidae), Venezuela (reported by Wenzel *et al.*,
        1966, as from *A. aculeata*, possibly a manuscript name, but in any
        event unknown to us)
    Exastinion clovisi (Streblidae), Venezuela (same as above)
    Nycterinastes primus (Trombiculidae), Venezuela
    Periglischrus vargasi (Spinturnicidae), Guatemala
Anoura cultrata Handley
    Anastrebla mattadeni (Streblidae), Panamá
    Exastinion clovisi (Streblidae), Panamá
    Periglischrus caligus (Streblidae), Venezuela
    Periglischrus vargasi (Streblidae), Panamá and Venezuela
Anoura caudifer (É. Geoffroy St.-Hilaire)
    Alabidocarpus furmani (Labidocarpidae), Venezuela
    Anastrebla mattadeni (Streblidae), Colombia
    Paraeuctenodes longipes (Streblidae), Brazil
    Parascoschoengastia aemulata (Trombiculidae), Venezuela
    Periglischrus caligus (Spinturnicidae), Venezuela
    Periglischrus vargasi (Spinturnicidae), Venezuela
    Strebla wiedemanni (Streblidae), Brazil
Anoura geoffroyi Gray
    Alabidocarpus furmani (Labidocarpidae), Nicaragua and Trinidad
    Anastrebla mattadeni (Streblidae), Panamá and Venezuela
    Anastrebla modestini (Streblidae), Guatemala, México, Panamá, and Trinidad
    Aspidoptera phyllostomatis (Streblidae), Trinidad (?)
    Basilia speiseri (Nycteribiidae)
    Exastinion clovisi (Streblidae), Brazil, Colombia, Panamá, Trinidad, and
        Venezuela
    Chirorhynchobia matsoni (Chirorhynchobiidae), Venezuela
    Ixodes downsi (Ixodidae), Trinidad
    Loomisia desmodus (Trombiculidae), Venezuela
    Nycterinastes primus (Trombiculidae), Venezuela
    Nycterinastes secundus (Trombiculidae), Costa Rica* and Venezuela
    Paradyschiria parvuloides (Streblidae)
    Paraeuctenodes longipes (Streblidae)
    Periglischrus paracutisternus (Spinturnicidae), Venezuela
    Periglischrus vargasi (Spinturnicidae), Colombia, Guatemala, México,
        Panamá, and Venezuela
    Radfordiella anourae (Macronyssidae), México
    Radfordiella oricola (Macronyssidae), México
    Speiseria ambigua (Streblidae), Trinidad
    Speleochir aitkeni (Ereynetidae), Trinidad
    Strebla wiedemanni (Streblidae)
    Trichobius dugesii (Streblidae), Trinidad
    Trichobius longipes (Streblidae), Trinidad
Artibeus sp.
    Aspidoptera buscki (Streblidae), Puerto Rico
    Aspidoptera phyllostomatis (Streblidae)
    Periglischrus iheringi (Spinturnicidae), Panamá
    Spelaeorhynchus praecursor (Spelaeorhynchidae), México
    Trichobius intermedius (Streblidae), Guatemala and El Salvador
Artibeus aztecus Anderson
    Eutrombicula alfreddugesi (Trombiculidae), México*
    Macronyssoides kochi (Macronyssidae), Panamá

Ornithodoros yumatensis (Argasidae), México
Paratrichobius sp. (Streblidae), Panamá
Parichoronyssus sp. (Macronyssidae), Panamá
Perates anophthalma (Trombiculidae), México*
Periglischrus iheringi (Spinturnicidae), México, Panamá, and
    Venezuela
Perissopalla beltrani (Trombiculidae), México*

Artibeus cinereus (Gervais)
Alabidocarpus guyanensis (Labidocarpidae), Surinam
Chirnyssoides caparti (Sarcoptidae), Panamá
Eutrombicula goeldii (Trombiculidae), Trinidad
Megistopoda sp. (Streblidae), Trinidad
Neotrichobius delicatus (Streblidae), Panamá and Trinidad
Periglischrus iheringi (Spinturnicidae), Panamá, Paraguay, and Venezuela

Artibeus concolor Peters
Periglischrus acutisternus (Spinturnicidae), Venezuela
Periglischrus iheringi (Spinturnicidae), Venezuela

Artibeus hirsutus Andersen
Perissopalla beltrani (Trombiculidae), México*
Trichobius intermedius (Streblidae), México

Artibeus jamaicensis Leach
Amblyomma sp. (Ixodidae), Venezuela
Aspidoptera buscki (Streblidae), Colombia, Cuba, Guatemala, México,
    and Panamá
Basilia bellardii (Nycteribiidae), Brazil
Basilia rondanii (Nycteribiidae)
Basilia wenzeli (Nycteribiidae), Panamá
Chirnyssoides caparti (Sarcoptidae), México** and Panamá
Chiroptella myops (Trombiculidae), México
Eudusbabekia viguerasi (Myobiidae), Cuba (Isla de Pinos) and México**
Eutrombicula alfreddugesi (Trombiculidae), Costa Rica*
Eutrombicula webbi (Trombiculidae), Venezuela
Hooperella saccopteryx (Trombiculidae), Costa Rica*
Hooperella vesperuginis (Trombiculidae), México, Nicaragua*, and Trinidad
Ixodes sp. (Ixodidae), Venezuela
Leptotrombidium hamaxiaium (Trombiculidae), Costa Rica* and Panamá
Macronyssoides kochi (Macronyssidae), Cuba, Panamá, and Trinidad
Megistopoda aranea (Streblidae), Brazil, Costa Rica, Colombia, El Salvador,
    Guatemala, México, Panamá, Puerto Rico, Surinam, Trinidad,
    and Venezuela
Metelasmus pseudopterus (Streblidae), Panamá
Microtrombicula carmenae (Trombiculidae), Panamá
Neotrichobius delicatus (Streblidae), Panamá
Nycterophilia coxata (Streblidae)
Ornithodoros azteci (Argasidae), Cuba, México, and Venezuela
Ornithodoros brodyi (Argasidae), México
Ornithodoros dusbabeki (Argasidae), Cuba (Isla de Pinos)
Ornithodoros hasei (Argasidae), Venezuela
Paralabidocarpus foxi (Labidocarpidae), Puerto Rico
Paratrichobius dunni (Streblidae)
Paratrichobius longicrus (Streblidae), Brazil, Colombia, and Panamá
Periglischrus iheringi (Spinturnicidae), Cuba, México, Panamá, Puerto
    Rico, Venezuela, and Virgin Islands
Periglischrus vargasi (Spinturnicidae), Cuba and Puerto Rico

Phyllostomonyssus conradyunkeri (Gastronyssidae), Venezuela

Spelaeorhynchus praecursor (Spelaeorhynchidae), Cuba, Dominican Republic, México**, and Puerto Rico

Speleochir brasiliensis (Ereynetidae), Brazil

Strebla carolliae (Streblidae), Panamá

Strebla hertigi (Streblidae), Panamá

Strebla wiedemanni (Streblidae), Panamá

Trichobius cernyi (Streblidae), Cuba

Trichobius dugesii (Streblidae), Cuba and Panamá

Trichobius frequens (Streblidae), Cuba and Dominican Republic

Trichobius intermedius (Streblidae), Bahamas, Cuba, Dominican Republic, Jamaica, México, Puerto Rico, and Virgin Islands

Trichobius joblingi (Streblidae), Panamá

Trichobius longipes (Streblidae), Cuba and Panamá

Trichobius pseudotruncatus (Streblidae)

Trichobius robynae (Streblidae), Puerto Rico

Trichobius truncatus (Streblidae)

Trichobius uniformis (Streblidae), Panamá

Whartonia nudosetosa (Trombiculidae), México

Artibeus lituratus (Olfers)

Amblyomma sp. (Ixodidae), Venezuela

Amblyomma longirostre (Ixodidae), Venezuela

Aspidoptera buscki (Streblidae), Panamá

Aspidoptera phyllostomatis (Streblidae)

Hooperella vesperuginis (Trombiculidae), México

Macronyssoides kochi (Macronyssidae), Brazil, Colombia, and Trinidad

Megistopoda aranea (Streblidae), Colombia, Panamá, and Trinidad

Metelasmus pseudopterus (Streblidae), Panama and Paraguay

Ornithodoros hasei (Argasidae), Costa Rica

Ornithodoros yumatensis (Argasidae), México

Paralabidocarpus artibei (Labidocarpidae), Trinidad

Paratrichobius sp. (Streblidae), Colombia and Panamá

Paratrichobius longicrus (Streblidae), El Salvador and Trinidad

Periglischrus iheringi (Spinturnicidae), Brazil, Colombia, Guatemala, Honduras, Panamá, Paraguay, Surinam, Trinidad, and Venezuela

Phyllostomonyssus conradyunkeri (Gastronyssidae), Surinam and Venezuela

Psorergatoides artibei (Psorergatidae), Surinam

Trichobius costalimai (Streblidae), Panamá

Trichobius intermedius (Streblidae), México

Trichobius joblingi (Streblidae), Panamá

Trichobius lonchophyllae (Streblidae), Panamá

Trichobius vampyropis (Streblidae), Panamá

Trichobius yunkeri (Streblidae), Panamá

Xenodontacarus serratus (Trombiculidae), México

Artibeus phaeotis (Miller)

Tecomatlana sandovali (Trombiculidae), México*

Artibeus toltecus (Saussure)

Chirnyssoides caparti (Sarcoptidae), México** and Panamá

Leptotrombidium hamaxiaium (Trombiculidae), Panamá

Loomisia desmodus (Trombiculidae), Costa Rica* and Nicaragua*

Macronyssoides kochi (Macronyssidae), Panamá

Microtrombicula boneti (Trombiculidae), México**
Paratrichobius sp. (Streblidae), Panamá
Parichoronyssus sp. (Macronyssidae), Panamá
Periglischrus iheringi (Spinturnicidae), Panamá and Venezuela
Periglischrus ojasti (Spinturnicidae), México**

Artibeus watsoni Thomas
Paratrichobius lowei (Streblidae), Panamá

Brachyphylla cavernarum Gray
Lawrenceocarpus micopilus (Labidocarpidae), Puerto Rico
Lawrenceocarpus puertoricensis (Labidocarpidae), Puerto Rico
Nycterophilia coxata (Steblidae), British West Indies
Ornithodoros hasei (Argasidae), Guadeloupe** and Martinique
Radfordiella oudemansi (Macronyssidae), Puerto Rico
Trichobius truncatus (Streblidae), Puerto Rico

Brachyphylla nana Miller
Eudusbabekia cernyi (Myobiidae), Cuba
Macronyssoides kochi (Macronyssidae), Cuba
Ornithodoros azteci (Argasidae), Cuba
Ornithodoros viguerasi (Argasidae), Cuba
Periglischrus cubanus (Spinturnicidae), Cuba
Trichobius frequens (Streblidae), Cuba

Brachyphylla pumila Miller
Trichobius frequens (Streblidae), Dominican Republic

Carollia sp.
Beamerella acutascuta (Trombiculidae), Costa Rica*
Chirnyssoides carolliae (Sarcoptidae), Panamá
Hooperella vesperuginis (Trombiculidae), Panamá
Loomisia alcithoae (Trombiculidae), Venezuela
Loomisia desmodus (Trombiculidae), Venezuela
Loomisia yunkeri (Trombiculidae), Venezuela
Ornithodoros azteci (Argasidae), Venezuela
Ornithodoros brodyi (Argasidae), Venezuela
Ornithodoros hasei (Argasidae), Venezuela
Strebla carolliae (Streblidae), Surinam
Whartonia nudosetosa (Trombiculidae), Costa Rica*

Carollia brevicauda (Schinz)
Alabidocarpus furmani (Labidocarpidae), Venezuela
Amblyomma sp. (Ixodidae), Venezuela
Eutrombicula goeldii (Trombiculidae), Venezuela
Eutrombicula pacae, (Trombiculidae), Venezuela
Parakosa tadarida (Labidocarpidae), Venezuela

Carollia castanea H. Allen
Hooperella vesperuginis (Trombiculidae), Nicaragua*
Loomisia desmodus (Trombiculidae), Costa Rica*
Loomisia sprocssi (Trombiculidae), Nicaragua*
Radfordiella corolliae (Macronyssidae), Panamá
Speiseria ambigua (Streblidae), Panamá
Speleocola secunda (Trombiculidae), Nicaragua*
Spelaeorhynchus praecursor (Spelaeorhynchidae), México
Strebla carolliae (Streblidae), Panamá
Trichobius joblingi (Streblidae), Panamá

Carollia perspicillata (Linnaeus)
Alabidocarpus furmani (Labidocarpidae), Venezuela
Alexfainia chilonycteris (Trombiculidae), Panamá

Amblyomma sp. (Ixodidae), Venezuela

Aspidoptera buscki (Streblidae), Panamá

Aspidoptera delatorrei (Streblidae), Panamá

Basilia speiseri (Nycteribiidae), Brazil

Beamerella acutascuta (Trombiculidae), Nicaragua*, Panamá, and
    Trinidad

Chirnyssoides sp. (Sarcoptidae), Brazil

Chirnyssoides amazonae (Sarcoptidae), Brazil

Chirnyssoides carolliae (Sarcoptidae), Panamá and Surinam

Chirnyssoides surinamensis (Sarcoptidae), Surinam

Chirnyssoides zanderyensis (Sarcoptidae), Surinam

Demodex carolliae (Demodicidae), Surinam

Demodex longissimus (Demodicidae), Surinam

Hooperella vesperuginis (Trombiculidae), Nicaragua*, Surinam,
    and Trinidad

Lawrenceocarpus lobus (Labidocarpidae), Nicaragua

Loomisia desmodus (Trombiculidae), Colombia, Nicaragua*, Trinidad,
    and Venezuela

Mastoptera guimaraesi (Streblidae), Panamá

Megistopoda aranea (Streblidae), Panamá

Metelasmus pseudopterus (Streblidae), Panamá

Nycterinastes primus (Trombiculidae), Venezuela

Nycterophilia parnelli (Streblidae), Panamá

Ornithodoros azteci (Argasidae), Panamá (Canal Zone)

Ornithodoros brodyi (Argasidae), Panamá and Venezuela

Ornithodoros hasei (Argasidae), Venezuela

Ornithodoros yumatensis (Argasidae), Venezuela

Paralabidocarpus carolliae (Labidocarpidae), Surinam

Parascoschoengastia megastyrax (Trombiculidae), Panamá

Paratrichobius longicrus (Streblidae)

Parichoronyssus crassipes (Macronyssidae), Panamá

Perates anophthalma (Trombiculidae), Trinidad

Periglischrus sp. (Spinturnicidae), Panamá

Perissopalla barticonycteris (Trombiculidae), Surinam

Perissopalla exhumatus (Trombiculidae), Perú and Trinidad

Perissopalla ipeani (Trombiculidae), Brazil and Surinam

Radfordiella carolliae (Macronyssidae), Panamá (Canal Zone)

Radfordiella desmodi (Macronyssidae), Trinidad

Speiseria ambigua (Streblidae), Colombia, Panamá, and Trinidad

Spelaeorhynchus sp. (Spelaeorhynchidae), Brazil

Spelaeorhynchus praecursor (Spelaeorhynchidae), Brazil, Colombia,
    México, and Venezuela

Speleochir carolliae (Ereynetidae), Surinam

Speleocola secunda (Trombiculidae), Surinam

Strebla altmani (Streblidae), Panamá

Strebla carolliae (Streblidae), Brazil, Colombia, Panamá, Trinidad,
    and Venezuela

Strebla consocius (Streblidae), Trinidad

Strebla mirabilis (Streblidae), Brazil, Panamá, and Trinidad

Trichobioides perspicillatus (Streblidae), Brazil, México, and Perú

Trichobius costalimai (Streblidae), Panamá

Trichobius degesii (Streblidae), Costa Rica, Nicaragua, Panamá,
    and Trinidad

Trichobius dugesioides (Streblidae), Panamá

   Trichobius joblingi (Streblidae), Brazil, Belize, Colombia,
     Costa Rica, El Salvador, Guatemala, Panamá, Perú, Surinam,
     Tobago, Trinidad, and Venezuela
   Trichobius johnsonae (Streblidae), Panamá
   Trichobius longipes (Streblidae), Panamá
   Trichobius macrophylli (Streblidae), Panamá
   Trichobius parasiticus (Streblidae), Trinidad
   Trichobius sparsus (Streblidae), Panamá
   Trichobius yunkeri (Streblidae), Panamá
   Whartonia nudosetosa (Trombiculidae), Costa Rica*, Guatemala,
     México, Nicaragua, and Trinidad
Carollia subrufa (Hahn)
   Chirnyssoides carolliae (Sarcoptidae), Panamá
   Hooperella vesperuginis (Trombiculidae), México* and Nicaragua*
   Loomisia desmodus (Trombiculidae), Nicaragua*, Panamá, and Venezuela
   Speiseria ambigua (Streblidae), Panamá
   Speleocola secunda (Trombiculidae), Nicaragua*
   Strebla carolliae (Streblidae), Panamá
   Trichobius joblingi (Streblidae), Panamá
   Whartonia nudosetosa (Trombiculidae), México*
Centurio senex Gray
   Basilia sp. (Nycteribiidae)
Chiroderma sp.
   Periglischrus iheringi (Spinturnicidae), Venezuela
Chiroderma salvini Dobson
   Chirnyssoides caparti (Sarcoptidae), Panamá
   Ornithodoros hasei (Argasidae), Venezuela
   Paratrichobius salvini (Streblidae), Panamá
   Periglischrus iheringi (Spinturnicidae), Panamá and Venezuela
Chiroderma villosum Peters
   Amblyomma sp. (Ixodidae), Venezuela
   Aspidoptera buscki (Streblidae), Panamá
   Paratrichobius sp. (Streblidae), Panamá
   Trichobius joblingi (Streblidae), Panamá
Choeroniscus minor (Peters)
   Amblyomma sp. (Ixodidae), Venezuela
Choeronycteris mexicana Tschudi
   Paratrichobius americanus (Streblidae), Arizona
   Trichobius longipes (Streblidae), Arizona
   Whartonia glenni californicus (Trombiculidae), México*
Chrotopterus auritus Peters
   Basilia hughscotti (Nycteribiidae), Brazil
   Hooperella vesperuginis (Trombiculidae), Nicaragua*
   Ornithodoros brodyi (Argasidae), México
   Strebla wiedemanni (Streblidae), Brazil
   Trichobius dugesioides (Streblidae), Panamá
Desmodus rotundus É. Geoffroy St.-Hilaire
   Basilia ferrisi (Nycteribiidae), Venezuela
   Chirnyssoides caparti (Sarcoptidae), Panamá
   Eudusbabekia arganoi (Myobiidae), México
   Hooperella saccopteryx (Trombiculidae), Trinidad
   Hooperella vesperuginis (Trombiculidae), Nicaragua* and Trinidad
   Loomisia desmodus (Trombiculidae), Guatemala, Nicaragua*, and Venezuela
   Macronyssoides kochi (Macronyssidae), Brazil and Trinidad

Megistopoda aranea (Streblidae), Panamá
Microtrombicula boneti (Trombiculidae), México*
Nycterinastes primus (Trombiculidae), Venezuela
Ornithodoros azteci (Argasidae), México, Panamá, and Trinidad
Ornithodoros peruvianus (Argasidae), Perú
Ornithodoros yumatensis (Argasidae), México
Paralabidocarpus desmodus (Labidocarpidae), Surinam
Parascoschoengastia megastyrax (Trombiculidae), Trinidad
Parasecia longicalcar (Trombiculidae), Trinidad
Perates anophthalma (Trombiculidae), México and Panamá
Periglischrus herrerai (Spinturnicidae), Panamá, Trinidad, and
    Venezuela
Periglischrus iheringi (Spinturnicidae), México and Panamá
Perissopalla exhumatus (Trombiculidae), Trinidad
Perissopalla precaria (Trombiculidae), Trinidad
Radfordiella desmodi (Macronyssidae), Panamá and Trinidad
Radfordiella oudemansi (Macronyssidae), Brazil
Speiseria ambigua (Streblidae), Panamá
Speleocola davisi (Trombiculidae), México
Speleocola secunda (Trombiculidae), Trinidad
Strebla carolliae (Streblidae), Panamá
Strebla diphyllae (Streblidae), Guatemala
Strebla hertigi (Streblidae), El Salvador and Panamá
Strebla mirabilis (Streblidae), Perú and Trinidad
Strebla wiedemanni (Streblidae), Colombia, Ecuador, El Salvador,
    Guatemala, Honduras, México, Panamá, Perú, Surinam, Trinidad,
    and Venezuela.
Tecomatlana sandovali (Trombiculidae), México*
Trichobioides perspicillatus (Streblidae), Panamá and Trinidad
Trichobius costalimai (Streblidae), Panamá
Trichobius dugesii (Streblidae), Trinidad
Trichobius furmani (Streblidae), Perú
Trichobius joblingi (Streblidae), Panamá and Trinidad
Trichobius parasiticus (Streblidae), Brazil, Colombia, Costa Rica,
    El Salvador, Guatemala, México, Panamá, Perú, Surinam,
    Trinidad, and Venezuela.
Trichobius uniformis (Streblidae), Panamá
Whartonia nudosetosa (Trombiculidae), México and Trinidad
Diaemus youngii (Jentink)
Nycteronyssus desmodus (Macronyssidae), Venezuela
Perissopalla exhumatus (Trombiculidae), Trinidad
Radfordiella oudemansi (Macronyssidae), Trinidad
Strebla sp. (Streblidae), Trinidad
Strebla diaemi (Streblidae), Colombia and Panamá
Trichobius dugesii (Streblidae), Trinidad
Trichobius parasiticus (Streblidae), Panamá
Diphylla ecaudata (Spix)
Strebla diphyllae (Streblidae), Guatemala and México
Strebla mirabilis (Streblidae)
Trichobius diphyllae (Streblidae), Guatemala, México, and
    Venezuela
Trichobius furmani (Streblidae), Colombia
Trichobius parasiticus, México
Enchisthenes hartii (Thomas)
Macronyssoides sp. (Macronyssidae), Panamá

    Parakosa maxima (Labidocarpidae), Venezuela
    Paratrichobius sanchezi (Streblidae), Panamá and Venezuela
    Periglischrus iheringi (Spinturnicidae), Panamá and Venezuela
    Trichobius dugesii (Streblidae), Trinidad
Erophylla bombifrons (Miller)
    Ornithodoros viguerasi (Argasidae), Puerto Rico
    Trichobius truncatus (Streblidae), Puerto Rico
Erophylla sezekorni Gundlach
    Loomisia desmodus (Trombiculidae), Bahamas
    Microtrombicula boneti (Trombiculidae), Bahamas
    Perates anophthalma (Trombiculidae), Bahamas
    Periglischrus cubanus (Spinturnicidae), Cuba
    Trichobius frequens (Streblidae), Cuba
    Trichobius intermedius (Streblidae), Cuba
    Trichobius robynae (Streblidae), Puerto Rico
    Whartonia guerrerensis (Trombiculidae), Bahamas
Glossophaga sp.
    Ornithodoros peruvianus (Argasidae), Perú
    Periglischrus caligus (Spinturnicidae), México and Panamá
Glossophaga alticola Davis
    Hooperella vesperuginis (Trombiculidae), México and Nicaragua
Glossophaga commissarisi Gardner
    Hooperella saccopteryx (Trombiculidae), México*
    Hooperella vesperuginis (Trombiculidae), Nicaragua*
    Speleocola secunda (Trombiculidae), Nicaragua*
Glossophaga longirostris Miller
    Alabidocarpus furmani (Labidocarpidae), Venezuela
    Amblyomma sp. (Ixodidae), Venezuela
    Eutrombicula goeldii (Trombiculidae), Venezuela
    Loomisia desmodus (Trombiculidae), Venezuela
    Ornithodoros azteci (Argasidae), Venezuela
    Ornithodoros hasei (Argasidae), Venezuela
    Ornithodoros rossi (Argasidae), Venezuela
    Parakosa maxima (Labidocarpidae), Venezuela
    Parakosa tadarida (Labidocarpidae), Venezuela
    Periglischrus caligus (Spinturnicidae), Venezuela
Glossophaga soricina (Pallas)
    Alabidocarpus furmani (Labidocarpidae), Nicaragua
    Amblyomma sp. (Ixodidae), Venezuela
    Beamerella acutascuta (Trombiculidae), México
    Chirnyssoides caparti (Sarcoptidae), Surinam
    Hooperella saccopteryx (Trombiculidae), Costa Rica*
    Hooperella vesperuginis (Trombiculidae), México*, Nicaragua*,
        Panamá, and Surinam
    Loomisia desmodus (Trombiculidae), México, Nicaragua*, Panamá,
        Surinam, and Venezuela
    Loomisia sprocssi (Trombiculidae), México*
    Loomisia univari (Trombiculidae), México*
    Macronyssoides kochi (Macronyssidae), Trinidad
    Microtrombicula boneti (Trombiculidae), México*
    Nycterinastes primus (Trombiculidae), Venezuela
    Ornithodoros azteci (Argasidae), Venezuela
    Paradyschiria parvuloides (Streblidae)
    Parichoronyssus sclerus (Macronyssidae), Panamá

Periglischrus caligus (Spinturnicidae), Brazil, Panamá, Surinam, Trinidad, and Venezuela

Perissopalla beltrani (Trombiculidae), México*

Perissopalla exhumatus (Trombiculidae), Trinidad

Perissopalla precaria (Trombiculidae), México

Psorergatoides glossophagae (Psorergatidae), Surinam

Speiseriae ambigua (Streblidae), Trinidad

Spelaeorhynchus praecursor (Spelaeorhynchidae), Amazon(?)

Speleocola davisi (Trombiculidae), México

Speleocola secunda (Trombiculidae), Nicaragua

Steatonyssus joaquimi (Macronyssidae), Brazil

Strebla carolliae (Streblidae), El Salvador, Panamá, and Venezuela

Strebla mirabilis (Streblidae), Trinidad

Trichobius dugesii (Streblidae), Colombia, El Salvador, Guatemala, México, Panamá, Perú, and Trinidad

Trichobius furmani (Streblidae), Paraguay

Trichobius joblingi (Streblidae), Panamá and Trinidad

Trichobius longipes (Streblidae)

Trichobius uniformis (Streblidae), Costa Rica, Guatemala, Guyana, México, Panamá, Perú, and Venezuela

Wagenaaria similis (Trombiculidae), México*

Whartonia nudosetosa (Trombiculidae), México and Nicaragua*

Hylonycteris underwoodi Thomas

Basilia rondanii (Nycteribiidae)

Leptonycteris curasoae Miller

Antricola sp. (Argasidae), Venezuela

Ornithodoros sp. (Argasidae), Venezuela

Leptonycteris nivalis Saussure

Basilia corynorhini (Nycteribiidae), Texas

Macronyssus unidens (Macronyssidae), Arizona

Ornithodoros rossi (Argasidae), Arizona

Periglischrus vargasi (Spinturnicidae), México and Texas

Radfordiella oricola (Macronyssidae), México

Trichobius sphaeronotus (Streblidae), México and Texas

Leptonycteris sanborni Hoffmeister

Basilia antrozoi (Nycteribiidae)

Periglischrus vargasi (Spinturnicidae), México

Speleocola davisi (Trombiculidae), México

Trichobius sphaeronotus (Streblidae), Arizona and New Mexico

Lionycteris spurrelli Thomas

Nycterinastes primus (Trombiculidae), Venezuela

Periglischrus hopkinsi (Spinturnicidae), Venezuela

Trichobius lionycteridis (Streblidae), Panamá and Perú

Lonchophylla concava Goldman

Beamerella acutascuta (Trombiculidae), Costa Rica*

Loomisia sprocssi (Trombiculidae), Costa Rica*

Lonchophylla robusta Miller

Anastrebla nycteridis (Streblidae), Panamá

Anatrichobius scorzai (Streblidae), Panamá

Chiroecetes lonchophylla (Macronyssidae), Venezuela

Eldunnia breviceps (Streblidae), Panama

Loomisia desmodus (Trombiculidae), Costa Rica* and Venezuela

Nycterinastes secundus (Trombiculidae), Costa Rica*

Periglischrus sp. (Spinturnicidae), Panamá

Speiseria ambigua (Streblidae), Panamá
Strebla carolliae (Streblidae), Panamá
Trichobius joblingi (Streblidae), Panamá
Trichobius johnsonae (Streblidae), Panamá
Trichobius lonchophyllae (Streblidae), Panamá
Trichobius uniformis (Streblidae), Panamá

Lonchorhina aurita Tomes

Basilia wenzeli (Nycteribiidae), Venezuela
Nycterinastes primus (Trombiculidae), Venezuela
Ornithodoros azteci (Argasidae), Cuba, Jamaica, Trinidad, and
     Venezuela
Ornithodoros brodyi (Argasidae), Venezuela
Ornithodoros hasei (Argasidae), Venezuela
Periglischrus gameroi (Spinturnicidae), Venezuela
Psorergatoides lonchorhinae (Psorergatidae), Venezuela
Speiseria ambigua (Streblidae), Panamá
Strebla altmani (Streblidae), Panamá and Venezuela
Strebla carolliae (Streblidae), Panamá
Trichobius dugesioides (Streblidae), Panamá
Trichobius joblingi (Streblidae), Panamá
Trichobius macrophylli (Streblidae), Panamá
Trichobius yunkeri (Streblidae), Panamá

Lonchorhina orinocensis Linares and Ojasti

Ornithodoros sp. (Argasidae), Venezuela
Ornithodoros hasei (Argasidae), Venezuela
Ornithodoros rossi (Argasidae), Venezuela

Macrophyllum macrophyllum (Schinz)

Basilia constricta (Nycteribiidae)
Eutrombicula variabilis (Trombiculidae), Venezuela
Ornithodoros azteci (Argasidae), Venezuela
Paralabidocarpus macrophyllum (Labidocarpidae), Surinam
Periglischrus sp. (Spinturnicidae), Panamá
Strebla altmani (Streblidae), Panamá
Strebla carolliae (Streblidae), Panamá
Trichobius joblingi (Streblidae), Panamá
Trichobius macrophylli (Streblidae), Panamá

Macrotus sp.

Whartonia nudosetosa (Trombiculidae), Jamaica

Macrotus californicus Baird

Loomisia sprocssi (Trombiculidae), California
Nycterophilia coxata (Streblidae), Arizona and California
Ornithodoros sp. (Argasidae), Arizona
Ornithodoros rossi (Argasidae), México
Periglischrus vargasi (Spinturnicidae), México
Perissopalla beltrani (Trombiculidae), Arizona*, California*,
     and México*
Tecomatlana watkinsi (Trombiculidae), Arizona*, California, and
     México
Trichobius adamsi (Streblidae), Arizona, California, and México
Whartonia glenni californica (Trombiculidae), Arizona*, California,
     and México*

Macrotus waterhousii Gray

Eudusbabekia samsinaki (Myobiidae), Cuba (Isla de Pinos)
Nycterophilia sp. (Streblidae), México*

    Nycterophilia coxata (Streblidae), México
    Nycterophilia parnelli (Streblidae), Cuba
    Ornithodoros azteci (Argasidae), Cuba
    Ornithodoros hasei (Argasidae), Jamaica**
    Periglischrus delfinadoae (Spinturnicidae), Cuba
    Periglischrus vargasi (Spinturnicidae), México
    Trichobius intermedius (Streblidae), Jamaica
    Trichobius macroti (Streblidae), Bahamas and Cuba
    Trichobius neotropicus (Streblidae), Dominican Republic
    Trichobius truncatus (Streblidae), Cuba

Micronycteris sp.
    Periglischrus parvus (Spinturnicidae), Venezuela

Micronycteris brachyotis (Dobson)
    Speiseriae ambigua (Streblidae), Trinidad   .
    Trichobius dugesii (Streblidae), Trinidad
    Trichobius joblingi (Streblidae), Trinidad

Micronycteris daviesi (Hill)
    Perissopalla barticonycteris (Trombiculidae), Brazil

Micronycteris hirsuta (Peters)
    Beamerella acutascuta (Trombiculidae), Panamá and Trinidad
    Beamerella subacutascuta (Trombiculidae), Trinidad
    Hooperella vesperuginis (Trombiculidae), Trinidad
    Lawrenceocarpus phyllostomus (Labidocarpidae), Venezuela
    Speleocola secunda (Trombiculidae), Trinidad

Micronycteris megalotis (Gray)
    Basilia bequaerti (Nycteribiidae)
    Beamerella acutascuta (Trombiculidae), Panamá
    Chirnyssoides carolliae (Sarcoptidae), Surinam
    Eutrombicula batatas (Trombiculidae), Venezuela
    Hooperella spinirostra (Trombiculidae), Brazil
    Hooperella vesperuginis (Trombiculidae), Trinidad
    Labodicarpus lukoschi (Labidocarpidae), Surinam
    Loomisia desmodus (Trombiculidae), Panamá and Trinidad
    Microtrombicula boneti (Trombiculidae), Curaçao
    Perates anophthalma (Trombiculidae), Colombia and Perú
    Periglischrus micronycteridis (Spinturnicidae), Panamá and
        Trinidad
    Periglischrus parvus (Spinturnicidae), Panamá and Trinidad
    Perissopalla deopertus (Trombiculidae), Perú
    Perissopalla exhumatus (Trombiculidae), Perú
    Perissopalla precaria (Trombiculidae), Panamá
    Speleocola secunda (Trombiculidae), Trinidad
    Strebla alvarezi (Streblidae), Panamá
    Trichobius keenani (Streblidae), Panamá
    Whartonia pachywhartoni (Trombiculidae), Brazil

Micronycteris minuta (Gervais)
    Periglischrus micronycteridis (Spinturnicidae), Panamá
    Periglischrus parvus (Spinturnicidae), Panamá
    Strebla machadoi (Streblidae), Venezuela

Micronycteris nicefori Sanborn
    Parastrebla handleyi (Streblidae), Panamá
    Strebla alvarezi (Streblidae), Panamá
    Trichobius joblingi (Streblidae), Panamá
    Trichobius keenani (Streblidae), Panamá

Micronycteris sylvestris (Thomas)
　　Strebla alvarezi (Streblidae), Panamá
Mimon cozumelae Goldman
　　Loomisia desmodus (Trombiculidae), México
　　Whartonia nudosetosa (Trombiculidae), México
Mimon crenulatum (É. Geoffroy St.-Hilaire)
　　Basilia tiptoni (Nycteribiidae), Panamá and Venezuela
　　Ioannela martae (Myobiidae), Venezuela
　　Ornithodoros sp. (Argasidae), Venezuela
　　Ornithodoros hasei (Argasidae), Venezuela
　　Ornithodoros mimon (Argasidae), Bolivia
　　Periglischrus dusbabeki (Spinturnicidae), Venezuela
　　Speleochir barbulata (Trombiculidae), Brazil
Monophyllus sp.
　　Trichobius dominicanus (Streblidae), Dominican Republic
Monophyllus cubanus Miller
　　Eudusbabekia rosickyi (Myobiidae), Cuba
　　Periglischrus vargasi (Spinturnicidae), Cuba
Monophyllus redmani Leach
　　Radfordiella monophylli (Macronyssidae), Cuba
　　Spelaeorhynchus monophylli (Spelaeorhynchidae), Puerto Rico
　　Trichobius cernyi (Streblidae), Cuba
　　Trichobius frequens (Streblidae), Cuba
　　Trichobius intermedius (Streblidae), Dominican Republic
　　Trichobius parasiticus (Streblidae), Jamaica
　　Trichobius robynae (Streblidae), Puerto Rico
　　Trichobius truncatus (Streblidae), Puerto Rico
Phylloderma stenops Peters
　　Strebla christinae (Streblidae), Panamá
Phyllonycteris aphylla (Miller)
　　Ornithodoros hasei (Argasidae), Jamaica**
Phyllonycteris poeyi Gundlach
　　Antricola marginatus (Argasidae), Cuba
　　Antricola silvai (Argasidae), Cuba
　　Eudusbabekia danieli (Myobiidae), Cuba
　　Macronyssoides kochi (Macronyssidae), Cuba
　　Ornithodoros viguerasi (Argasidae), Cuba and Haiti**
　　Periglischrus cubanus (Spinturnicidae), Cuba
　　Trichobius cernyi (Streblidae), Cuba
　　Trichobius frequens (Streblidae), Cuba and Dominican Republic
　　Trichobius intermedius (Streblidae), Cuba and Dominican Republic
　　Trichobius parasiticus (Streblidae)
　　Trichobius truncatus (Streblidae)
Phyllostomus sp.
　　Aspidoptera phyllostomatis (Streblidae), Brazil
　　Basilia bellardii (Nycteribiidae), Brazil
　　Basilia speiseri (Nycteribiidae)
　　Mastoptera guimaraesi (Streblidae), Panamá
　　Megistopoda aranea (Streblidae), Brazil and Cuba
　　Parichoronyssus sclerus (Macronyssidae), Costa Rica
　　Strebla consocius (Streblidae), Perú and Surinam
　　Strebla mirabilis (Streblidae), Brazil, Panamá, and Perú
　　Trichobius longipes (Streblidae), Panamá
　　Trichobius phyllostomae (Streblidae), Brazil

Phyllostomus discolor (Wagner)

    Aspidoptera buscki (Streblidae), Panamá

    Beamerella acutascuta (Trombiculidae), Nicaragua*

    Eudusbabekia phyllostomi (Myobiidae), Nicaragua

    Eutrombicula goeldii (Trombiculidae), Venezuela

    Hooperella vesperuginis (Trombiculidae), Nicaragua*

    Megistopoda aranea (Streblidae), Panamá

    Microtrombicula carmenae (Trombiculidae), Costa Rica, Nicaragua, and Trinidad

    Periglischrus acutisternus (Spinturnicidae), Trinidad and Venezuela

    Periglischrus torrealbai (Spinturnicidae), Venezuela

    Pseudoalabidocarpus secus (Labidocarpidae), Venezuela

    Strebla consocius (Streblidae), Colombia

    Strebla hertigi (Streblidae), Colombia, Panamá, Perú, Surinam, Trinidad, and Venezuela

    Strebla mirabilis (Streblidae), Brazil, Panamá, and Trinidad

    Trichobioides perspicillatus (Streblidae), Colombia, Panamá, and Trinidad

    Trichobius costalimai (Streblidae), Colombia, El Salvador, Guatemala, Panamá, Perú, Puerto Rico, Trinidad, and Venezuela

    Trichobius longipes (Streblidae), Trinidad

Phyllostomus elongatus (É. Geoffroy St.-Hilaire)

    Lawrenceocarpus phyllostomus (Labidocarpidae), Venezuela

    Periglischrus acutisternus (Spinturnicidae), Trinidad and Venezuela

    Pseudoalabidocarpus secus (Labidocarpidae), Venezuela

    Strebla mirabilis (Streblidae)

    Trichobioides perspicillatus (Streblidae), Colombia

Phyllostomus hastatus (Pallas)

    Alabidocarpus phyllostomi (Labidocarpidae), Surinam

    Blankaartia sinnamaryi (Trombiculidae), Panamá

    Demodex phyllostomatis (Demodicidae), Surinam

    Eutrombicula goeldii (Trombiculidae), Venezuela

    Mastoptera guimaraesi (Streblidae), Colombia and Panamá

    Mastoptera minuta (Streblidae), Colombia

    Microtrombicula boneti (Trombiculidae), Panamá

    Microtrombicula carmenae (Trombiculidae), Panamá

    Nasicola annereauxi (Trombiculidae), Venezuela

    Neotrichobius delicatus (Streblidae), Surinam

    Ornithodoros azteci (Argasidae), Venezuela

    Ornithodoros hasei (Argasidae), Venezuela

    Paraeuctenodes longipes (Streblidae), Brazil

    Periglischrus acutisternus (Spinturnicidae), Colombia, Panamá, Trinidad, and Venezuela

    Periglischrus torrealbai (Spinturnicidae), Panamá, Trinidad, and Venezuela

    Speiseria ambigua (Streblidae), Panamá

    Speleochir phyllostomi (Ereynetidae), Colombia

    Strebla carolliae (Streblidae), Panamá

    Strebla consocius (Streblidae), Surinam, Trinidad, and Venezuela

    Strebla hertigi (Streblidae), Costa Rica, Nicaragua, and Panamá

    Strebla mirabilis (Streblidae), Colombia, Panamá, Perú, and Trinidad

    Trichobioides perspicillatus (Streblidae), Surinam

    Trichobius dugesii (Streblidae), Trinidad

    Trichobius joblingi (Streblidae), Panamá and Trinidad

    Trichobius longipes (Streblidae), Bolivia, Costa Rica, Colombia, Guatemala, Panamá, Perú, Surinam, Trinidad, and Venezuela

Trichobius parasiticus (Streblidae), Panamá
Trichobius phyllostomae (Streblidae)

Rhinophylla pumilio Peters

Periglischrus hopkinsi (Spinturnicidae), Brazil and Venezuela
Periglischrus ramirezi (Spinturnicidae), Brazil and Venezuela

Stenoderma rufum Desmarest

Paralabidocarpus artibei (Labidocarpidae), Puerto Rico
Paralabidocarpus foxi (Labidocarpidae), Puerto Rico
Paralabidocarpus stenodermi (Labidocarpidae), Puerto Rico
Periglischrus iheringi (Spinturnicidae), Puerto Rico

Sturnira lilium (É. Geoffroy St.-Hilaire)

Aspidoptera delatorrei (Streblidae), Guatemala and Panamá
Aspidoptera phyllostomatis (Streblidae), Paraguay
Chirnyssoides brasiliensis (Sarcoptidae), Brazil
Eudusbabekia lepidoseta (Macronyssidae), Nicaragua
Eutrombicula goeldii (Trombiculidae), Venezuela
Exastinion clovisi (Streblidae)
Hooperella vesperuginis (Trombiculidae), Nicaragua*
Ixodes sp. (Ixodidae), Venezuela
Loomisia desmodus (Trombiculidae), Venezuela
Megistopoda proxima (Streblidae), Colombia and Panamá
Microtrombiula sturnirae (Trombiculidae), México and Nicaragua
Nycteriglyphus sturnirae (Rosensteiniidae), Brazil
Ornithodoros sp. (Argasidae), Venezuela
Ornithodoros hasei (Argasidae), Venezuela
Parakosa tadarida (Labidocarpidae), Venezuela
Paralabidocarpus artibei (Labidocarpidae), Nicaragua
Periglischrus iheringi (Spinturnicidae), México
Periglischrus ojasti (Spinturnicidae), Panamá, Trinidad, and
    Venezuela
Periglischrus vargasi (Spinturnicidae), México
Trichobioides perspicillatus (Streblidae), Panamá

Sturnira ludovici Anthony

Ixodes sp. (Ixodidae), Venezuela
Megistopoda proxima (Streblidae), Costa Rica
Megistopoda theodori (Streblidae), Panamá
Microtrombicula carmenae (Trombiculidae), Costa Rica and Panamá
Microtrombicula sturnirae (Trombiculidae), Costa Rica and Panamá
Ornithodoros hasei (Argasidae), Venezuela
Parasecia soucouyanti (Trombiculidae), Panamá
Parichoronyssus euthysternum (Macronyssidae), Panamá
Periglischrus iheringi (Spinturnicidae), Colombia and Venezuela
Periglischrus ojasti (Spinturnicidae), Panamá
Pseudoschoengastia bulbifera (Trombiculidae), Panamá
Trichobius brennani (Streblidae), Panamá
Trichobius yunkeri (Streblidae), Panamá

Sturnira mordax (Goodwin)

Microtrombicula carmenae (Trombiculidae), Costa Rica
Microtrombicula sturnirae (Trombiculidae), Costa Rica

Sturnira tildae de la Torre

Amblyomma sp. (Ixodidae), Venezuela

Tonatia sp.

Mastoptera minuta (Streblidae), Bolivia, Colombia, Ecuador, Perú,
    and Surinam

Stizostrebla longirostris (Streblidae), Brazil and Colombia
Strebla galindoi (Streblidae), Trinidad
Strebla mirabilis (Streblidae), Colombia
Tonatia bidens (Spix)
Speiseria ambigua (Streblidae)
Strebla galindoi (Steblidae), Panamá
Strebla mirabilis (Streblidae)
Strebla tonatiae (Streblidae)
Trichobius bequaerti (Streblidae), Panamá
Tonatia brasiliense (Peters)
Strebla tonatiae (Streblidae), Ecuador and Panamá
Tonatia nicaraguae Goodwin
Mastoptera minuta (Streblidae), Panamá
Pseudostrebla greenwelli (Streblidae), Panamá
Strebla hoogstraali (Streblidae), Panamá
Trichobius mendezi (Streblidae), Panamá
Tonatia sylvicola (D'Orbigny)
Basilia constricta (Nycteribiidae)
Mastoptera minuta (Streblidae), Brazil and Panamá
Ornithodoros hasei (Argasidae), Panamá
Pseudostrebla ribeiroi (Streblidae), Brazil and Panamá
Strebla kohlsi (Streblidae), Colombia and Panamá
Trichobius dybasi (Streblidae), Panamá
Trichobius joblingi (Streblidae), Panamá
Trichobius parasiticus (Streblidae), Brazil
Tonatia venezuelae (Robinson and Lyon)
Chirnyssoides venezuelae (Sarcoptidae), Venezuela
Paralabidocarpus tonatiae (Labidocarpidae), Venezuela
Trachops sp.
Strebla consocius (Streblidae), Perú
Trachops cirrhosus (Spix)
Loomisia desmodus (Trombiculidae), México*
Ornithodoros sp. (Argasidae), Venezuela
Ornithodoros azteci (Argasidae), Venezuela
Ornithodoros brodyi (Argasidae), Panamá
Paralabidocarpus trachops (Labidocarpidae), Surinam
Periglischrus paracutisternus (Spinturnicidae), Venezuela
Periglischrus vargasi (Spinturnicidae), Panamá
Speiseria ambigua (Streblidae), Panamá
Strebla altmani (Streblidae), Panamá
Strebla carolliae (Streblidae), Panamá
Strebla diphyllae (Streblidae), Guatemala
Trichobius dugesii (Streblidae), Panamá
Trichobius dugesioides (Streblidae), Panamá
Trichobius joblingi (Streblidae), Panamá
Uroderma bilobatum Peters
Alabidocarpus nicaraguae (Labidocarpidae), Nicaragua
Amblyomma sp. (Ixodidae), Venezuela
Basilia constricta (Nycteribiidae)
Basilia myotis (Nycteribiidae)
Chirorhynchobia urodermae (Chirorhynchobiidae), Panamá
Eutrombicula batatas (Trombiculidae), Trinidad
Macronyssoides sp. (Macronyssidae), Panamá
Neotrichobius delicatus (Streblidae), Panamá

Ornithodoros hasei (Argasidae), Panamá
Parasecia manueli (Trombiculidae), Costa Rica*
Paratrichobius dunni (Streblidae), Panamá
Paratrichobius longicrus (Streblidae)
Periglischrus iheringi (Spinturnicidae), Guatemala, Panamá,
    Paraguay, and Venezuela
Phyllostomonyssus conradyunkeri (Gastronyssidae), Surinam
Trichobius costalimai (Streblidae), Panamá
Trichobius joblingi (Streblidae), Panamá
Trichobius keenani (Streblidae), Panamá
Trichobius urodermae (Streblidae), Panamá and Venezuela

Uroderma magnirostrum Davis
Alabidocarpus nicaraguae (Labidocarpidae), Venezuela
Eudusbabekia urodermae (Myobiidae), Brazil
Ornithodoros hasei (Argasidae), Venezuela

Vampyressa nymphaea Thomas
Aspidoptera buscki (Streblidae), Panamá
Metelasmus pseudopterus (Streblidae), Panamá

Vampyressa pusilla (Wagner)
Chirnyssoides caparti (Sarcoptidae), Panamá
Macronyssoides sp. (Macronyssidae), Panamá
Neotrichobius delicatus (Streblidae), Panamá and Venezuela
Periglischrus iheringi (Spinturnicidae), Panamá
Trombicula dunni (Trombiculidae), Panamá

Vampyrodes caraccioloi Thomas
Chirnyssoides caparti (Sarcoptidae), Panamá
Parichoronyssus sp. (Macronyssidae), Panamá
Periglischrus iheringi (Spinturnicidae), Panamá
Speleochir brasiliensis (Ereynetidae), Brazil

Vampyrops sp.
Periglischrus iheringi (Spinturnicidae), Paraguay

Vampyrops dorsalis Thomas
Periglischrus iheringi (Spinturnicidae), Venezuela

Vampyrops helleri Peters
Alabidocarpus furmani (Labidocarpidae), Venezuela
Alabidocarpus jonesi (Lapidocarpidae), Nicaragua and Venezuela
Amblyomma sp. (Ixodidae), Venezuela
Basilia astochia (Nycteribiidae), Colombia
Eutrombicula nadchatrami (Trombiculidae), Venezuela
Ornithodoros hasei (Argasidae), Panamá
Paratrichobius sp. (Streblidae), Panamá
Periglischrus iheringi (Spinturnicidae), México and Panamá
Phyllostomonyssus conradyunkeri (Gastronyssidae), Surinam

Vampyrops lineatus É. Geoffroy St.-Hilaire
Megistopoda pilatei (Streblidae), Brazil, Cuba, México, and U.S.A.
Paratrichobius longicrus (Streblidae)
Periglischrus iheringi (Spinturnicidae), Brazil
Strebla wiedemanni (Streblidae), Brazil

Vampyrops vittatus Peters
Chirnyssoides caparti (Sarcoptidae), Panamá
Loomisia desmodus (Trombiculidae), Costa Rica*
Macronyssoides consiliatus (Macronyssidae), Panamá
Paratrichobius sp. (Streblidae), Panamá
Speiseria ambigua (Streblidae), Panamá
Trichobius vampyropis (Streblidae), Panamá and Venezuela

Vampyrum spectrum (Linnaeus)

Hooperella vesperuginis (Trombiculidae), Panamá and Trinidad
Parasecia longicalcar (Trombiculidae), Panamá
Trichobius parasiticus (Streblidae)

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ORAL BIOLOGY

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Mammalian dentitions have attracted considerable attention from paleontologists and taxonomists. This mainly is because jaws and associated teeth are the most commonly found remains of mammals in fossil beds and, thus, the materials most readily available for comparison with extant species.

The degree to which occlusal patterns or coronal shapes have differentiated, even at the specific or subspecific levels, has been the subject of many investigations. However, relatively little is known about other aspects of oral anatomy and biology of the oral environment in most mammals. Dental researchers, on the other hand, generally have approached the study of mammalian dentitions from a medical or clinical point of view at the tissue, cellular, and subcellular levels. Until recently, researchers have been inclined to study only selected laboratory rodents, a few species of primates, and a variety of domestic forms. The blending together of these two basic orientations results in a much broader, interdisciplinary approach that can be termed "oral biology."

In view of the wealth of information available about teeth and associated structures and the wide variety of sophisticated techniques now at hand, it no longer suffices to undertake only highly specialized, traditional investigations. Thus, in this paper we have attempted to utilize a broader biological approach to a subject that a few years ago would have been limited to a discussion of coronal patterns and their taxonomic implications. Until now, no efforts have been made to study comparatively the oral biology of a group of wild, free-living species of mammals. It is our contention, however, that such studies are necessary if we are to overcome the artificiality of investigating only selected components of a system as if they exist individually in nature. We agree with Romer's classic comment that many of our colleagues seem to view teeth as though they in themselves act as species.

Among the Chiroptera, the Phyllostomatidae are perhaps the best suited of all families for comparative analysis of oral biology. Within this one family there are species that have extremely diverse feeding habits, which if not obligate, certainly are restricted. Diets are known to include essentially carnivorous, frugivorous, omnivorous, nectarivorous, and sanguivorous modes. Indeed, the adaptive radiation within these Neotropical bats is extensive even though they have a relatively close genetic affinity and a common ancestry. It is especially important, of course, to underscore the significant relationship between this divergence and the biology and structural characteristics of the oral systems. It is unlikely that any other natural assemblage of mammals could provide a more suitable or potentially rewarding source for an evolutionarily oriented study of the biology of oral systems.

Ideally the present report would follow the traditional format of a review paper. Unfortunately, however, the opportunity to write this particular report

came a few years too soon for us to use such a format exclusively. Much important information has not been published elsewhere so as to be available for review. One possibility was for us to write a shorter version of this chapter on a restricted aspect while knowing that considerable salient additional data would be published shortly, making the present paper almost immediately obsolete, or at least seriously inadequate. We have chosen instead to write a chapter with a somewhat variable format that ranges from portions which are a typical review to portions composed entirely of our unpublished data. Consequently, some sections and subsections will seem to the reader to be somewhat disproportionate in length and detail.

In our view, most of what can be said at this time about dental gross anatomy, abnormalities, and taxonomic arrangements based on coronal patterns has been published elsewhere by Slaughter (1970) and Phillips (1971). Although these areas lend themselves to promising additional work, relatively little has been published since these earlier studies. We have chosen, therefore, to summarize in a review style the available information on these matters. Consequently, our emphasis is on the more poorly known aspects of chiropteran oral biology such as evolutionary mechanisms, general dental microanatomy, and comparative studies of salivary glands. Sections of this paper covering these topics report much previously unpublished information or ideas essential to an understanding of the oral biology of phyllostomatid bats and are, therefore, more detailed.

Lastly, a word about the authors is relevant. The senior author initiated the research program and is responsible for most of the interpretations presented herein. The section on transmission electron microscopy of the parotid and submandibular salivary glands of *Artibeus phaeotis*, which is the first such published information for phyllostomatids, was written by Carleton J. Phillips and Gary W. Grimes. The summary of phyllostomatid masticatory apparatus (tongues, neck, and throat musculature) was written by G. Lawrence Forman.

MATERIALS AND METHODS

Specimens used for portions of this paper that report previously unpublished information about phyllostomatid oral biology were collected in the Mexican states of Nuevo León, Hidalgo, Nayarit, and Jalisco, in 1972 and 1973 or in Jamaica, in 1974. In addition to specialized preparative techniques, which are detailed below, many specimens were preserved either as typical museum study specimens (skins and skulls) or as fluid-preserved specimens. Samples from each of the species collections have been deposited as voucher specimens in The Museum, Texas Tech University. Slides, in the case of histological preparations, have been deposited in the Department of Biology, Hofstra University.

General Histology

Specimens selected for general histological studies with the light microscope (LM) were killed in the field; tissues were removed, placed in individual containers, and fixed in one of the following solutions: 10 per cent nonbuffered or buffered formalin; Carnoy's fixative; or alcohol-formalin-acetic acid. Some

specimens were fixed *in toto*. All materials subsequently were stored in 70 per cent ethyl alcohol until studied. Calcified tissues were prepared for embedding by one of the following two methods: tissues were placed for at least 20 days in 10 per cent ethylenediamine tetra-acetic acid (versene) adjusted to pH 7 or they were placed in Decal (Scientific Products) for two to six hours depending on outcome of tests for calcium (Lillie, 1965). Following decalcification, the specimens were washed, dehydrated, and cleared in xylene for at least 30 minutes. Vacuum infiltration for 30 to 45 minutes at 25 inches mercury was followed by embedding in paraplast. Sections were cut at five to seven micrometers.

Selected slides were prepared for study with the light microscope by staining with a variety of general histological procedures as follows: Harris' hematoxylin and eosin-Y (H&E), the periodic acid-Schiff (PAS) reaction, azure-A and eosin-B (pH 4.8-5.0), Masson's trichrome stains (using Harris' hematoxylin for two minutes), Mallory triple connective tissues stains (Humason, 1972), aldehyde-fuchsin following oxidation for 30 minutes in peracetic acid (Fullmer and Lillie, 1958), and silver impregnation. Unless otherwise noted, formulae, times and interpretations of tinctorial results of these techniques were based on those of Lillie (1965).

Transmission Electron Microscopy

Transmission electron micrographs are included in this report. Materials for this technique were partially prepared in the field. Glands were removed from bats at time of death, minced, and fixed in 2 per cent glutaraldehyde in 0.1 M PO_4 buffer. Although not wholly desirable, some specimens were stored in this fixative for as long as three weeks prior to embedding. The materials were washed in 0.1 M PO_4 buffer for two hours, post-fixed in one percent OsO_4 in 0.05 M PO_4 buffer for one hour, and embedded in Epon. Additional details of technique can be found in Pease (1964) and Hayat (1972). Sections were made on a Porter-Blum MT-2 ultramicrotome and stained with uranyl acetate and lead citrate. Observation and photographs were made on an RCA EMU 3-G electron microscope (TEM) operated at 50 kilovolts (KV).

Scanning Electron Microscopy

Critical point drying was used for preparation of soft tissues for the scanning electron microscope (SEM). Specimens were embedded (subsequent to decalcification in the case of jaws) in the manner described above (General Histology) and the blocks were sectioned to the desired plane. In this way, it was possible to retain prepared slides that could be stained with general histological procedures for comparison to the three-dimensional view obtained with the scanning electron microscope. The blocks then were deparafinized in xylene (usually two hours in two or three changes), dehydrated in ethyl alcohol, placed in successive changes of 50, 60, 70, 90 and 100 per cent amyl acetate: ethanol and, finally, dried in a CO_2 critical point drying apparatus. The dried specimens were mounted on aluminum stubs and coated lightly with carbon and gold:palladium (60:40). With exception of decalcification, embedding, and critical point

drying, the same procedures were used to prepare hard materials such as teeth. The materials were studied with an Hitachi HHS 2-R scanning electron microscope at 10 or 20 KV and photographed with either Polaroid PN/55 or Kodak 4127 film. Excellent detailed techniques can be found in Anderson (1951), Boyde and Wood (1969), and Hayes (1973).

Terminology

Dental nomenclature is highly complex; the terminology employed here for descriptions of coronal patterns essentially is that of Van Valen (1966a) and Herskovitz (1971); an additional, fairly detailed explanation can be found in Phillips (1971). Basic terminology for dental microanatomy is that used in the standard textbook edited by Sicher and Bhaskar (1972). Dental formulae are used only sparingly in this chapter, but when presented they do have phylogenetic implications. By convention, lower-case letters have been used for lower teeth, and upper-case for upper teeth. Thus, the last upper premolar is labeled with an uppercase P and the number 4; the latter suggesting an evolutionary status for the tooth. We have followed Handley (1959) and Phillips (1971) in regarding the I3 as the missing incisor in those species having only two upper incisors. A lower-case d denotes deciduous teeth. With regard to the salivary glands, we have not followed Wimsatt (1955) and DiSanto (1960), who also have studied these structures in phyllostomatids. These authors used the names parotid, principle submaxillary, and accessory submaxillary for the major salivary glands of bats. In so doing, they cited Robin (1881). Herein, we have used the names parotid, submandibular, and sublingual for these same glands because the term submaxillary is not descriptive for a gland generally located near the angle of the mandible, and the name sublingual is used most often in literature for the pair of large salivary glands positioned between the dentaries at the base of the tongue. The nomenclature for throat and cervical musculature is based on that used by Wille (1954).

Histologists traditionally have used the terms serous and mucous to describe cells comprising secretory acini of salivary glands. These terms have been valuable for easily communicating the general appearance of cells. Mucous cells, for example, have a clear, almost achromatic cytoplasm when fixed with formalin and stained with hematoxylin and eosin-Y, whereas serous cells generally have a relatively dense, chromatic cytoplasm and a large concentration of basophilic material in the basal ergastoplasm (Sicher and Bhaskar, 1972). Numerous studies have indicated, however, that this classification scheme is inadequate regarding nomenclature of secretory products (see Junqueira *et al.*, 1951; Leblond, 1950; Wimsatt, 1956; DiSanto, 1960). Cells having the appearance of mucous type cytoplasm in the parotid gland of *Artibeus jamaicensis*, for example, apparently do not secrete mucins and, thus, have been termed pseudomucous by Wimsatt (1956). We agree with the comments of Shackleford and Wilborn (1968) in not following Wimsatt in using this term. For the purposes of this report we have chosen to use the traditional terms mucous and serous in the descriptive way stated by Sicher and Bhaskar (1972) without implication of knowledge of the chemistry of the secretory products. Additionally, we have followed others

(see Shackleford and Wilborn, 1968) in referring to those secretory cells having combined morphological or tinctorial characteristics (or both) of classical serous and mucous cells as being seromucoid.

DECIDUOUS DENTITIONS

The deciduous (primary) dentitions of phyllostomatid bats are highly specialized and strikingly different from the permanent dentitions. Unlike the deciduous teeth of most mammals, those in bats are not directly functional in comminution of food material. Instead, chiropteran deciduous teeth generally are regarded as modified for use as instruments for clinging to the female (see Allen, 1939; Reeder, 1953; Friant, 1963). In this connection, it is interesting that in some rhinolophid species the deciduous teeth are resorbed prior to birth (Grassé, 1955; Spillmann, 1927; Dorst, 1953), and in at least one molossid (*Mops*) some, but not all, of the deciduous teeth are resorbed prenatally (Dorst, 1957a). Each species of phyllostomatid thus far studied apparently possesses a full complement of deciduous teeth that are retained after birth. However, the lower first deciduous premolar (dp2) has not been observed and possibly either is lost shortly after birth or is resorbed prenatally, if it forms at all.

The deciduous teeth of phyllostomatids generally are smaller and morphologically less complex than those of vespertilionids and molossids (see Phillips, 1971, for a summary). The simplicity of deciduous teeth in the phyllostomatids is consistent with their comparatively reduced permanent dentitions; only the Phyllostomatinae have permanent teeth with fairly complex coronal patterns (see next section).

From an evolutionary and systematic point of view, there are two especially noteworthy features in the known phyllostomatid deciduous dentitions. As described below, morphological differences in the upper deciduous incisors suggest different systematic relationships among the phyllostomatids than are implied by the current scheme of classification. It is important to note that such discontinuities have been indicated by a variety of other investigations based on such diverse approaches as comparative serology, chromosomal morphology, and osteology (Gerber and Leone, 1971; Baker, 1967; Walton and Walton, 1970). Secondly, the presence in many phyllostomatid species of three upper deciduous premolars (dP2, dP3, and dP4) is of evolutionary significance because the normal permanent dentitions include only two upper premolars. The only known exceptions to this configuration apparently result from abnormalities such as double initiation and atavism (Phillips, 1971). The presence of a small and unreplaced upper deciduous premolar directly posterior to the canine provides strong evidence, in the absence of an adequate fossil record, that the two remaining permanent premolars can, in fact, be regarded as P3 and P4, in the evolutionary sense.

The following paragraphs summarize current knowledge about the deciduous dentitions in the various phyllostomatid subfamilies.

Among the Phyllostomatinae, the known deciduous dental formula is 2/3; 1/1; 3/2-3?. This subfamily is of special interest because of differences in shape

of the first upper deciduous incisors in *Macrotus* in comparison to those of *Tonatia*, *Mimon*, *Chrotopterus*, and *Phyllostomus*. In *Phyllostomus*, the second upper deciduous incisor is longer and more greatly curved than the inner one, which is thin and tapers to a fine, recurved point at the tip (Miller, 1907). In *Mimon* (Phillips, 1971), *Tonatia* (Dorst, 1957*b*), and *Chrotopterus* (Leche, 1878), the inner upper incisors resemble those in *Phyllostomus* in being smaller than the outer ones and in having a fine, recurved point. In *Macrotus*, on the other hand, the first upper deciduous incisor is as large as the outer one and is forked, with the mesial lobe being somewhat larger than the lateral one (Nelson, 1966). It also is of interest that in *Macrotus* the three lower incisors have only two permanent replacements (Phillips, 1971). The first and second lower deciduous incisors are trilobed, like their permanent replacements, whereas the third, which is shed but not replaced, is a small, simple spicule. This disparity between numbers of deciduous and permanent teeth is yet another example of the value of the analysis of deciduous teeth toward deciphering evolutionary sequences.

The deciduous dental formula in the Glossophaginae is 2/2; 1/1; 3/2-3. Among the 13 genera of glossophagine bats, the deciduous dentitions of only *Glossophaga*, *Leptonycteris*, and *Choeronycteris* have been studied and described (Phillips, 1971; Stains and Baker, 1954). All three apparently have at least 22 such teeth; the first lower deciduous premolar (dp2) has not been found and possibly is either resorbed or shed early in life. The major difference within these genera is in the shape of the upper deciduous incisors. In *Glossophaga* and *Leptonycteris* (Fig. 1) these teeth are forked, whereas in *Choeronycteris* they are pointed and recurved.

Within the Carolliinae, only the genus *Carollia* has been studied; the deciduous dental formula is 2/2; 1/1; 2/2-3. In *Carollia*, the first upper deciduous incisor is the most noteworthy component because it is thin and the apical end comes to a fine, recurved point (Leche, 1878; Miller, 1907). This deciduous tooth thus resembles the inner upper deciduous incisor in some species of Phyllostomatinae as well as at least *Choeronycteris* in the Glossophaginae.

The deciduous dental formula in the Stenoderminae is 2/2; 1/1; 2/2. In the two genera of this subfamily (*Artibeus* and *Ametrida*) for which data are available, the first upper deciduous incisor is forked, as in *Macrotus* (Leche, 1878; Miller, 1907).

The deciduous teeth in species of Phyllonycterinae have not yet been investigated. In the Desmodontinae, both *Desmodus* and *Diphylla* have a deciduous dental formula of 2/2; 1/1; 2/2. The teeth are small and greatly simplified; apparently the two upper deciduous incisors, both of which are the same size and are simple hooklike spicules, are functional (Miller, 1896; Birney and Timm, 1975). The remaining deciduous teeth are extremely small, barely penetrating the gingivum, and apparently are shed rather soon after birth (Birney and Timm, 1975).
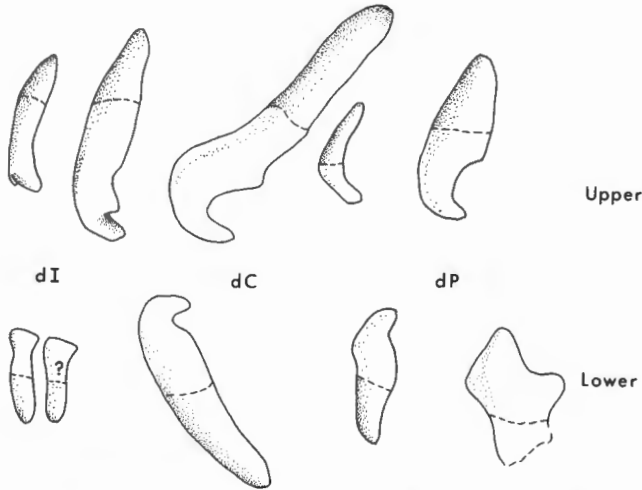
FIG. 1.—An example of deciduous teeth in the Mexican long-nosed bat, *Leptonycteris nivalis*. The tooth marked with a ? has not actually been seen in available specimens. From Phillips, 1971.

PERMANENT DENTITIONS

Development

Dental development is a complex process that is almost unstudied in phyllostomatid bats. This is unfortunate because full understanding of comparative dental ontogeny probably would be of considerable value to interpretation of evolutionary mechanisms and relationships. This is especially true regarding interpretation of such abnormalities as double initiation, incomplete dichotomy, and atavism. Furthermore, the direct relationship between morphogenetic integration and the process of dental ontogeny is readily apparent (Phillips, 1971). Bats remain almost unknown in this regard, although development of molars in relationship to integration of coronal configurations has been investigated in a horseshoe bat, *Hipposideros beatus* (Marshall and Butler, 1966). Studies on other mammals, particularly insectivores and marsupials, further underscore the importance of an understanding of dental ontogenesis to the determination of dental evolutionary mechanisms (Ziegler, 1972*a*, 1972*b*; Kindhal, 1963; Berkovitz, 1967, 1972; Osborn, 1970, 1973).

Three readily recognizable formative stages of dental development generally can be used to delineate aspects of mammalian tooth development (Sicher and Bhaskar, 1972). It must be remembered, however, that ontogenesis is a continuous process rather than stepwise, as might be implied by common use of the term stage.

Dental lamina stage.—Initiation of the teeth results from cellular proliferation within the epithelial dental lamina, which is of ectodermal origin. Dental buds, which are the primordia of individual teeth, develop simultaneously with differentiation of the dental lamina.

Dental cap stage.—This developmental phase is characterized by uneven cellular proliferation resulting in formation of an outer and inner enamel epithelium. It is especially important to note that development of the dental cap influences the mesodermal mesenchyme, which in turn condenses to form the dental papilla. The dental papilla provides the primordium for both the dentin and pulp; it is this mesodermal component, through the process of dentinogenesis, that actually sets the size and occlusal pattern of the finished tooth (Tonge, 1971; Osborn, 1973).

Dental bell stage.—This stage is characterized by both histodifferentiation and morphodifferentiation that results in formation and alignment of ameloblasts and odontoblasts, which in turn will form the matrices of enamel and dentin, respectively.

A remarkable SEM micrograph of a developing permanent upper premolar in a near-term fetus of a specimen of the Jamaican fig-eating bat, *Ariteus flavescens*, is shown in Fig. 2. In this instance, enamel and dentin formation has reached the cement-enamel junction, and root formation is well underway. A distinct, smooth-surfaced epithelial diaphragm can be seen at the root apex. A dense band representing the columnar enamel-producing ameloblasts and stratum intermedium also can be distinguished easily in this electron micrograph. The developing tooth is cushioned by the stellate reticulum, also well illustrated by this figure. The long processes that connect the component cells, together with the fact that the stellate reticulum is fluid rich, gives this layer a "lacy" appearance.

Within the Phyllostomatidae, dental development in relationship to age has been investigated histologically only in the Jamaican fruit bat, *Artibeus jamaicensis*. The following summary comments are based on this study (Farney, 1975). Because ages of individual bats cannot be determined with precision, Farney (1975) used the standard measurement of crown-rump length in his report. At some future date, it might be possible to relate these measurements to actual age; at best, they currently provide chronological indications. In the 9-millimeter embryo, a dental lamina was evident; tooth buds could be distinguished anteriorly. In an embryo that measured 13.5 millimeters Farney (1975) was able to identify typical bell stage primordia, again representing only anterior teeth. At this time in growth of the embryo, the lower first molar was in the cap stage, suggesting early initiation of the molar field. It probably is true that in phyllostomatids in general the upper and lower first molars develop and erupt early. This possibility is strongly supported by earlier studies (Phillips, 1971) of tooth eruption sequences in three glossophagine genera (*Glossophaga, Leptonycteris*, and *Choeronycteris*). The importance of this finding is reflected in terms of morphogenetic fields and, consequently, dental evolution. The upper and lower first molars in phyllostomatids can be regarded as molar determinants as discussed by Osborn (1973) and, thus, are pivotal in additional studies of developmental interrelationships of permanent teeth in these bats.

An embryo of *Artibeus jamaicensis* that measured 20.5 millimeters was found
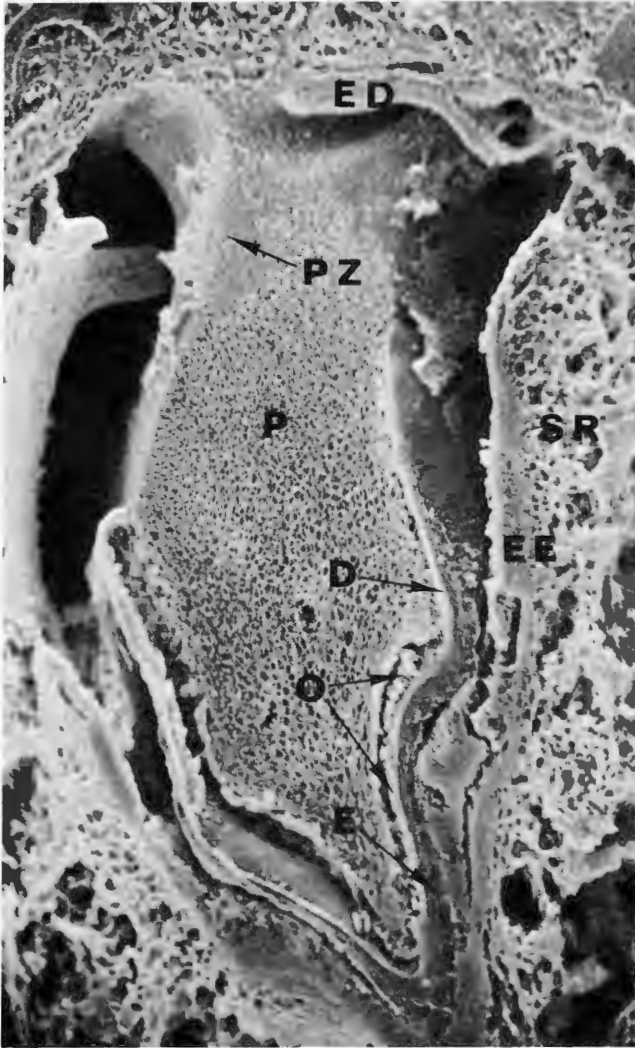
Fig. 2.—Scanning electron micrograph of a developing upper premolar in *Ariteus flavescens*. Abbreviations are: D, dentin; E, enamel; EE, enamel epithelium; ED, epithelial diaphram; O, odontoblasts; P, pulp; PZ, proliferative zone; SR, stellate reticulum. 109×.

to have deciduous teeth in a late bell stage; buds representing permanent teeth were detected anterior to the first molar (Farney, 1975). In a 31.5 millimeter embryo, the deciduous incisors and canines were fully formed; the permanent incisors were in the bell stage and the permanent canines were in the cap stage. The first permanent premolars were reported to be in an early bud phase, whereas the second premolars were somewhat more developed; this latter finding strongly suggests that the last premolar (P4) can be regarded as a premolar determinant.

Eruption and Shedding

Among the phyllostomatids, eruption and shedding has been studied only in three genera of glossophagines (*Glossophaga, Leptonycteris,* and *Choeronycteris*) and, therefore, is a topic still largely unknown (Phillips, 1971).

In general, eruption is a continuous process that can be divided into three stages (Sicher and Bhaskar, 1972): a pre-eruptive phase during which the dental organ completes development and enamel and dentin are formed; a prefunctional eruptive phase during which the root(s) forms and the new tooth moves to the occlusal plane; and the functional eruptive phase, which begins after the tooth reaches the occlusal plane. The first two of these phases are of primary concern to the present discussion; the third phase, which involves the complex movements of mature, functional teeth is of interest in investigations of changes that take place in the dental arcade as responses to stresses and attrition. For example, in the common vampire bat (*Desmodus rotundus*), the mature permanent teeth continue to move into the occlusal plane as considerable attrition due to thegosis reduces the crowns of the enamel-less teeth (Phillips and Steinberg, 1976). Regarding developmental problems of the first two eruptive phases, there presently are three main topics of considerable interest. How and why do developing teeth undergo the initial process of eruption, what is the relationship of erupting permanent teeth to the shedding of the deciduous teeth, what is the process of passage of the permanent teeth through the oral epithelium and the mechanism of epithelial attachment to the surface of the tooth?

Many mechanisms of eruption have been suggested and studied experimentally but the problem is far from resolved (see Sicher and Bhaskar, 1972; Phillips and Oxberry, 1972). Studies of the glossophagine long-tongued bat, *Choeronycteris mexicana,* provide the only information on this subject for phyllostomatids (Phillips, 1971). Analysis of these materials reveals no trace of a hammock ligament, as reported by Sicher (1942) for certain rodents. It is of further interest that there is no indication of a vascular role in eruption because the pulp and connective tissue adjacent to the developing apical foramen are not highly vascularized, at least in the studied specimens of *Choeronycteris.*

The relationship of the newly erupting permanent teeth to the deciduous teeth in *Choeronycteris* is more straight forward. In conjunction with enamel maturation, the stratum intermedium and ameloblasts, and perhaps the reduced outer enamel epithelium, become indistinguishable due to changes in cellular morphology (Figs. 3, 4). Both cell types appear to develop large, clear (formalin fixed and stained with hematoxylin and eosin-Y) vesicles within the cytoplasm. In most of the cells, the vesicle is so large that the heterochromatic nucleus is basally restricted and crescent shaped (Figs. 3, 4). Additionally, in these specimens there is a distinct, thick proliferative zone of cells at the coronal apex of the developing permanent tooth (Figs. 3, 5). The mesodermal connective tissue that surrounds the developing tooth following the loss of the stellate reticulum and reduction of the outer enamel epithelium shows considerable alteration in those areas adjacent to the proliferative zone (see Phillips, 1971). It has been suggested elsewhere (Sicher and Bhaskar, 1972) that cells of the prolifera-

tive zone produce an enzyme (possibly hyaluronidase) that leads to a loss of the ground substance within the collagenous fibers that comprise the principle fiber bundles. The previously dense connective tissue thus becomes a loose, fluid-rich tissue with fine argyrophilic fibers. This presumed process of proteolysis allows for passage of the new tooth toward the oral cavity. Although lymphocytes have been reported from regions of connective tissue degradation in other species (Fullmer, 1967), no inflammatory cells have been observed in such areas in young of *Choeronycteris* (Phillips, 1971) and are not generally regarded to be a factor in this developmental process. In sections from a newborn *Choeronycteris* stained with the periodic acid-Schiff reaction (PAS), the region of connective tissue undergoing degradation is PAS negative or, at most, only moderately PAS positive. This is in contrast to the unaffected adjacent tissue, which generally is strongly to moderately PAS positive. Following Spicer *et al.* (1965), it can be said that connective tissue undergoing degradation is low in mucosubstance.

Based on studies of *Choeronycteris* (Phillips, 1971), it also can be suggested that the process of initial eruption of permanent teeth in phyllostomatids is fairly rapid. Unlike the process in man, there are no histological indications of periods during which areas of resorption are partially repaired.

The eruptive process of permanent teeth directly affects shedding of deciduous teeth (Sicher and Bhaskar, 1972). Although the mechanisms have not yet been established, it is clear that in young phyllostomatids the proximity of a permanent tooth results in resorption of the root of the deciduous tooth (Phillips, 1971). As is visible in Fig. 5, the medial surface of the root of a deciduous upper premolar was undergoing resorption; it is of additional interest that multinucleated cells that morphologically and tinctorially resemble osteoclasts can be seen within the resorbed area. It has been suggested, but not confirmed, that pressure exerted by the permanent teeth causes osteoclasts to differentiate from the surrounding mesodermal connective tissue (Sicher and Bhaskar, 1972).

Coronal Configurations

The coronal configurations of secondary teeth of many phyllostomatid species have been described, figured, and discussed in a wide variety of publications (Hall and Kelson, 1959; Slaughter, 1970; Miller, 1971; Phillips, 1971; Winkelmann, 1971; Farney, 1975). Consequently, the following generalized comments are not descriptively detailed but instead are intended as a review and background.

Traditionally, knowledge about dental morphology of bats has had great practical value because of the use of dental characteristics in taxonomy. This aspect is underscored by an examination of books such as Hall and Kelson (1959), in which keys to families, genera, and species frequently are based mostly on dental characters. However, as we learn more about various inherited characters of phyllostomatids, it is likely that features of secondary dentitions taken alone will fall short of providing adequate and accurate presentations of real genetic relationships.
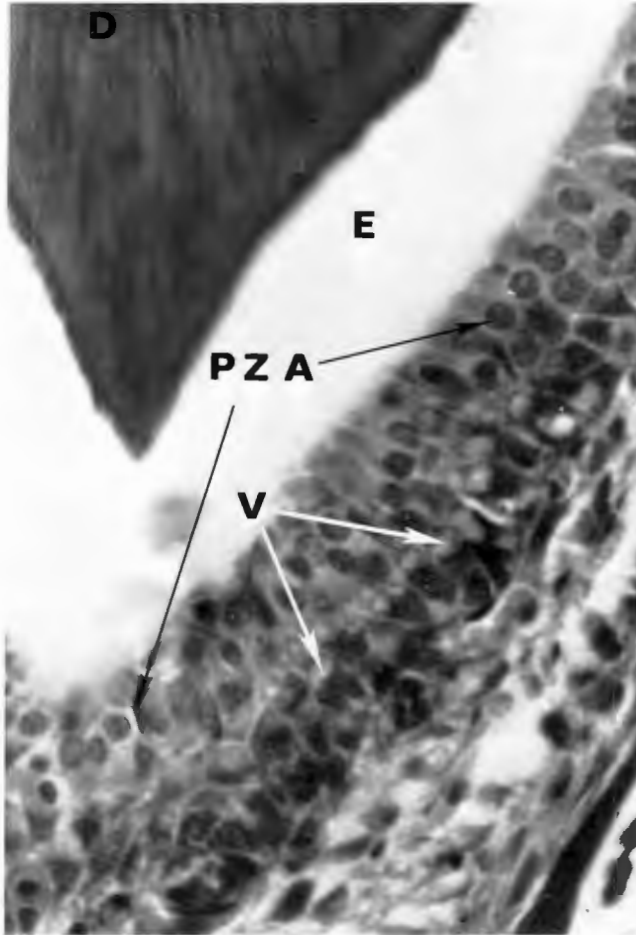
FIG. 3.—Reduced enamel epithelium of developing permanent premolar in *Choeronycteris mexicana*. Abbreviations are: D, dentin; E, enamel space; PZA, proliferative zone of amelo-blasts; V, vesicles. Hematoxylin and eosin-Y. 662 ×.

Phyllostomatinae.—Dental formula: I 2/1-2; C1/1; P 2/2-3; M 3/3. The teeth of all species in this subfamily are robust and relatively primitive. The inner upper and lower incisors typically are larger and more developed than are the outer ones (when the latter are present). The canine teeth tend to be thick based and have notable cingula. The height of the canines is not appreciably greater than is the height of the premolars and molars. The upper molars are nearly square; the ectoloph is primitively W-shaped and is considerably higher than the remainder of the tooth. In occlusal aspect, the ectoloph occupies approximately one-half of the tooth. The lower molars also are primitive; the trigonid has the typical triangular shape as does the talonid, giving these molars a W-shaped appearance. The cusps and commissures of both upper and lower molars normally are relatively sharp, regardless of the individual's age. Sharp-
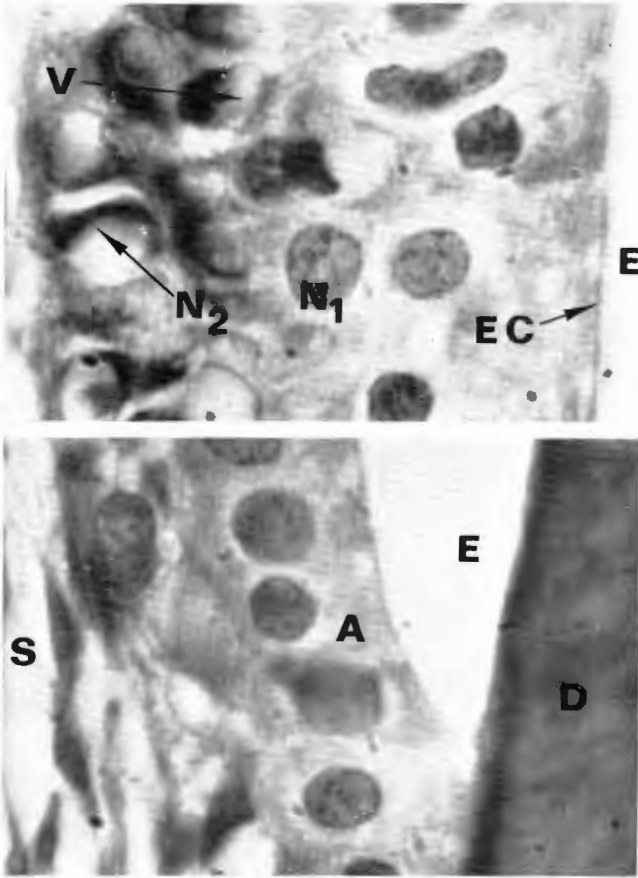
FIG. 4.—Details of reduced enamel epithelium in *Choeronycteris mexicana*. *Top*: near coronal apex. *Bottom*: junction of crown and root surface. Abbreviations are: A, amelo-blasts; D, dentin; E, enamel spaces; EC, enamel cuticle; N, euchromatic nucleus of amelo-blast; N2, heterochromatic nucleus of vesiculated cell; S, stellate reticulum; V, cytoplasmic vesicle. Hematoxylin and eosin-Y. 1299×.

ness is maintained by thegosis, which in turn is a consequence of the occlusal pattern.

Glossophaginae.—Dental formula: I 2/0-2; C1/1; P 2-3/2-3; M 2-3/2-3. The genera comprising this subfamily can be divided into at least three distinct groups based on dental characteristics; if all aspects of dental morphology are considered equally, the pattern is even more complex (see Phillips, 1971). In all studied species, the teeth are relatively small and in some they actually are minute in comparison to those of the Phyllostomatinae. Among the glossophagines (Fig. 6), the upper inner incisors are either large to moderate in size (for instance, *Glossophaga*, *Leptonycteris*, and *Platalina*) or much reduced and separated by a distinct median gap (for instance, *Anoura*, *Hylonycteris*, and *Choeronycteris*). The canines in all of the species are high and slender. Three or four groupings of
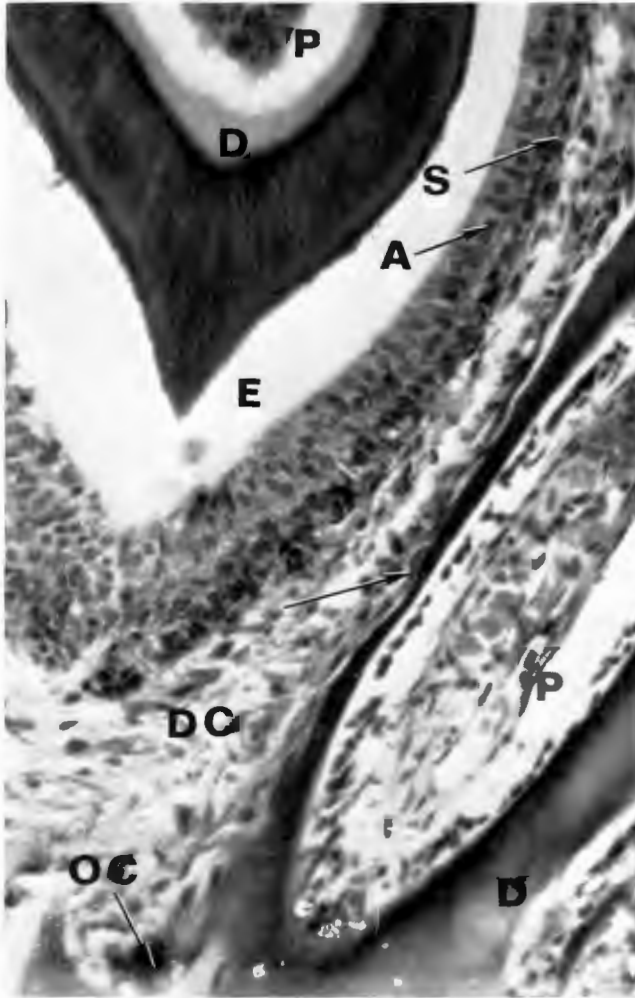
FIG. 5.—Developing permanent premolar and resorbing adjacent deciduous tooth (arrow) in *Choeronycteris mexicana*. Abbreviations are: A, ameloblasts; D, dentin; DC, altered connective tissue; E, enamel space; OC, "osteoclast;" P, pulp; S, stratum intermedium. Hematoxylin and eosin-Y. 304×.

molars can be distinguished within the subfamily, as currently defined. Within the first group of genera, *Anoura*, *Lionycteris*, and *Lonchophylla* have the most primitive configuration. A relatively high, W-shaped ectoloph is present, and the metastyle is prominent. In *Glossophaga*, *Monophyllus*, and *Leptonycteris*, the ectoloph also is W-shaped (although considerably elongated in the last genus) but is lower, and the metastyle is much reduced in comparison to the first group of genera. In yet another grouping (*Lichonycteris*, *Scleronycteris*, and *Hylonycteris*), the ectoloph is low and has been modified considerably, especially in the anterior elements; the paracone apparently has been lost, leaving a distinct parastyle on the anterior element. Determination of whether or not the paracone or parastyle

A **B**
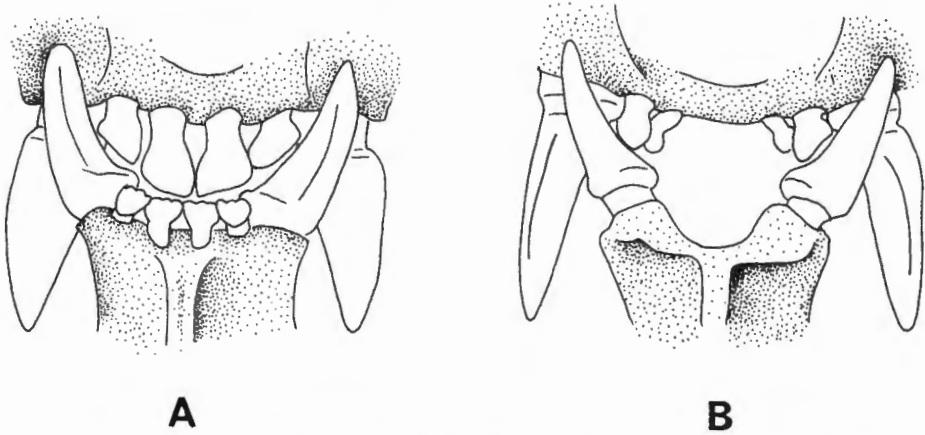
FIG. 6.—An example of the extremes in arrangement of permanent upper and lower incisors in glossophagines. A: *Lonchophylla robusta*. B: *Anoura geoffroyi*. From Phillips, 1971.

was lost (in absence of a fossil record) was based primarily on a remarkable series of *Lichonycteris* that has been described elsewhere (Phillips, 1971). It should be noted, however, that Winkelmann (1971) apparently disagreed with this interpretation, although he has not offered other evidence or an explanation for his opinion. The posterior element of the ectoloph in these genera still is nearly triangular.

The genera *Platalina*, *Musonycteris*, *Choeronycteris*, and *Choeroniscus* all have highly modified upper molars, in which the labial edge consists of a raised lip with an anterior parastyle and posteriorly positioned metacone.

In contrast to the extremely complex evolutionary pattern found in the upper molars of glossophagines, the lower molars are remarkably uniform. Variation in configuration mostly is in size and height of the cusps and is relatable to the degree of modification from the primitive pattern found in the upper molars.

Carolliinae.—Dental formula: I 2/2; C1/1; P 2/2; M 3/3. The dentitions in species of *Carollia* and *Rhinophylla* have been influenced by shortening of the upper and lower jaws. The upper inner incisor is large and somewhat procumbent, whereas the second incisor is much reduced and almost peglike. The lower incisors also are small. The upper and lower premolars are robust and high-crowned. The upper molars are considerably modified from what must have been the primitive configuration. The W-shaped ectoloph usually is reduced, or indistinguishable. The stylar shelf is high; the paracone and metacone often are almost linearly arranged along the labial border (depending on species). The protocone is absent, and, in fact, the entire lingual portion of the molars is anteroposteriorly narrowed. The lower molars also are highly modified; in *Carollia*, the lingual cusps (metaconid and entoconid) are much reduced, and in *Rhinophylla* they have been lost altogether.

Stenoderminae.—Dental formula: I 2/2; C 1/1; P 2/2; M 2-3/2-3. The dentitions of the large and variable number of species in this subfamily have been greatly influenced by both widening and shortening of the upper and lower

jaws. The basic phyllostomatid pattern of large inner and small outer upper incisors and relatively small lower incisors has been maintained. The canines usually are extremely robust and broad based as also are the upper and lower premolars. The upper molars in these species typically have a low profile and lack the primitive W-shaped ectoloph. Instead, the teeth either are narrow and long or nearly cuboidal (as in *Sturnira*). The paracone and metacone have been shifted to the labial margin, forming a longitudinal lip. The lower molars also are broad and clearly designed for crushing fruit; the trigonid, however, generally has been maintained and is easily distinguished. Thegosis is insignificant, probably because of the occlusal pattern, and, thus, the molar surfaces of steno-dermines have a rounded appearance rather than the distinct, sharpened cutting edges characteristic of the Phyllostomatinae.

Phyllonycterinae.—Dental formula: I 2/2; C 1/1; P 2/2; M 3/3. The three genera (*Brachyphylla*, *Erophylla*, and *Phyllonycteris*) tentatively classified in this subfamily (Jones and Carter, 1976) present two basically different dental patterns. In *Brachyphylla*, the upper and lower jaws have been shortened and widened, as is typical of the stenodermines. The dental arcade has been modified considerably but in overview also is similar to those found among species of this subfamily. The major difference, visible in the upper molars, is that the protocone and a relatively large metaconule are found in the basin between the lingual and labial borders.

The other two phyllonycterines, *Erophylla* and *Phyllonycteris*, have narrow, elongate upper and lower jaws, and the teeth are greatly reduced in size in accordance with an evolutionary trend possibly toward nectar feeding. The upper molars in these bats are relatively broad and exhibit, in reduced form, the pattern found in the stenodermines; the teeth have a distinct labial edge and broad concave basin.

Desmodontinae.—Dental formula: I 1-2/2; C 1/1; P 1/2; M 1-2/1-2. The three genera of vampire bats obviously have the most strikingly modified dentitions among the phyllostomatids. The cheek teeth are much reduced in number and size because selective emphasis has been placed on the upper inner incisors (which are procumbent) and upper and lower canines. These teeth are large and have extremely sharp cutting edges maintained by thegosis (see Phillips and Steinberg, 1976).

EVOLUTIONARY MECHANISMS

A survey of the highly variable dental configurations found in extant species of phyllostomatids produces a striking example of adaptive radiation of coronal dental anatomy in at least partial relationship to modifications in diet. Evolutionary patterns are relatively easy to decipher, even in the absence of a useful fossil record. Likewise, development of possible evolutionary scenarios and logical arguments for various genetic relationships among the species, based on dentitions, are reasonably straight forward, even if incomplete. The most significant problem, as yet essentially unanswered, is: how did the teeth evolve, or, what are the mechanisms of dental evolution? The following comments are

intended to supply some ideas on, and review some of the conceptual aspects of, this subject.

Two questions of special interest regarding evolutionary mechanisms are: how are teeth lost (keeping in mind that many phyllostomatids have lost one or more permanent teeth or have variable numbers of teeth); and how are coronal configurations modified?

Loss of certain permanent teeth is a characteristic shared by all phyllostomatids. Several mechanisms potentially are involved and although some mammalian taxonomists seem to believe that teeth simply become smaller and eventually disappear, the actual factors are more interesting and certainly more complex. As pointed out in the section on deciduous teeth, the pattern of loss of permanent teeth can in some instances be deciphered by the presence of unreplaced deciduous teeth. Relatively few workers have emphasized the fact that species of several chiropteran genera have unreplaced deciduous teeth. Such inconsistencies between number of deciduous teeth and number of permanent teeth are not restricted to the Chiroptera (Berkovitz, 1968). Among the glossophagines, which have been studied most intensively, *Choeronycteris mexicana* usually retains some of its four lower deciduous incisors in adulthood, and, furthermore, histological studies have revealed that permanent incisors form but do not erupt (Phillips, 1971). Thus, in this species at least, the permanent lower incisors have not really been lost. The mechanism involved is unknown but possibly a mutation has caused a localized biochemical alteration that results in destruction of partially developed permanent teeth at a time when they are in an advanced stage of morphogenesis. Grewal (1962) reported a similar instance in certain strains of laboratory mice (*Mus musculus*).

Extension of the mechanism(s) that cause permanent teeth to fail to develop fully and erupt, even though their morphogenesis is normally initiated, raises the question of whether other missing permanent teeth in phyllostomatids have been lost completely in the sense that morphogenesis is not even initiated. The high incidence of an atavistic P2 in some glossophagines (Phillips, 1971) indicates that the potential for development and eruption of this tooth still is present. Krutzsch (1953), Johnson (1952), and Sheppe (1964) debated the evolutionary importance of supernumerary and atavistic teeth in rodents, but the situation does not appear totally analagous to that found in phyllostomatids. In phyllostomatids, supernumerary teeth (Fig. 7) resulting from double initiation or from some abnormality during differentiation can be recognized because they are morphological duplicates of another tooth or because they actually are a part of another tooth. The theory that the small, single-rooted, permanent tooth formed between the P3 and canine in many glossophagine species most likely represents the permanent P2, and thus is atavistic, also is supported by the fact that in at least three genera (*Glossophaga, Leptonycteris*, and *Choeronycteris*) there is a deciduous P2.

Sheppe (1964:35) stated that "in the evolutionary history of a tooth there is a time when it occurs in almost all individuals. If for some reason the genes necessary for its development begin to be lost by the population. . . . eventually
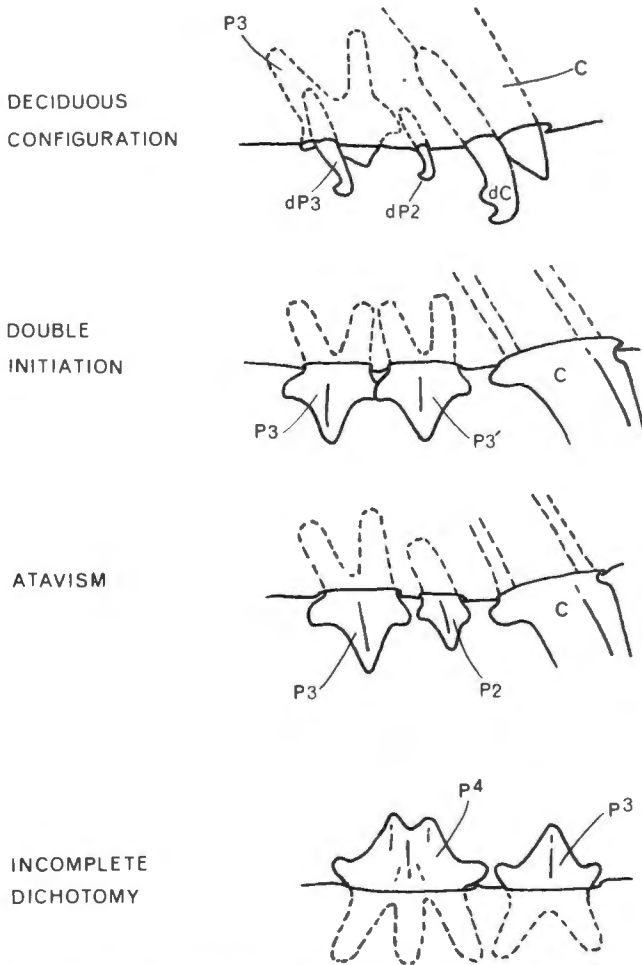
FIG. 7.—A comparison of normal deciduous configurations and abnormal or unusual permanent configurations of potential evolutionary importance. From Phillips, 1971.

all genetic basis for the tooth will be lost ... [and] if a tooth later appears in the same place it will be because of either a new mutation or some developmental accident without genetic basis." In fact, however, the factors controlling initiation, development, and eruption of teeth are considerably more complicated than this statement would suggest. Loss of various permanent teeth in the evolution of phyllostomatids clearly has been a complex process and not simply a matter of losing necessary genes. Among other mammals, Kurtén (1963) discussed the loss and return of m2 in the evolution of certain felids; he pointed out that the return of a tooth could have been the product of activation of the field of molarization, which presupposed that the genotype for m2 had never been lost although the tooth had been lacking.

This topic is brought into sharper focus when viewed in light of data from current developmental studies. The role of mesenchymal papillae in determina-

tion of tooth size, shape, and presence or absence (Kollar, 1972, 1975) is so considerable that in our view models of the evolutionary process can use this single component as a cornerstone. For example, Glasstone (1965) has shown that mechanical division of a papilla into halves will result in development of two half-sized but morphologically normal, teeth. Reduction of a mesenchymal papilla into fragments of less than one-half its normal size will cause an abortion of the developmental process (Glasstone, 1965; Kollar, 1975). From experimental data such as these, it can be theorized that intrinsic or extrinsic factors limiting mesenchymal cell division (during proliferation) to a level below a critical mass will result in the phenotypic absence of a given tooth. Such intrinsic or extrinsic factors presumably are reversible; the model thus derived is theoretically sound and easily applicable to descriptive data such as those presented by Kurtén (1963). Additionally, a model based on Glasstone's (1965) studies also enables us to offer a solution to the puzzle of how teeth disappear following an apparent trend toward reduction. Teeth can become phenotypically absent when proliferation of mesenchyme is limited to production of a mass of cells below threshold level. Most importantly, when developmental data are integrated into studies of evolutionary mechanisms, it becomes clear that loss of genes is not necessarily a factor. Teeth can be phenotypically absent even though development of their ectodermal (epithelial) component is initiated in the dental lamina.

When the above model is considered with regard to atavistic teeth in glossophagines (in conjunction with the presence of a dP2), the case for atavism is greatly strengthened. It also is applicable to instances where teeth apparently have been crowded out by narrowing of the jaw bones. Any intrinsic factor (such as DNA mutation within specific mesenchymal cells) or extrinsic factor (such as mechanical limitation, innervation, circulatory pattern, or influencing product released by adjacent cells) that causes limitation of mesenchymal proliferation can have a major influence on size and even presence or absence of teeth in the phyllostomatids.

Our model of mesenchymal proliferation also can be applied to problems in geographic variation. For example, Jones and Phillips (1976) recently presented a taxonomic review of the genus *Sturnira* in the Antilles. In this study, coronal differences between samples of *Sturnira lilium* were consistent enough to suggest limited interbreeding between insular populations. Consequently, subspecific designations were warranted. Differences in size, occlusal patterns, and even presence or absence of the last molars clearly are nonrandom in this phyllostomatid species. Indeed, consideration of data in terms of evolutionary mechanisms allows us to elaborate on the taxonomically important patterns reported by Jones and Phillips (1976). Thus, we now can delineate the levels to which such variation can be traced.

Variation in upper and lower molars in Antillean *Sturnira lilium* probably has the following sources: 1) Variation in occlusal pattern (size and shape of cusps) in ml and Ml results from variation in arrangement of the mesenchymal papillae of these teeth. Size, and to some extent shape, can be modified by a simple, slight increase or decrease in number of cells; that is, the exact cut-off point of mitotic division during proliferation of the mesenchymal papilla. What-

ever the factors determining cessation of division, their effect varies between populations. 2) The upper and lower third molars are smaller than the other molars. Geographically, specimens from Dominica and Martinique have smaller third molars than do specimens from more southerly islands, such as St. Lucia (Jones and Phillips, 1976). Additionally, some specimens from Dominica and Martinique bilaterally or unilaterally lack m3. Again, these patterns of variation can be traced initially to the mesodermal component. Loss of cusps might partially be a function of reduction in size (number of cells) of the mesenchymal papilla due to early cessation of mitotic division. *In vitro* studies with mechanically reduced mesenchyme would suggest, however, that more is involved than a severe reduction in number of cells (Glasstone, 1965). Consequently, the answer might be that an additional component such as a lessening in organizational control is the cause in loss of cusps. Osborn and Crompton (1973) referred to this process as an aging of the dental lamina. Actual absence of one or both m3 quite possibly reflects an inadequate mass of cells in the mesenchymal papilla of the tooth germ. Again this would be attributed by us to intrinsic or extrinsic factors causing early cessation of mitotic division within the proliferating mesenchymal papillae.

Overall, the basic model explained here is especially important relative to the phyllostomatids. It seems clear, furthermore, that loss of a particular tooth involves much more than loss of genes.

Pilbeam and Gould (1974) recently pointed out certain pitfalls to interpretation of apparent evolutionary changes in tooth size. Their mathematical analysis was applied to human evolution but clearly has important implications for the present discussion. These authors presented data that, although somewhat inconclusive (by their own judgement) in terms of statistical significance, nevertheless, clearly supported their contention that positive allometry between tooth size and overall body size can be an important factor and certainly worthy of consideration in making an evolutionary analysis. If these authors are correct, one would expect an increase in tooth size and possibly modification in shape in conjunction with selection for increase in body size. In absence of useful data on body weight, Pilbeam and Gould (1974) used length of skull as one criterion of size in determination of geometric scaling of teeth. We regard this as especially noteworthy in view of the common role of mesoderm in both bone formation and determination of tooth size and shape. This developmental commonality reflects the potential for a common controlling, or influencing, factor in terms of size, as outlined in our model discussed above.

Although we have not yet run regression analyses on any of the phyllostomatids, it is reasonably apparent that the role of positive allometry must be considered in our effort to understand dental evolution in these species. The stenodermines perhaps will provide the best example of positive allometry. In this group of species, there is a fairly wide range in size, and it is quite probable that many of the dental differences are more nearly a consequence of selection for size than they are the product of direct selectional pressure on the teeth. Additionally, the loss of third molars in the largest species and in small species

having the broadest rostra might paradoxically be coupled with geometric scaling. In most (probably all) phyllostomatids the first molars are the determinant teeth in the permanent dental arcade. That is, these teeth develop first and directly or indirectly influence the other cheekteeth and maybe even the anterior teeth, although the latter seems doubtful (this interdental relationship is discussed more fully in following paragraphs on morphogenetic fields). The role of determinants was not explored by Pilbeam and Gould (1974), but clearly their analysis of positive allometry is directly applicable. The paradox is that although positive allometry can result in larger and more robust teeth in conjunction with increased body size, it probably also can cause reduction and even loss of third molars.

It apparently is typical for Ml and ml to form first (Osborn, 1970) and influence the others; the reduction of coronal pattern in the posterior-most molars has been related by us to alterations in the mesenchymal papilla and referred to as an aging of the dental lamina by Osborn and Crompton (1973). Extension of these various data clearly suggest that apparent loss of third molars can be presumed to be a secondary impact of selection for increased body size or increased rostral length or width simply because their development is retarded, retrogressed, or even eliminated through resulting lack of space or even mechanical or biochemical influences from the preceding molars. This model seems especially applicable in studies of the genus *Artibeus*, in which species of various sizes currently are classified. Additionally, it probably is noteworthy that the third molars have been lost in species of the glossophagine genus *Leptonycteris* (Fig. 8). An evolutionary trend toward increase in body size (in comparison to other species in the subfamily) is readily apparent in these species. The most intriguing outcome of this logic is that we are presented with a sound model for explaining loss of posterior molars and once again reminded that teeth can be altered in size and shape as well as in presence or absence without any direct selective pressure on their own genetic complement.

Reduction in size of incisors for certain of the glossophagine species probably reflects what Pilbeam and Gould (1974) regard as "absolutely small" in contrast to geometric scaling. We have not tested our hypothesis mathematically for purposes of the present discussion but, nevertheless, would suggest that the evolutionary trends in these teeth for those species in which they are small or missing reflect direct selective pressure. In terms of evolutionary mechanisms, this scenario contrasts sharply with that presented for the trend toward loss of third molars.

The subject of Morphogenetic integration of developmental fields is another major component of a discussion on evolutionary mechanisms involved with dental coronal patterns. The phyllostomatid bats have been little studied in this regard, except for an earlier analysis of several glossophagine species by the senior author (Phillips, 1971). Many workers have pointed out that interpretation of dental evolution requires analysis of coronal patterns in terms of complex interrelationships between developing permanent teeth rather than in a simplistic fashion whereby genes are tied to particular characters by direct, complete causation (see Gould and Garwood, 1969; Olson and Miller, 1958; Kurtén, 1963; Van Valen, 1965, 1970). At the same time, however, the mechanisms involved in
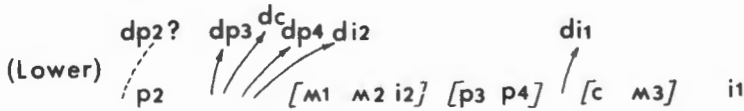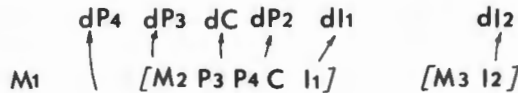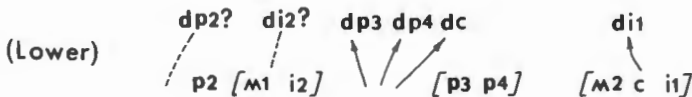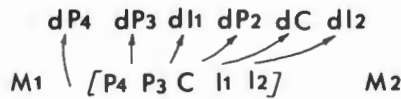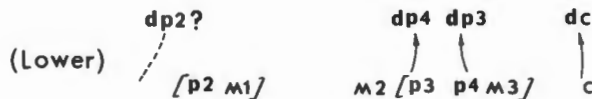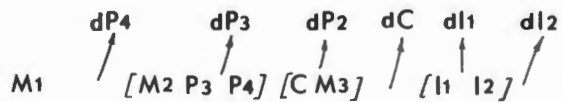
FIG. 8.—Comparative eruption sequences for three genera of glossophagines. Note the early eruption of the M1, which apparently is the molar determinate, and the relatively late eruption of M2 in *Leptonycteris*. From Phillips, 1971.

developmental interrelationships remain far from being established. As Van Valen (1970) indicated, current models requiring gradients might not be widely applicable but, nevertheless, are useful in helping to explain some developmental patterns that in themselves certainly do exist.

Three aspects of morphogenetic integration have been demonstrated in glossophagine bats (Phillips, 1971): at least some significant correlations are found between coronal features of different molars; interpretation of the correlation patterns is facilitated by inferential knowledge of developmental sequences (Fig. 8), suggesting that certain teeth could act as determinants; and in evolution of longer jaws and decreased complexity of occlusion, one also finds a decrease in significant correlations between dimensions of upper and lower molars.

The factors controlling relationships suggested by significant correlations within and between mature teeth are uncertain. It must be remembered, of course, that significant positive or negative correlation coefficients suggest, but do not prove, a causal relationship. Various workers have cited "intraembryonic compensation" (Van Valen, 1962) or "reciprocal variation in odontogenesis" (Garn et al., 1966) as possible mechanical factors and enzymatic, hormonal, or neural controls as organizers and indirect factors (Schour, 1934; White, 1959; Van Valen, 1966b).

Although it once was widely assumed that directional selection would result in a decrease in genetic and phenotypic variation, Guthrie (1965) and Bader and Lehmann (1965) obtained data that strongly suggested an increase in variation in dental characters within species undergoing rapid evolution. Application of this finding to analysis of dimensional variation in coronal components in several species of glossophagines led the senior author (Phillips, 1971) to hypothesize that the paracone rather than the parastyle has been lost from the upper molars in some of these species. The arguments for this opinion are based mainly on two findings: a definite pattern of high coefficients of variation in the paracone-parastyle length in those species having both elements; and individual variation in specimens of *Lichonycteris obscura* in which all conditions, including intermediates, were found and studied (Fig. 9). In this regard, it should be remembered that Winkelmann (1971) has disagreed, or at least has not followed this hypothesis. He has not, however, offered a counter argument.

Future comparative statistical and morphological studies of coronal features undoubtedly will be valuable in efforts to determine evolutionary pathways and mechanisms. Presently, however, limitations in knowledge of developmental biology and tissues pose the greatest problems to delineation of evolutionary mechanisms. One apparent solution is to combine histological and histochemical information with available developmental data for mammalian dentitions. This method was employed, for example, in preparation of a model for evolution of ever-growing molars in certain microtine rodents (Phillips and Oxberry, 1972). In studies of phyllostomatid dentitions, this approach has offered some insights into the evolution of enamel-less, self-sharpening permanent teeth in the common vampire bat, *Desmodus rotundus* (Phillips and Steinberg, 1976). In this instance, histological and scanning electron microscopic analyses were compared with basic developmental information derived from studies on other mammals. Certain patterns of developmental biology could thus be shown to have been of preadaptive value in evolution of enamel-less but cement-covered permanent teeth. Consequently, it should be possible in the near future to delineate an evolutionary model incorporating the actual mechanisms that in a sense set the stage for the process of natural selection.

In the case of *Desmodus*, it can be shown that the preadaptive features that facilitated the evolution of a highly specialized dentition very likely included the following: 1) Mammalian teeth are not dependent upon enamel, or, more strictly, ectoderm for determination of tooth shape (Sicher and Bhaskar, 1972; Kollar, 1975; Osborn, 1973). Thus, even in absence of the enamel-producing
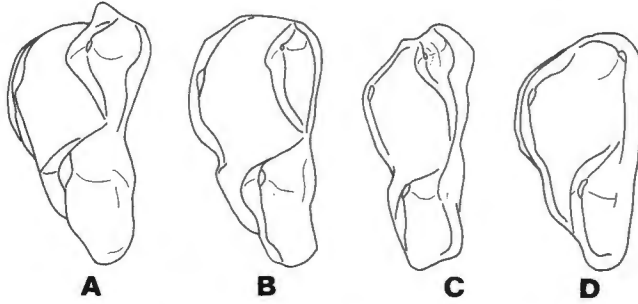
FIG. 9.—Variation in the first upper molar in four different specimens of *Lichonycteris obscura.* From Phillips, 1971.

ectodermal component, a mesodermal tooth germ will still result in an essentially normal tooth, insofar as the crown is concerned. This factor, which probably is common to mammalian dental morphogenesis, obviously allows for selection of enamel-less, but otherwise normal, teeth in any given species. 2) Cementoblasts will differentiate and produce a cementoid layer if enamel or dentin come into contact with periodontal tissue in the course of dental morphogenesis (Sicher and Bhaskar, 1972; Phillips and Oxberry, 1972). The coronal cementoid layer on permanent teeth in *Desmodus* apparently results because of a lack of protective, reduced enamel epithelium. 3) Active attrition of coronal surfaces eventually would result in loss of a crown, were it not for continuing eruption and consequent replacement of tissue. Based on studies of laboratory species, it generally is agreed that even non-ever-growing mammalian teeth normally continue to erupt throughout life (see Glickman, 1972). Teeth continue to shift position in response to a wide variety of factors subsequent to termination of the active eruptive phase, during which, teeth move into the occlusal eruptive plane. Cement added onto roots of teeth has the effect of maintaining the length of the rooted portion. In the common vampire bat, the anatomical root becomes crown as the original anatomical crown is worn away by thegosis, which is the most significant component of bimodal attrition in this species (Phillips and Steinberg, 1976).

The continuing search for solutions to evolutionary puzzles clearly requires analysis of phenotypic data within a framework of developmental biology. In this regard we are fortunate that the needs of medical science have produced a relatively large body of supportive information, particularly in the area of oral anatomy. Although lack of information about controlling factors in morphogenetic "fields" or gradients remains a major problem with interpretation of apparently real relationships between individual teeth within an arcade, it nevertheless is apparent that combination of phenotypic realities with applicable data on developmental systems is a valuable trend in research.

DENTAL MICROANATOMY

Dental histology has been investigated in considerable detail in a variety of mammalian species, with exception of the Chiroptera. In view of the variety
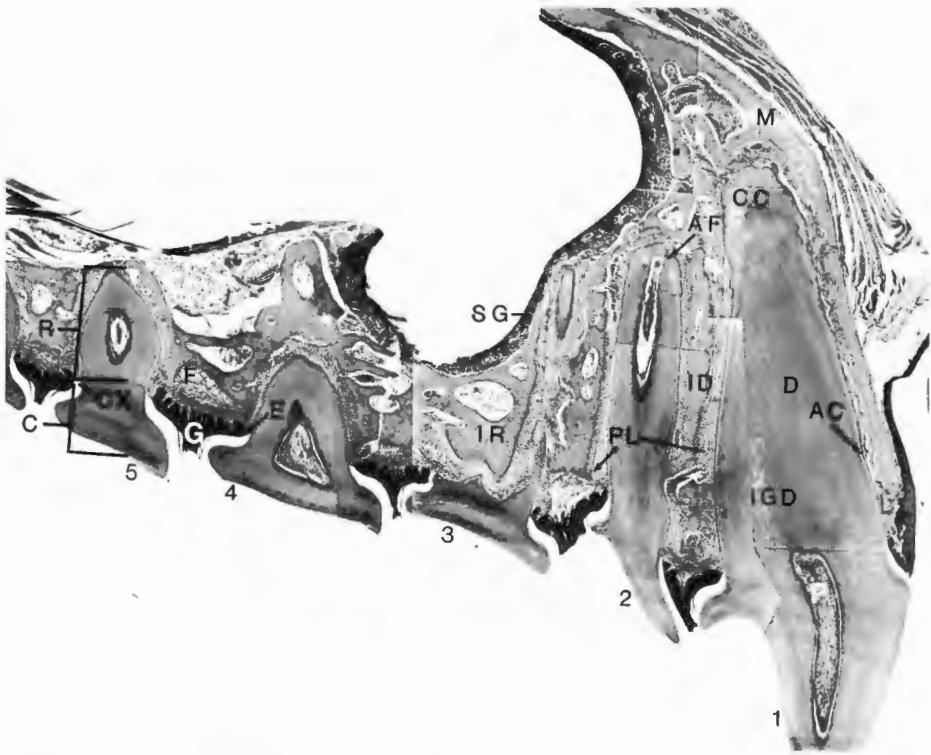
Fig. 10.—Composite microanatomical overview of maxillary teeth in a specimen of *Sturnira ludovici*. Abbreviations are: AC, acellular cement; AF, apical foramen; C, crown; CC, cellular cement; CX, cervix; D, dentin; EA, epithelial attachment; F, fat cells; G, gingivum; ID, interdental septum; IGD, interglobular dentin; IR, interradicular septum; M, maxillary bone; PL, periodontal ligament; R, root; SG, minor salivary glands. Hematoxylin and eosin-Y. 19×.

of dental configurations found in the Phyllostomatidae, careful comparative histological studies not only are warranted but likely will prove valuable in expanding our knowledge about dental evolution and comparative oral biology.

Fig. 10 presents an overview of the basic microanatomical features of the upper jaw of a specimen of *Sturnira*. In this composite photograph one can study the spatial relationships and general histological characteristics of the tissues.

Enamel

Enamel typically provides the outer protective covering for mammalian teeth. Among the phyllostomatids, only the common vampire bat, *Desmodus rotundus*, has been shown either to lack enamel or at most to have an enamel covering only over the apical portion of newly formed permanent teeth (Phillips and Steinberg, 1976). In this species, continuing eruption and concomitant attrition due to thegosis, quickly eliminate the original coronal apices. Although its sister genera, *Diaemus* and *Diphylla*, have yet to be studied in this regard, it seems likely that they too have at least a reduced enamel layer.
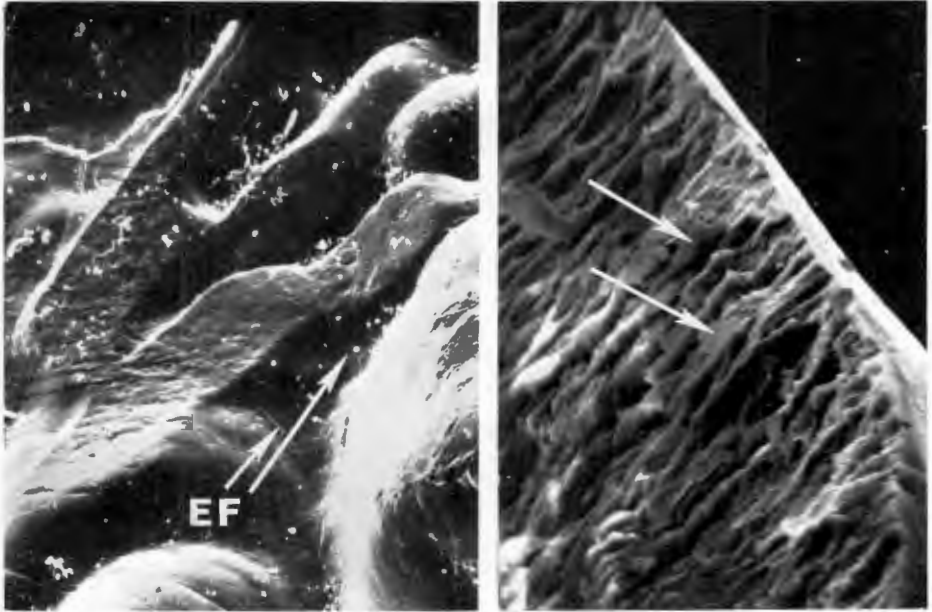
FIG. 11.—*Left:* Scanning electron micrograph of occlusal surface of M1 in *Artibeus jamaicensis.* Note the enamel ridges and small surface inconsistencies or fractures (EF). 2000×. *Right:* Scanning electron micrograph of fractured enamel in an upper canine from *Glossophaga soricina* showing the interrow sheets (arrows). 1480×.

Biochemically, human enamel is known to consist mainly of inorganic materials similar to apatite and to be semipermeable (Sicher and Bhaskar, 1972; Zimmerman, 1968). As of this writing, essentially nothing is known about the biochemistry of enamel of the Phyllostomatidae or other chiropterans. Among the phyllostomatids, specific differences in feeding habits (and, thus, availability of calcium, phosphorous, and Vitamin D) and the general oral environments would suggest that this particular subject could provide an intriguing opportunity for future comparative study.

Relatively little is known about the detail of enamel structure in most kinds of mammals although a few species are notable exceptions to this statement; in these kinds the structural arrangement of enamel has been investigated intensively by means of X-ray diffraction, histochemistry, and electron microscopy (for example, see Gustafson and Gustafson, 1967; Helmcke, 1967). General correlative studies (ordinal level) of cross-sectional configurations of enamel have been undertaken by Shobusawa (1952) and Boyde (1964, 1971). According to Boyde (1971), enamel prisms in the Chiroptera are essentially the same as those usually found in the Cetacea, Sirenia, and Insectivora. He (Boyde, 1964, 1971) has described the enamel prisms as hexagonally packed, nearly straight in course, and having distinct cylindrical boundaries that allow for easy recognition of interprismatic regions. In the course of our investigations on phyllostomatids, only the long-tongued bat, *Glossophaga soricina*, has been examined (Fig. 11). The portion of enamel shown was exposed by fracturing of an upper
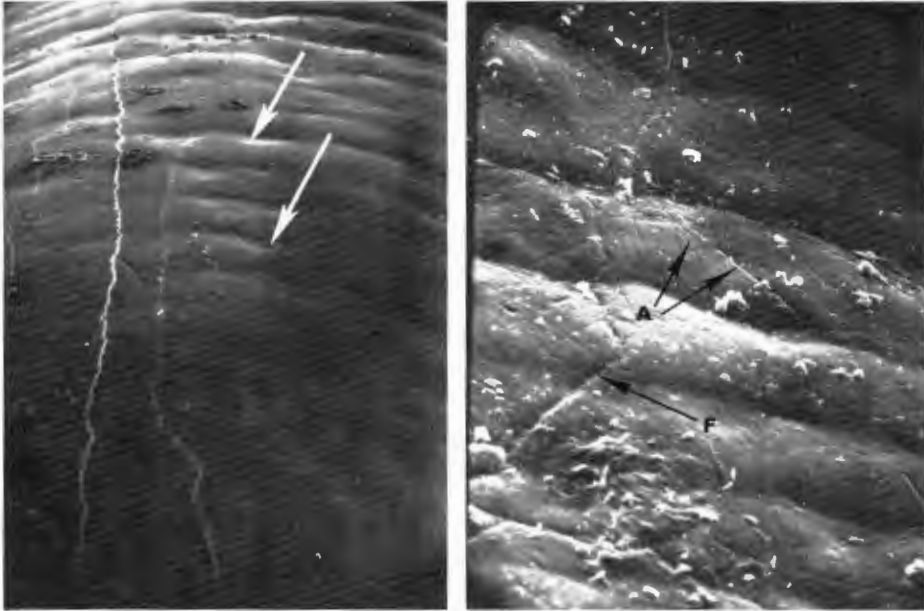
FIG. 12.—*Left*: Scanning electron micrograph of the anterior surface of an upper canine from *Artibeus jamaicensis* showing ridgelike perikymata (arrows). The longitudinal fracture line at the left resulted from vacuum processing. 111×. *Right*: Scanning electron micrograph of perikymata, surface scratches (A) and a groovelike inconsistency in the enamel surface (F). 370×.

canine, which occurred in a vacuum chamber during preparation for study with the scanning electron microscope. The course of the enamel prisms is apparently nearly straight. The interprismatic material was found to be in the form of inter-row sheets, some of which were left standing and clearly visible when the canine fractured (Fig. 11). This structural feature is at variance with what Boyde (1971) reported for the Chiroptera, however, structural variation could easily occur between species within an order. Ordinal comparisons (Shobusawa, 1952; Boyde, 1971) have resulted in groupings that most certainly do not reflect phylogenetic relationships. Thus, at least at the ordinal level, structural differences or similarities are difficult to interpret and a given species probably cannot be considered indicative of an order without a considerable survey of species.

Although the structural characteristics of enamel remain essentially unknown, the subject has considerable promise. Farney (1975) undertook a detailed scanning electron microscopic analysis of enamel of the Jamaican fruit bat, *Artibeus jamaicensis*.

Surface features of enamel in phyllostomatids are poorly known. Prior to widespread use of the scanning electron microscope, teeth were studied by means of dissecting microscopes. This instrument is inadequate, however, because of the extremely small size and reflective qualities of the teeth. Examination of the outer enamel covering with the scanning electron microscope typically reveals a coronal surface that is far from smooth (Figs. 11, 12). In adult speci-

mens, one usually can identify the perikymata, particularly on the sides of the crowns (Fig. 12). Perikymata, which have the appearance of being transverse, wavelike grooves, are regarded as external indications of the striae of Retzius (Sicher and Bhaskar, 1972). The ends of enamel rods and edges of lamellae are visible in human teeth at various states of erosion (Scott and Wyckoff, 1949; Scott *et al.*, 1949) but have not yet been observed in any of the phyllostomatids examined with scanning electron microscope. Numerous scratches and irregular grooves are common, however, and easily visible (Fig. 12). Some phyllosto-matids, particularly *Artibeus*, have notable surface modifications in the form of high interconnected ridges of enamel between the cusps (Fig. 11). These ridges become flattened due to abrasion and probably serve as treads that increase friction for holding hard rinded fruits in place when they are being crushed by the molars.

Dentin

Dentin is the major component of teeth in phyllostomatids. Although its chemical composition in these bats is unknown, in man it consists of approxi-mately 30 per cent organic material and water and 70 per cent inorganic material (Sicher and Bhaskar, 1972). The shape of the dentin is maintained by the organic constituents of decalcified teeth in histological preparations. The presence of mucosubstances is indicated by a PAS-positive staining reaction, which ranges from moderate to intense with phyllostomatids. Collagenous fibrils also are present in the organic dentin, as is indicated by green or blue staining of dentin with Masson's trichrome or Mallory triple, respectively.

In all phyllostomatids studied histologically thus far (*Artibeus, Sturnira, Phyllostomus, Desmodus, Glossophaga, Leptonycteris, Anoura,* and *Choeronyc-teris*), the coronal portion of the dentin is characterized by distinct dentinal tubules that follow a general S-shaped path from the pulpal chamber to the dentino-enamel junction (Fig. 13). These tubules tend to be highly arborized, especially near the enamel junction. This especially is true in vampire bats (*Desmodus*) although there is an absence of a definite layer of enamel. In this particular spe-cies, the tubules begin to branch at approximately one-half the distance between the pulpal chamber and outer coronal surface. In contrast to the coronal dentin, dentin comprising the roots of teeth in phyllostomatids does not contain so reg-ular a series of tubules. Instead, the tubules are sparse and usually have a twisted and irregular course. In the healthy teeth from phyllostomatid bats, the dentinal tubules contain a cytoplasmic process from an odontoblastic cell, positioned at the lining of the pulpal chamber (Fig. 13).

Interglobular dentin, which results from incomplete fusion during the process of dentinal mineralization (Sicher and Bhaskar, 1972), is found commonly in coronal dentin in phyllostomatids (Figs. 10, 14). Hypomineralized and hyper-mineralized globules stain differently due to the differing amounts of organic ground substance left after decalcification. It is perhaps noteworthy that differ-ences in amounts of interglobular dentin cannot readily be related to diet, at least based on comparison of the nectarivorous *Leptonycteris* to frugivorous *Artibeus* or insectivorous vespertilionid species.
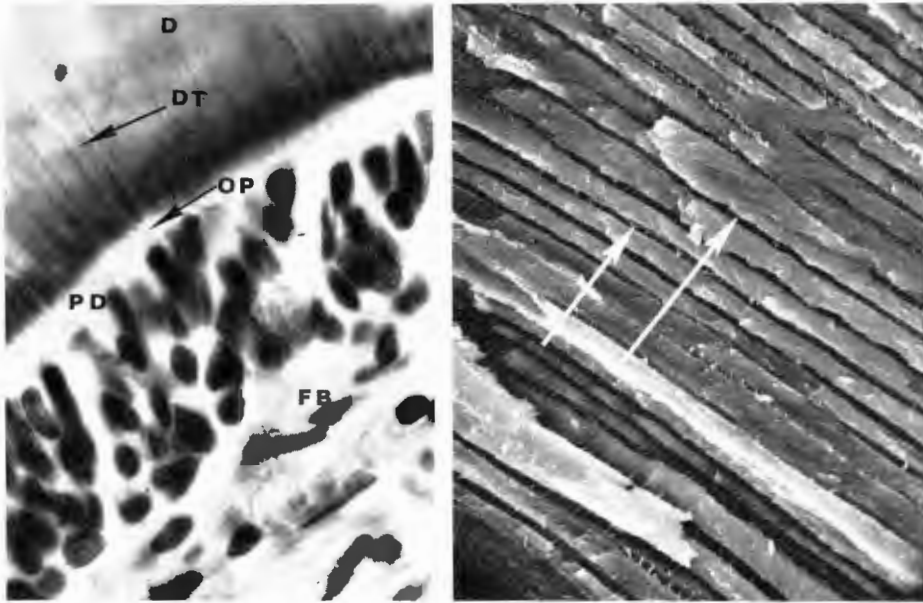
FIG. 13.—*Left:* Histological view of dentin and associated odontoblasts in *Sturnira ludovici.* Abbreviations are: D, dentin; DT, dentinal tubules; FB, fibroblasts; OP, odontoblastic process; PD, pre-dentin. Hematoxylin and eosin-Y. 942×. *Right:* Scanning electron micrograph of fractured dentin in *Glossophaga soricina.* Arrows denote dentinal tubules. 1900×.

Irregular, or reparative, dentin is found in instances where attrition is high due either to thegosis or abrasion. This type of dentin is formed quickly and serves to block the pulp chamber and, thus, prevent exposure of the pulp (Phillips and Oxberry, 1972). Among the various phyllostomatids that have been studied histologically, reparative dentin is found most commonly in the vampire bat (*Desmodus*). This undoubtedly is the result of relatively rapid, continuing eruption into the occlusal plane and a reflection of the considerable thegosis that planes the permanent dentition (Phillips and Steinberg, 1976).

Christian (1956) reported that he could determine age in the vespertilionid big brown bat (*Eptesicus fuscus*) by counting annular rings in dentin. According to Christian (1956), "a wide band of dentin is deposited during summer months followed by a dense zone during periods of hibernation." Although secondary dentin can be demonstrated histologically in most phyllostomatids, there is no evidence that it conforms to age except in a most general way. Bands, or areas, of secondary dentin vary in number and width both within a given tooth and among different teeth. Overall, it can be stated that secondary dentin, which usually is found adjacent to the coronal pulp chamber, seems most common in older individuals. Absence in the phyllostomatids of a marked annual physiological change such as hibernation essentially eliminates the possibility of using annual dentinal changes for age determination.
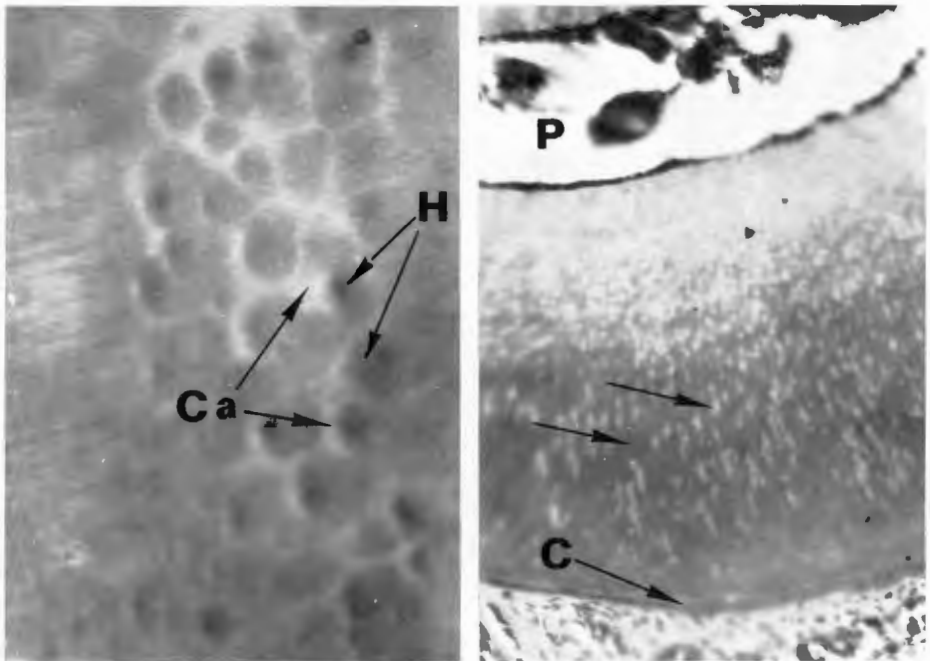
FIG. 14.—*Left:* Histological view of interglobular dentin in *Sturnira ludovici.* Abbreviations are: CA, hypercalcified area; H, hypocalcified area. Hematoxylin and eosin-Y. 388×. *Right:* Inconsistencies in dentin mineralization in *Desmodus rotundus.* Pale areas (arrow) are hypomineralized; other abbreviations are: P, pulp; C, cement. Masson's trichrome. 232×.

Cementum

The cementum is the softest of the three types of hard dental tissue. It is permeable and in man at least, is comprised of about 55 per cent organic material and water and 45 per cent mineral (Sicher and Bhaskar, 1972). A cementoid layer of variable thickness covers the roots of the teeth in the phyllostomatids. With the exception of *Desmodus,* the pattern is essentially the same in all other species that have been examined. The cementoid layer (along the sides of the root) is thin and acellular. Cementoblasts, characterized by small, ovoid, and somewhat heterochromatic nuclei, are found aligned along the root surface, even in adults (Figs. 15, 16). Typically, high magnification with the light microscope (1500×) reveals the elaboration of collagen into the cementoid tissue between the cementoblasts and cementoid layer (Fig. 15). The weak, or negative, PAS response in the cementoid tissue apparently reflects the polymerization of connective tissue mucosubstances (see Sicher and Bhaskar, 1972).

Among the phyllostomatids studied thus far, the cementoid layer appears thin in the glossophagines (specifically, *Glossophaga, Anoura, Leptonycteris,* and *Choeronycteris*) and of moderate thickness in *Phyllostomus, Artibeus,* and *Sturnira.* A strikingly different situation is found in *Desmodus* (Phillips and Steinberg, 1976). A thin layer of cement extends onto the coronal surface, where in absence of enamel it covers the dentin. The cementum covering the
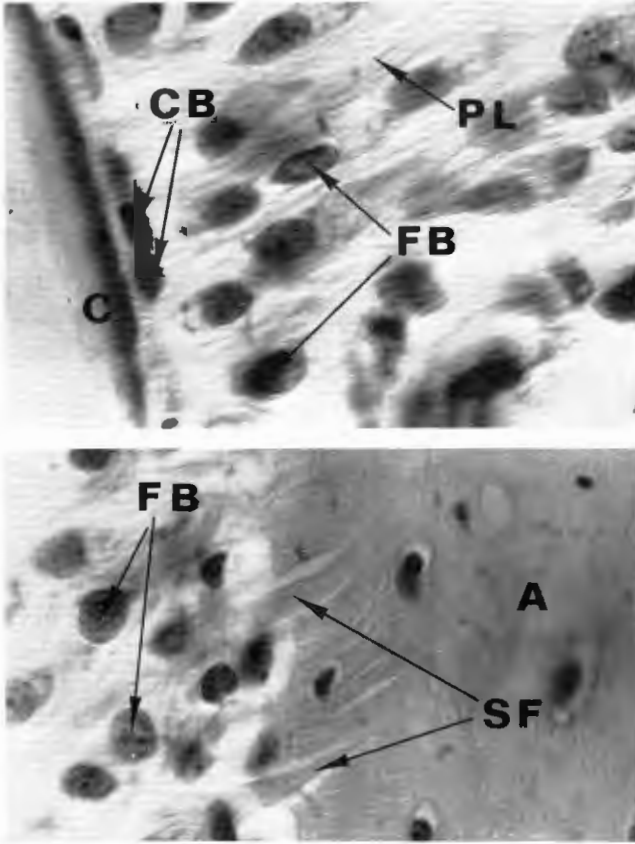
FIG. 15.—*Top*: Histological view of periodontal ligaments investing root surface (*Sturnira ludovici*). Abbreviations are: C, cement; CB, nuclei of cementoblasts; FB, fibroblasts; PL, periodontal ligament. Hematoxylin and eosin-Y. 1110×. *Bottom*: Histological view of periodontal ligaments investing alveolar bone (*S. ludovici*). Abbreviations are: A, alveolar bone; FB, fibroblasts; SF, Sharpey's fibers. Hematoxylin and eosin-Y. 1110×.

roots tends to be thick and is characterized by definite incremental lines (Fig. 16) that reflect periodic deposition in response to both stress and eruption. Although numerous workers have suggested (and, in some cases, actually tested) the value of incremental lines in cementum as a means of age determination (Klevezal and Kleinenberg, 1966), such a technique cannot be employed with *Desmodus*(Phillips and Steinberg, 1976). The numbers of incremental lines in the cementum varies both within teeth and, especially, among different teeth. Resorption and remolding of cementum, in addition to deposition of new cementum, can be related to dental drift by comparison to changes in adjacent alevolar bone.

Dental Pulp

The pulpal cavity in mammalian teeth typically is filled with a complex soft tissue that is continuous with the periapical tissue through the apical fora-
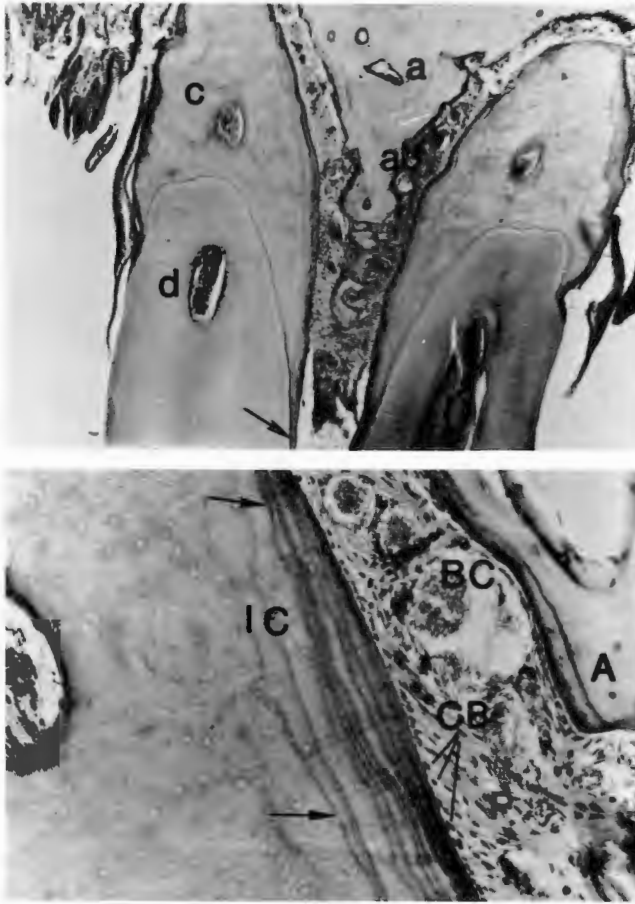
FIG. 16.—*Top*: Histological view of cementoid covering on upper incisors in *Desmodus.* Cementum (arrow) extends well onto the medial surface of the crown. Abbreviations are: A, alveolar bone; AB, alveolar bone resorption; C, cement; D, dentin; P, pulp. Hematoxylin and eosin-Y. 41×. *Bottom*: Higher magnification of irregular incremental lines in cement (arrows). Abbreviations are: A, alveolar bone; BC, blood vessels; CB, cementoblasts; IC, incremental cellular cement; P, periodontal ligaments. Hematoxylin and eosin-Y. 157×. Both photographs from Phillips and Steinberg (1976).

men of the root. Thus, the pulp is a continuation of the soft tissues that surround teeth and is histologically and, to some extent, biochemically similar to that connective tissue. It generally is agreed (Ogilvie and Ingle, 1965; Sicher and Bhaskar, 1972) that the pulp, which is histologically simple, but nevertheless dynamic, serves four basic functions: formative, defensive, nutritive, and sensory.

The formative function of the dental pulp probably should be regarded as the principle one among the four. Basically, the pulp develops from a mesodermal aggregation of cells that gives rise to fibroblasts, which elaborate the collagenous pulpal matrix, and to odontoblasts, which are directly involved with formation of dentin. The latter process is initiated by interaction between odonto-
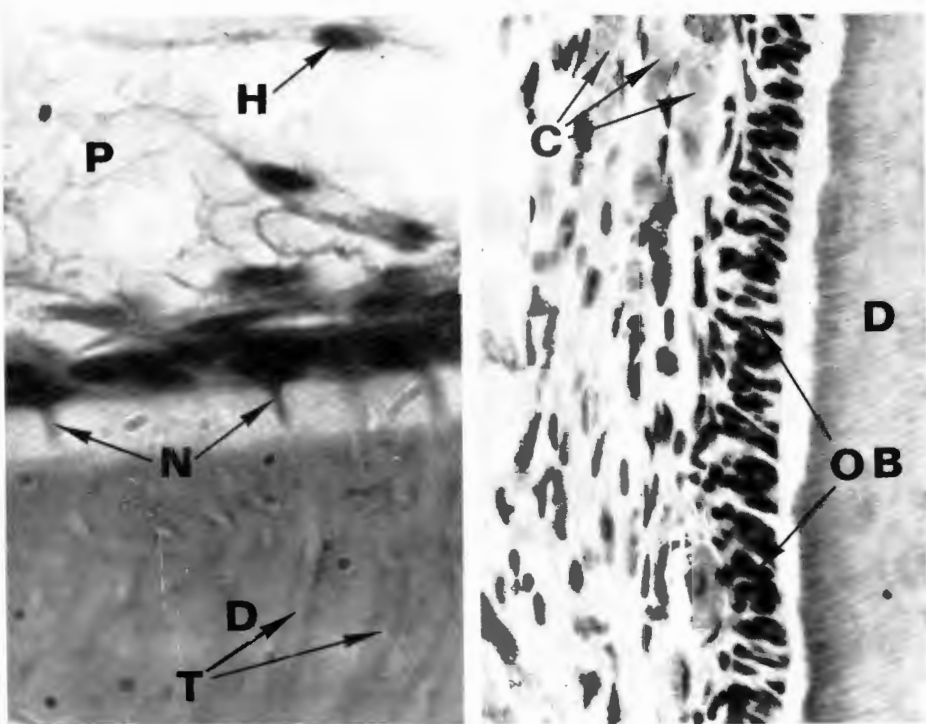
FIG. 17—*Left*: Pulpal pathology with displaced odontoblast nuclei (N) in a specimen of *Glossophaga soricina*. Abbrevations are: D, dentin; H, histiocyte (macrophage); P, pulp; T, dentinal tubules. Hematoxylin and eosin-Y. 1544×. *Right*: Normal (healthy) pulp in *Sturnira ludovici*. Abbreviations are: C, capillaries; D, dentin; OB, odontoblasts. Hematoxylin and eosin-Y. 760×.

blastic cells and ectodermal elements during tooth development (Stanley and Ranney, 1962). The highly specialized odontoblasts line the walls of the pulpal cavity in the normal (healthy) state and, thus, are a major histological feature (Fig. 17). In the phyllostomatid species studied, there were no interspecific differences apparent with light microscopy. As can be seen in Fig. 17, active odontoblasts are columnar in shape and have ovoid, heterochromatic nuclei. In specimens of bats displaying severe pulpal pathology of variable etiology, the odontoblasts frequently are flattened along their long axes. In fruit-eating phyllostomatids having relatively robust teeth (such as *Artibeus* and *Sturnira*), the pulp most often is healthy and odontoblastic cells essentially normal. Based on the genera of Glossophaginae that have been studied (*Leptonycteris, Anoura, Glossophaga*, and *Choeronycteris*), it is apparent that the pulp frequently is pathologic in wild individuals of these species. Each of these species is characterized by small teeth that are not especially important for feeding and, therefore, not under considerable coronal stress. Nuclei of odontoblasts frequently are displaced and, in fact, located within adjacent dentinal tubules (Fig. 17). Such a displacement (or, perhaps, migration) is thought to result from an increase in intrapulpal pressure, due to inflammation or pulpitis and is an initial pulpal
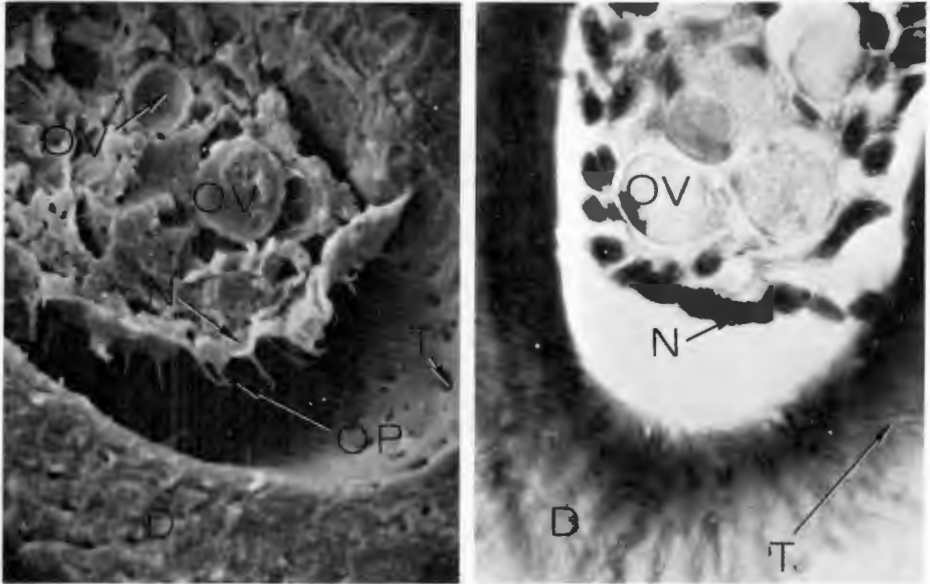
Fig. 18.—*Left:* Scanning electron micrograph of pulp chamber in an upper third premolar of *Leptonycteris nivalis*. 1242×. *Right:* histological section 5 micrometers away from view shown on left. Hematoxylin and eosin-Y. 1242×. Abbreviations for both are: D, dentin; OP, odontoblastic processes; OV, occluded vessel; N, nuclei of odontoblasts; T, dentinal tubule.

reaction to injury (Ogilvie and Ingle, 1965; Beveridge and Brown, 1965; Ostrom, 1963). Although the body of the odontoblastic cells is most prominent histologically, a moderate amount of cytoplasm is incorporated within the dentin in the form of processes that extend from the wall of the pulpal chamber to the dentinoenamel junction. In phyllostomatids, the processes were found to arborize considerably, especially near their termini. This feature apparently is typical in mammalian teeth (see Ogilvie and Ingle, 1965). The pulp of one species (*Leptonycteris nivalis*) has been studied with the scanning electron microscope, following decalcification of the teeth, standard sectioning down to the desired level, and critical point drying. This material affords a remarkable view of the odontoblastic cells and their processes (Fig. 18). Additionally, it is possible to compare the SEM photographs with a histological view, made from directly adjacent tissue. The odontoblasts in this instance were flattened, possibly as a result of certain pathologic features (thrombosis) within the pulp or adjacent to the rooted portion of the tooth (lesions in the oral mucosa). Among the odontoblastic processes exposed by the retraction of the cells from the wall of the pulp chamber, which is a common artifact of nonperfused histological preparations, at least one clearly is divided at its base. The process of this particular cell apparently matched the paired dentinal tracts, also visible with the SEM. In the SEM photograph, the odontoblasts appear to rest on a distinct, continuous membranelike layer that would serve to separate the main portion of the cells from the wall of the pulpal cavity. Such a structure has not been

reported previously even in recent, detailed TEM and autoradiographic studies (see Weinstock and Leblond, 1974), and it thus is possible that what appears to be a continuous membrane actually is either the apical portion of the cell membranes of adjacent cells or, perhaps, a layer of predentin.

Fibroblasts were found to be the second-most numerous cell type in the healthy pulp in phyllostomatids (Fig. 19). Such also is the case in man and rodents and, presumably, other mammals as well (Ogilvie and Ingle, 1965; Phillips and Oxberry, 1972). Numbers of fibroblasts clearly were greatest in developing teeth and least numerous in permanent teeth of old bats. Again, this pattern is essentially the same as in man and other mammals (Sicher and Bhaskar, 1972; Phillips and Oxberry, 1972).

Histologically, fibroblasts are easily identified within the dental pulp of bats. The nucleus is large, ovoid, and euchromatic. Additionally, the nucleus to cytoplasm ratio is high and, therefore, the latter is difficult to distinguish. Collagenous fibers, which are produced by the pulpal fibroblasts (Avery and Han, 1961), are found throughout the healthy pulpal stroma in phyllostomatids. Such fibers, which can be seen clearly with the PAS procedure, vary in abundance from individual to individual, as well as from tooth to tooth within a given specimen. It seems likely that both age and position of individual teeth within the dental arcade have an influence on abundance of fibers (Sicher and Bhaskar, 1972; Stanley and Ranney, 1962).

Staining of the pulp in *Artibeus, Sturnira,* and *Leptonycteris* with aldehyde-fuchsin alone or with aldehyde-fuchsin following oxidation with peracetic acid failed to reveal either elastic or oxytalan fibers. Neither type of fiber has been demonstrated in the dental pulp of other species of mammals (Ogilvie and Ingle, 1965).

Korff's fibers, which are reticular and apparently become part of the collagenous matrix of the dentin (Bevelander, 1941), probably are present in the normal pulp of all phyllostomatids, especially in instances where new dentin is being formed. We have studied them only in *Leptonycteris nivalis*, where they were revealed by silver impregnation.

Histiocytes, which can become macrophages, and lymphoid wandering cells, are found regularly in apparently normal (healthy) pulp in the phyllostomatids (Fig. 19). Neither of these types of cells (especially the second) is so common as the fibroblasts, but, nevertheless, they are easily identifiable. Both the histiocytes and lymphoid cells have defensive roles; the former remove dead cells, bacteria, and foreign materials by phagocytosis and the latter possibly are a source of antibodies and plasma cells (Zander, 1946; Bloom and Fawcett, 1968).

The dental pulp and dentin are nourished by a complex network of blood vessels, some of which are extremely small (Figs. 18, 19). The details of pulpal circulation in phyllostomatids are as yet unstudied but it is likely that, as in man, the pulpal capillaries are contractile with numerous arteriovenous connections (A-V shunts) as well (Han and Avery, 1963). In contrast to man (Ogilvie and Ingle, 1965; Provenza, 1958), the phyllostomatids apparently lack a distinct subodontoblastic plexus and zone of Weil. Such a plexus and cell-free zone are thought to reflect the nutritive requirements of the odontoblastic cells. Possibly,
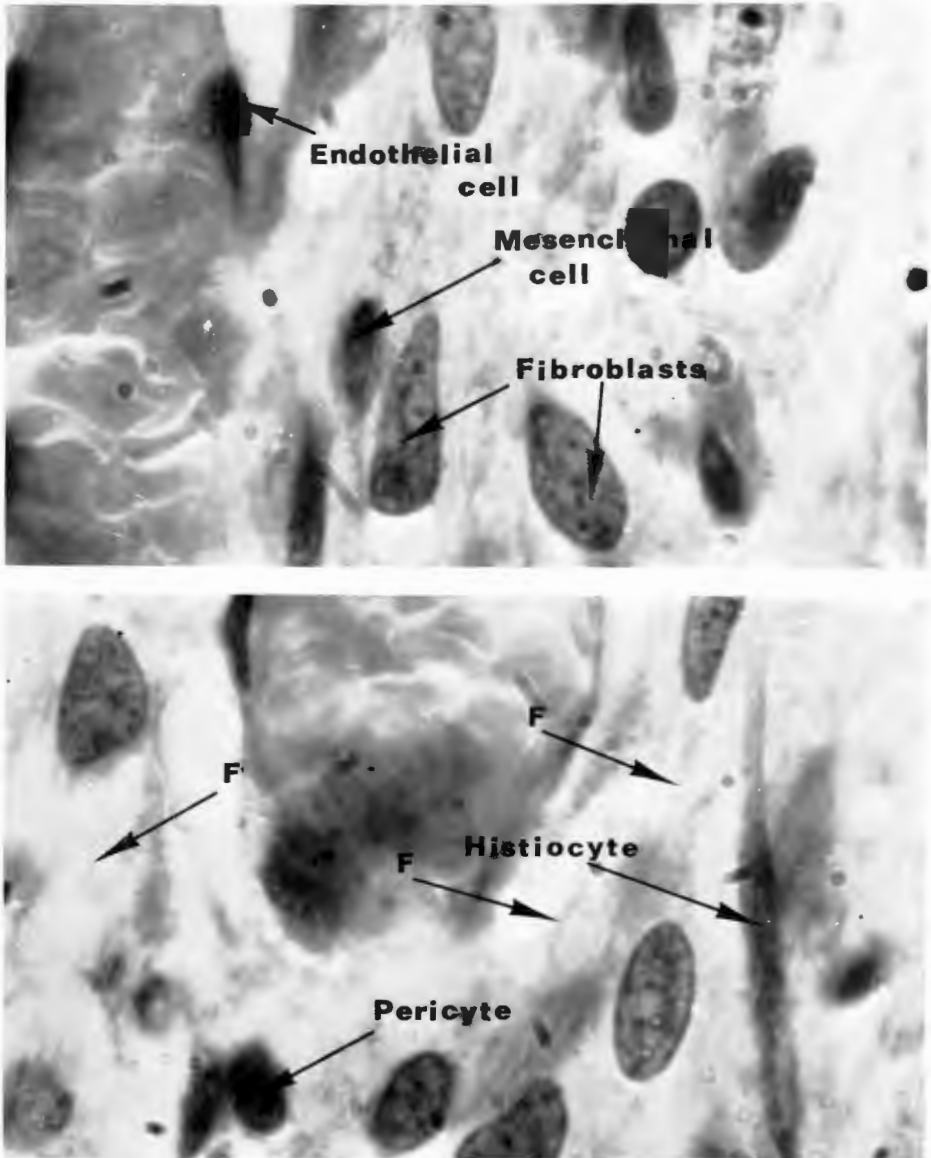
FIG. 19.—Histological examples of typical components of healthy pulp in a molar from an adult *Sturnira ludovici*; small collagenous fibrils are labeled with an *F*. Hematoxylin and eosin-Y. Both are 3300×.

the extremely small size of the pulp chamber in these bats negates the importance of a subodontoblastic plexus. On the other hand, a distinct zone of Weil is found in the pulp of the molossid genus *Tadarida*, which also has an extremely small pulpal chamber (Phillips, unpublished data).

Two circulatory abnormalities frequently are noted in the phyllostomatids. Many specimens contain a high percentage of dental pulpal blood vessels that

are either totally or partially occluded by a thrombus or hyaline material (Fig. 18). Extensive hyperemia (dilation of capillaries) is commonly found in specimens of *Phyllostomus*, *Sturnira*, and *Leptonycteris*. This condition has been shown to be either transitory or an indication of early pulpitis (Ogilvie and Ingle, 1965). Which is the case in a given specimen is not always clear.

The sensory aspect of the dental pulp in phyllostomids is as yet unstudied. The pulp undoubtedly is richly innervated and it is likely that, as in man, sensory nerve endings extend peripherally into the layer of odontoblastic cells and, possibly, into the predentin (Ogilvie and Ingle, 1965; Sicher and Bhaskar, 1972).

Periodontium

The periodontal membrane consists of connective tissue fiber bundles that connect teeth to surrounding alveolar bone. Connective tissue cells, blood and lymphatic vessels, nerves, and a variety of intercellular substances form the principle constituents of this membrane. In previously studied mammals, collagen, oxytalan and elastic fibers, and acid mucopolysaccharides have been found extracellularly (Fullmer, 1967). Embryologically, the periodontal ligaments are derived from the dental sac that envelops the developing tooth. The fibrous connective tissue of the sac differentiates into three layers; the outer is adjacent to alveolar bone, the inner lies adjacent to the cementum, and the intermediate layer of unorganized fibers becomes rearranged and thickened to periodontal ligaments (Orban, 1927; Glickman, 1972). Groups of collagenous fibers that form the principal fiber bundles can be grouped according to orientation (Sicher and Bhaskar, 1972). Gingival ligaments attach the gingivum to cementum; trans-septal (interdental) ligaments are found between adjacent teeth; and a group of alveolodental ligaments connect cementum directly to alveolar bone. Principle fiber bundles representative of each of these categories, have been demonstrated in all species of phyllostomatids thus far studied. It is apparent, however, that among the alveolodental group, the oblique fiber bundles are least common. Instead, the principle fiber bundles frequently can be traced from within alveolar bone (Sharpey's fibers) to their point of attachment in cementum (Figs. 15, 20). Additionally, scanning electron microscopy reveals at moderate magnifications (4000 ×) that many of the principle fiber bundles are interconnected by a network of fine connective tissue fibers (Fig. 21). The exact structural constituents of the fine interlacing fibers of the phyllostomatid periodontium are unknown, and cannot be determined by scanning electron microscopy alone because the SEM does not reveal the typical periodicity of collagen. Comparison of the SEM micrographs of *Leptonycteris* to those of other mammals (for example, man, dogs, and armadillos) suggests that these interlacing fibers represent the indifferent fiber plexus described by Shackleford (1971), who suggested that the density of the indifferent fiber plexus is directly related to amount of stress placed on the coronal surfaces. In the specimen of *Leptonycteris* illustrated in Fig. 20, staining of the histological material with silver impregnation indicates that at least some of the fine interconnecting fibers might be reticular. Two types of reticulin (precollagenous and basement membrane) usually are present in the periodontium (Fullmer, 1967). Both are found in phyllostomatid bats. The pre-
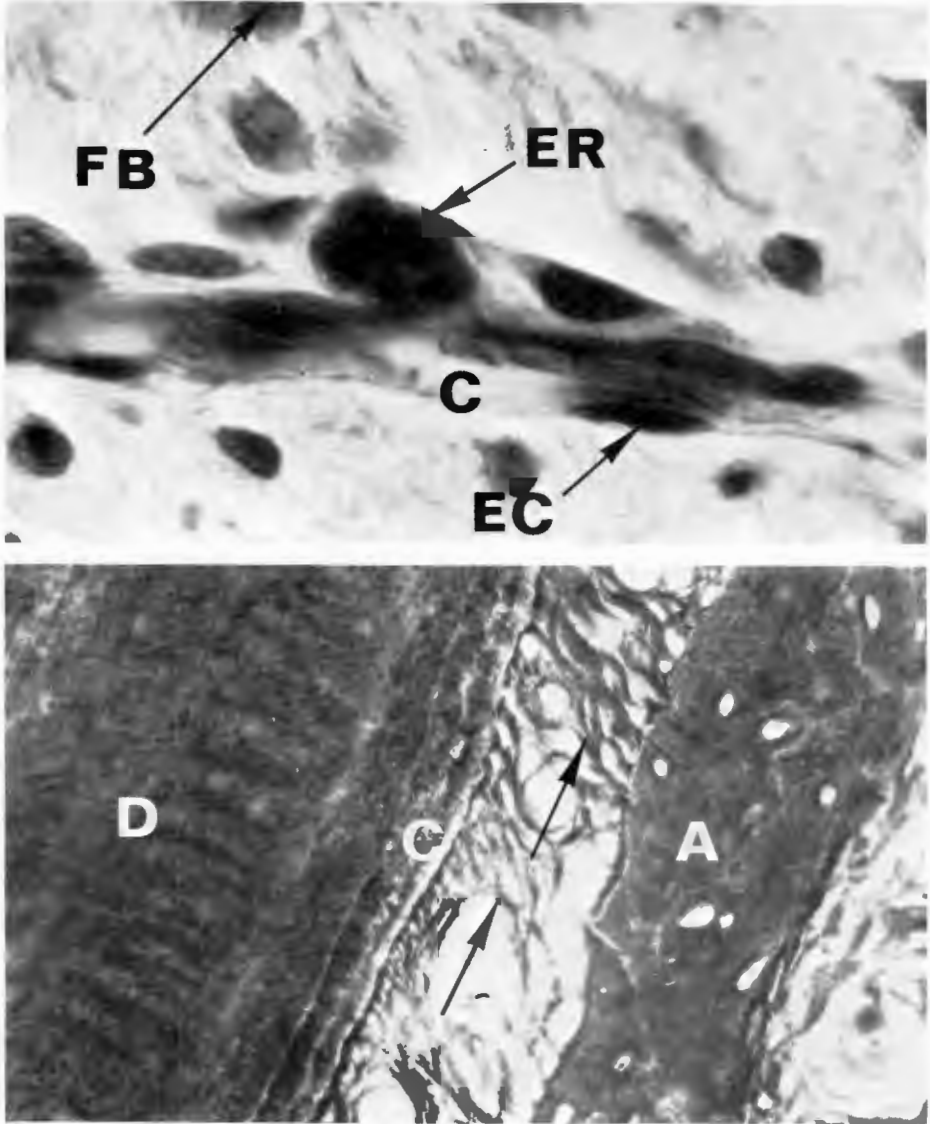
FIG. 20.—*Top*: Histological view of components of the periodontium (in *Artibeus jamaicensis*). Abbreviations are: EC, endothelial cells; ER, epithelial rest; FB, fibroblast. Hematoxylin and eosin-Y. 1284×. *Bottom*: Silver impregnation staining of collagenous principle fiber bundles (arrows) in *Leptonycteris nivalis*. Abbreviations are: A, alveolar bone; C, cement; D, dentin. 375×.

collagenous (or argyrophil) reticular fibers become black with silver impregnation (Fullmer, 1967; Lillie, 1965). Consequently, they can be distinguished fairly easily from the collagenous principle fiber bundles, which are larger and stain pale red-brown or violet. Few species of phyllostomatids have been studied with silver impregnation, and, thus, no specific comparisons of numbers and distribution of periodontal reticular fibers can yet be made.
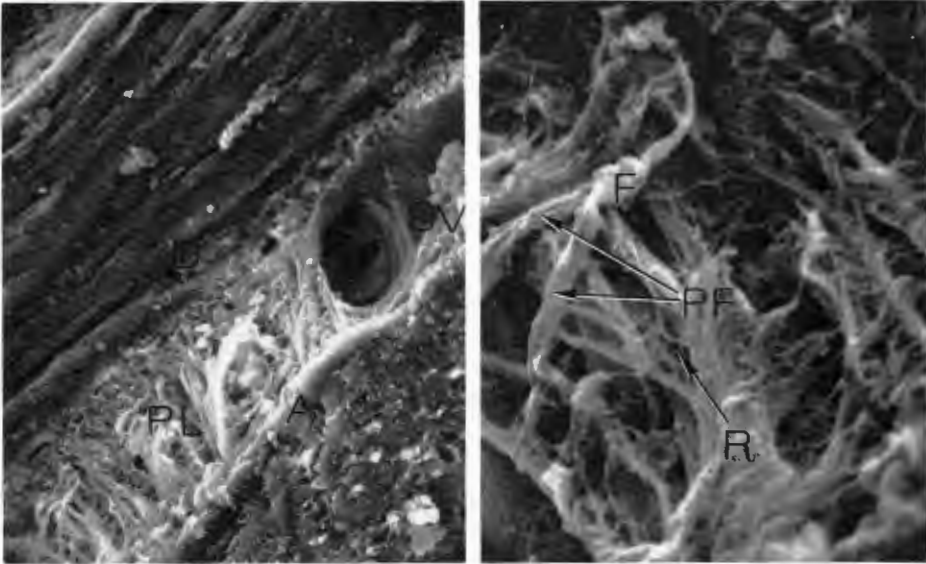
FIG. 21.—*Left*: Scanning electron micrograph of typical periodontium in a specimen of *Leptonycteris nivalis*. Abbreviations are: A, alveolar bone; BV, blood vessel; D, dentin; PL, periodontal ligaments. 700×. *Right*: Detail of periodontium showing fibroblasts (F), collagenous principle fiber bundles (PF), and "reticular" fibrils of the indifferent fiber plexus (R). 2800×.

Overall, the principal fiber bundles of representatives of the genera *Artibeus, Phyllostomus, Sturnira, Desmodus, Leptonycteris, Anoura,* and *Choeronycteris* are essentially the same in basic histological features, staining reaction, density, and distribution. Observed individual differences generally were relatable to unusual or pathological conditions.

Fullmer and Lillie (1958) and Fullmer (1967 and elsewhere) have found and studied in detail a type of connective tissue fiber that they termed oxytalan fiber. Although these fibers, which apparently are related to elastic fibers and possibly are their precursors, are common in the periodontium of several unrelated species of mammals, they have not been found in the periodontium of phyllostomatid bats. Staining with aldehyde fuchsin following oxidation with peracetic acid has revealed a relatively small number of oxytalan fibers in the submucosa of the oral epithelium in phyllostomatids. Absence of oxytalan fibers in the periodontium of those species in which the teeth are under considerable stress (for example, *Desmodus*; Phillips and Steinberg, 1976) is of interest in view of the fact that these fibers reportedly are abundant in high stress regions in other mammals (Fullmer, 1967). In low stress situations such as developing teeth or adult teeth in such species as the armadillo, the oxytalan fibers, if present, tend to be nonaligned (Shackleford, 1971).

The cellular components of the periodontium of phyllostomatids are essentially the same as in other mammals. Long, slender, fixed fibroblasts comprise the majority cell type directly associated with periodontal ligaments in phyllostomatids having normal (healthy) periodontium. These cells have large,

ovoid nuclei (Figs. 15, 20) and appear, in histological preparations, to be interspersed with principle fiber bundles. The cytoplasm, which is eosinophilic and sparse in comparison to the nucleus, is difficult or impossible to distinguish with standard stains such as hematoxylin and eosin. When studied by scanning electron microscopy, the stellate shape of fixed fibroblasts can be readily distinguished (Fig. 21). Usually these cells are associated with principle fiber bundles; elongate cytoplasmic processes and formative bundles of collagen (reticular fibers) are visible at $4000 \times$. Cells resembling fibroblasts but having smaller, more elongate nuclei frequently can be found in association with blood vessels, particularly capillaries, in the periodontium of adult (fully grown) phyllostomatids. These cells apparently are undifferentiated mesenchymal cells that persist into a bat's adulthood. If they are in fact mesenchymal cells, it is likely that they are important in response to local inflammatory or pathological conditions (Bloom and Fawcett, 1968).

The periodontal ligament is known to serve as the periosteum for alveolar bone (Fullmer, 1967). It is not surprising, therefore, that osteoblasts and osteoclasts are found in the periodontium adjacent to alveolar bone in phyllostomatid bats. The presence of these cells is related either to apposition of new bone or resorption of old bone and, thus, their occurrence frequently reflects degree and directionality of stresses on teeth. The general phenomenon of alveolar responses to stresses has been studied intensively in other mammals, particularly with regard to human dental medicine (for example, see Fullmer, 1967; Sicher and Bhaskar, 1972). Variations in activities of cellular enzymes (certain dehydrogenases and nonspecific esterases) have been related to the process of bone remolding (Glickman, 1972). Marked alveolar resorption is common, for example, adjacent to teeth that have become nonfunctional due to acute dental caries in *Phyllostomus hastatus* (Phillips and Jones, 1970). Atrophy of periodontal ligaments also results from loss of function and is common in this species, which exhibits an unusually high incidence of dental caries in nature. Resorption of alveolar bone in conjunction with periodontal inflammation caused by infestations of oral mites also is common in three glossophagine genera (*Leptonycteris, Anoura, Monophyllus*); in these species, large numbers of multinucleate osteoclasts are found adjacent to alveolar bone (Phillips *et al.*, 1969; Phillips, 1971).

Among the phyllostomatids thus far studied, alveolar bone remolding (Fig. 16) typically is most extensive in the common vampire bat, *Desmodus rotundus* (Phillips and Steinberg, 1976). In this instance the teeth undergo considerable coronal stresses as a result of thegosis (tooth sharpening) and, therefore, drift and continuing eruptive movements into the occlusal plane have considerable effect on alveolar bone.

Cementoblasts are yet another type of cell commonly found in the periodontium of phyllostomatid bats (Figs. 15, 16). They typically are found along the surfaces of roots and are characterized by spherical or slightly ovoid nuclei. As visible in Fig. 15, they are notably smaller than fibroblasts and are easily distinguished. Cementogenesis, especially at root apices, apparently continues throughout the life of individual bats. Resorption and deposition of cement

is influenced by essentially the same factors that influence remolding of bone (Glickman, 1972). For example, marked deposition by cementoblasts was found to be a usual response to extreme coronal stress in *Phyllostomus hastatus* (Phillips and Jones, 1970) and *Desmodus rotundus* (Phillips and Steinberg, 1976).

Alveolar Process

The portions of the mandible and maxilla that support the sockets into which teeth are set are termed the alveolar process. In man and other primates for which data are available, the process can be divided into two components: alveolar bone, which surrounds the roots and provides a site for attachment of the periodontal ligaments; and supporting alveolar bone, which consists of both cortical plates (compact bone) and spongy bone (see Sicher and Bhaskar, 1972). In phyllostomatid bats, the alveolar process differs somewhat from this model in that spongy bone is minimized, and the typical interdental and interradicular septa are characterized by extensive amounts of compact bone (Figs. 10, 16). The only exception among the species that have been studied histologically seems to be the large spear-nosed bat (*Phyllostomus hastatus*). In this species, one can find moderately extensive spongy bone, but, even so, the specimen of *Sturnira* illustrated in Fig. 10 is a better example of the typical alveolar process in phyllostomatids.

Oral Epithelium and Gingivum

The oral mucous membrane is a structurally variable lining of this cavity in mammals. The morphological characteristics of the membrane are thought to reflect specific functions or mechanical influences related to position within the oral cavity as well as to feeding habits (Sicher and Bhaskar, 1972). The oral epithelium of phyllostomatid bats has not been studied previously in detail.

Structurally, the oral mucous membrane can be divided into three components: an outer layer of stratified squamous epithelium; an intermediate lamina propria; and a variable submucosa layer comprised of connective tissue. In all species of bats studied for this report, the squamous epithelium was found to consist of a basal cell layer, an intermediate cell layer, and either an orthokeratinous (totally keratinous), parakeratinous, or nonkeratinized outer surface (Figs. 22, 23). The gingivum, which is the portion of the oral mucous membrane that surrounds the teeth and, thus, usually is subjected to a variety of mechanical forces, and the prominent palatal ridges were found to be either orthokeratotic or parakerototic. Orthokeratotic tissue typically is comprised of scalelike cells apparently lacking nuclei (Fig. 23), whereas the parakeratotic layer is characterized by the presence of flattened, heterochromatic (hematoxylin and eosin) nuclei within the epithelial cells (Fig. 22). In the phyllostomatids, the gingivum is most commonly parakeratotic, whereas the palatal ridges are about 50 per cent parakeratotic and otherwise orthokeratotic. As might be predicted, the degree of keratinization of the hard palate in these bats can be related directly to food habits. Consequently, the hard palate of *Artibeus jamaicensis*, which feeds on fruits that sometimes have
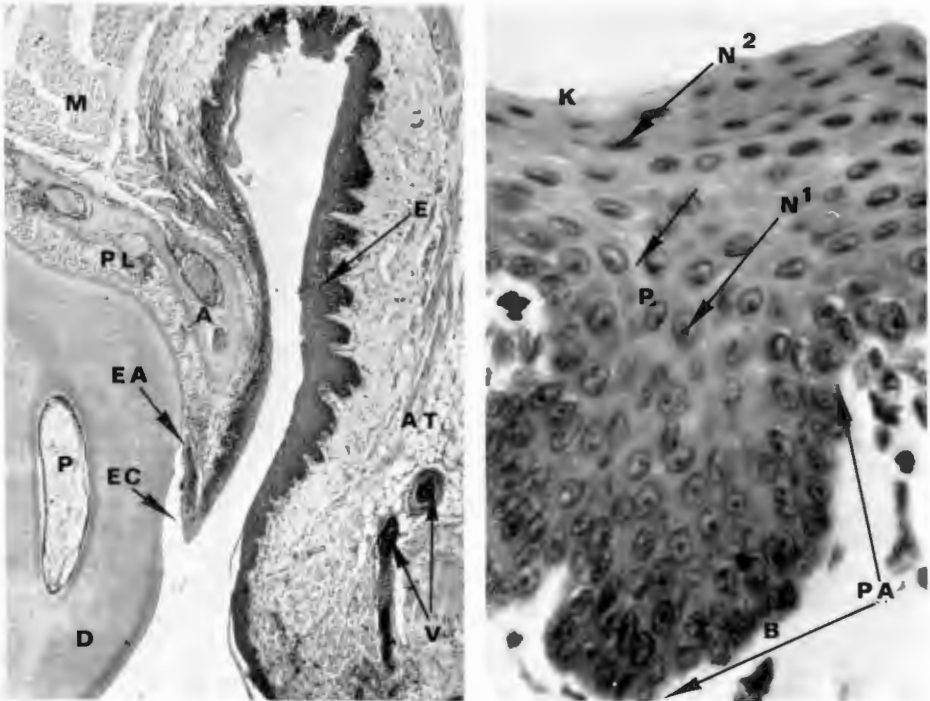
FIG. 22.—*Left*: Histological overview of gingivum and oral epithelium of the lip in a specimen of *Anoura geoffroyi.* Abbreviations are: A, alveolar bone; AT, adipose tissue; D, dentin; EA, epithelial attachment; EC, epithelial cuff; E, epithelium; M, muscle; P, pulp; PL, periodontal ligaments; V, bases and shafts of vibrissae. Hematoxylin and eosin-Y. 63×. *Right*: Gingivum in *Leptonycteris nivalis.* Abbreviations are: B, basal cells; K, keratinized surface; P, prickle cells; PA, papilla; N_1, euchromatic nuclei of prickle cell; N_2, heterochromatic nuclei of perakeratotic layer; arrow, space between prickle cells. Hematoxylin and eosin-Y. 876×.

hard rinds, is considerably more keratinized than is the hard palate of *Leptonycteris,* which feeds almost exclusively on pollen and nectar. It seems possible that keratinization is a local response to mechanical stress, and, thus, the more mechanical force applied, the thicker and more keratinized the outer layer of epithelium.

The basal cell layer of the mucous membrane, which is separated from the lamina propria by a distinct PAS-positive basement membrane, is structurally variable within a given bat. Generally, the cells are cuboidal and the nuclei relatively euchromatic (Figs. 22, 23). On the other hand, in some areas (particularly the gingivum), the cells tend to be elongate with relatively little cytoplasm and heterochromatic nuclei. A prickle cell layer also is present, as it is in other mammals. In man, this layer of stratified epithelium is most distinguishable in areas of orthokeratotic or parakeratotic mucosa. When viewed with oil immersion microscopy, large numbers of intercellular "bridges" or tonofibrils are easily distinguishable in phyllostomatids (Fig. 24). In the specimen of a long-nosed bat (*Leptonycteris nivalis*) shown in Fig. 24, the tonofibrils connect the elongate cells
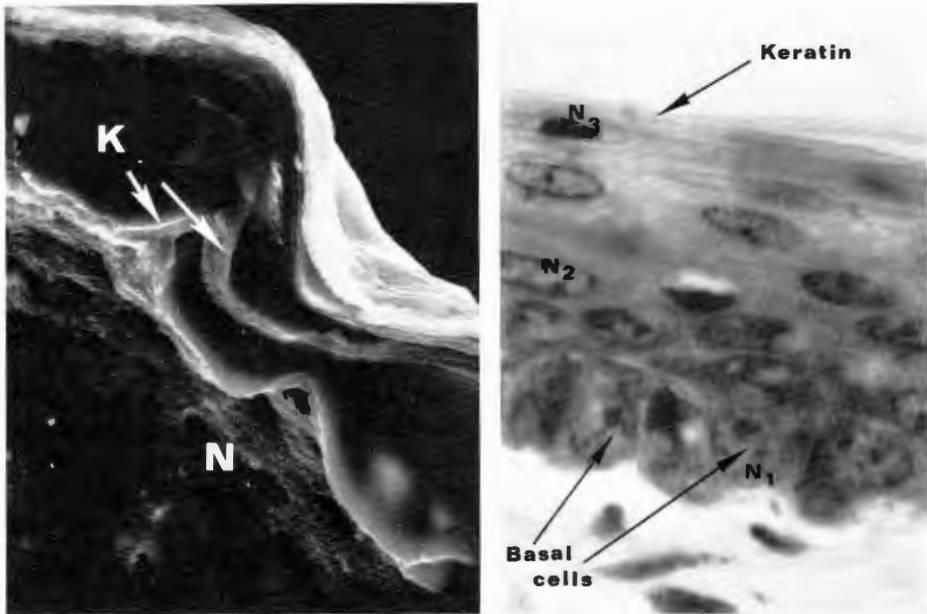
FIG. 23.—*Left:* Scanning electron micrograph of orthokeratotic layer (K) in *Leptonycteris nivalis.* Nuclei of prickle cells also can be distinguished in this view (N). 1850×. *Right:* Oral epithelium in *Sturnira ludovici* showing round, euchromatic nuclei of basal cells (N_1), elongate euchromatic nuclei of prickle cells (N_2), and a single heterochromatic nucleus (N_3) of a cell within the otherwise orthokeratotic outer layer. Hematoxylin and eosin-Y. 1628×.

across a distinct intercellular space, forming a network of interfacial canals. Although these cells in phyllostomatids have not yet been investigated by means of the transmission electron microscope, it is likely that the arrangement of tonofibrils and desmosomes is similar to that in other mammals (Bloom and Fawcett, 1968).

The orthokeratotic outer layer differs from the parakeratotic layer not only in presence or absence of nuclei, but also in staining characteristics. With the standard hematoxylin and eosin-Y, for example, the orthokeratotic layer is pale yellow or essentially not stained, whereas the cytoplasm of cells comprising the parakeratotic layer stains the characteristic pink. The scanning electron microscope provides a striking view of structural features of an orthokeratotic outer layer (Fig. 23). The extremely flat, scalelike condition of the cells can be seen readily; in this instance, which is representative of the masticatory mucosa of the hard palate of a specimen of *Leptonycteris nivalis*, at least seven distinct layers can be distinguished. Dark, ovoid areas below the orthokeratotic surface layer, represent the nuclei of prickle cells, apparently altered by critical point drying or some other aspect of the SEM technique (Fig. 23). Fullmer and Lillie (1958) discovered and studied oxytalan fibers in the periodontium of several species of mammals. In the course of the present study it was found that occasionally the outline of cells in parakeratotic layers of the oral epithelium of phyllostomatids
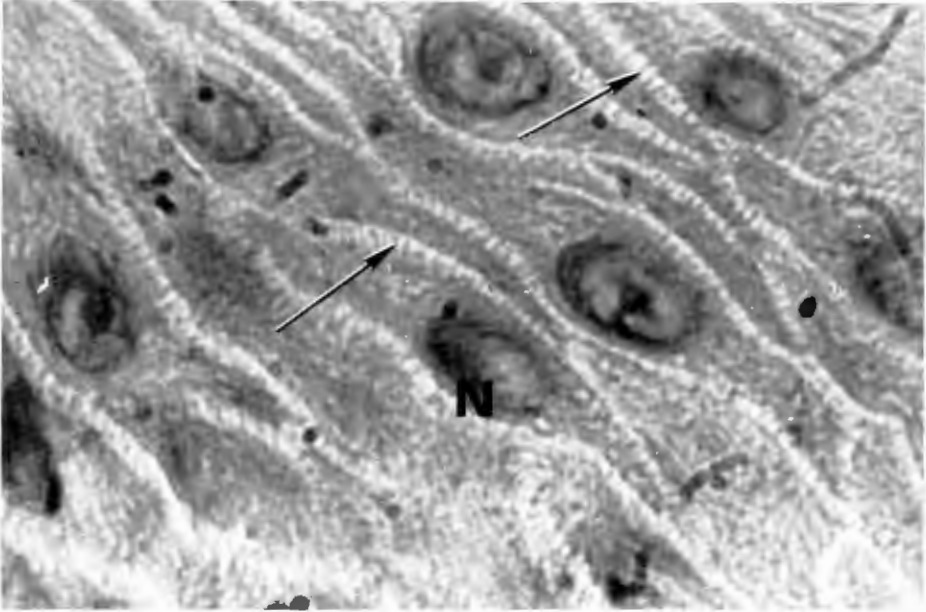
FIG. 24.—Histological view of the prickle cell layer in oral epithelium of *Leptonycteris nivalis*; these cells are characterized by ovoid euchromatic nuclei (N) and interconnecting tonofibrils (arrows). Hematoxylin and eosin-Y. 2500 ×.

would stain deep purple following the peracetic acid-aldehyde fuchsin procedure for oxytalan fibers. The reason for this reaction is unknown, although Fullmer (personal communication) also has noted such a reaction in other kinds of mammals. None of the other staining techniques employed in this study (see the section on materials and methods) produced similar results.

The epithelial attachement to teeth has received considerable attention from dental researchers (for example, see Sicher and Bhaskar, 1972; Löe, 1967; Glickman, 1972, for citations). The area of attachment has the form of a cuff in which debris and bacteria can accumulate and, thus, is a primary site for inflammation. In the phyllostomatids, the actual form of the epithelial attachment varies individually as well as interspecifically. Most commonly, the junction between enamel and cementum provides the site of attachment (Fig. 25). In some specimens the attachment is below this level, probably as a consequence of continuing eruption into the occlusal plane. In vampire bats (*Desmodus*), as shown in Fig. 25, the epithelial attachment differs dramatically because the permanent teeth lack enamel (Phillips and Steinberg, 1976). In *Desmodus*, the attachment always is directly to the cementoid layer.

Mast cells and numerous polymorphonuclear leukocytes, indicative of inflammation, generally are found within the area of the epithelial attachment to teeth (Fig. 25). It seems likely that low grade inflammation is a normal state of affairs in phyllostomatid bats.
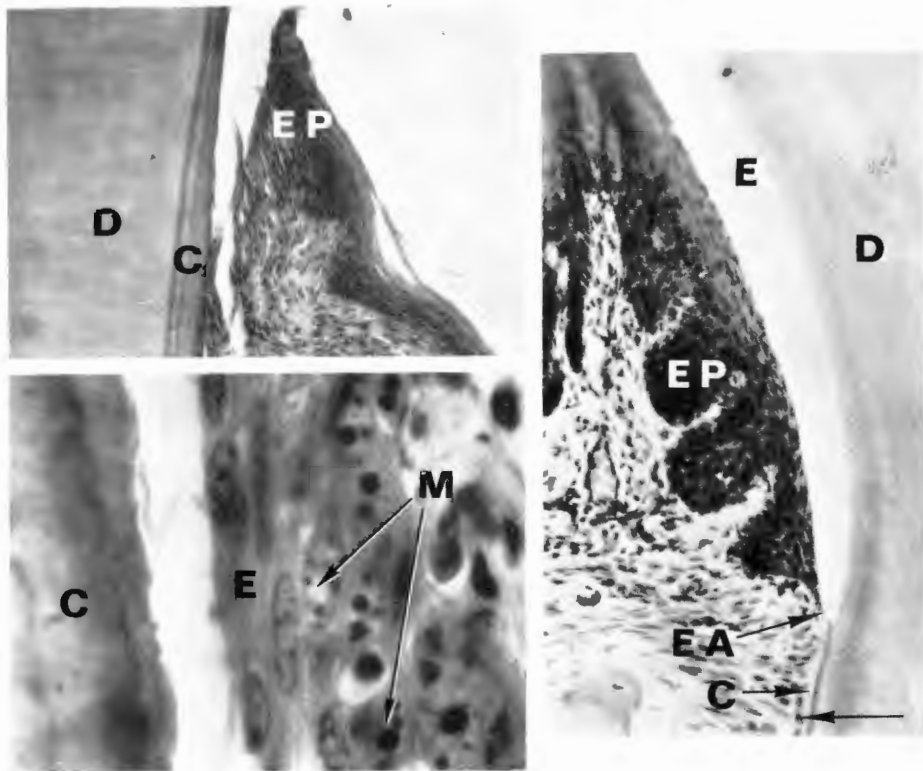
FIG. 25.—*Top left*: Epithelial attachment in *Desmodus rotundus*. Note the cementoid layer that extends up the coronal surface. Hematoxylin and eosin-Y. 148×. *Lower left*: High magnification (light microscope) view of granular mast cells in the gingivum of *Desmodus rotundus*. Hematoxylin, eosin-Y, and PAS. 2072×. *Right*: The epithelial attachment in *Glossophaga soricina*, which is more typical of phyllostomatids because of the lack of coronal cementum. Hematoxylin and eosin-Y. 370×. Abbreviations for all illustrations are: C, cementum; D, dentin; EA, epithelial attachment; ES, enamel space; E, epithelial cells; EP, epithelium; M, mast cells; arrow, cementoblasts.

PATHOLOGY

Oral and dental disease in wild mammals has not been studied to the extent warranted by the potential value of such data to our understanding of systematic and evolutionary biology. Among the several papers dealing with oral and dental diseases in wild species, the volume by Colyer (1936), although somewhat outdated, is by far the most complete. Publications by Hall (1940, 1945) also are valuable even though limited to relatively few species. Insofar as the Chiroptera are concerned, the only available information (aside from incidental comments) is that published by Phillips and Jones (1969, 1970), Phillips *et al.* (1969), and Phillips (1971). The first of these papers deals with nonphyllostomatid bats, the second with *Phyllostomus hastatus* and the last two with glossophagines only. Consequently, the following overview reflects this disparity and is based pri-

marily on Phillips (1971), although a considerable amount of previously un-published histological data on periodontal disease has been included here.

Dental Caries

Dental caries involves many etiological factors, including bacteria, substrate characteristics (diet), and surface and structural aspects of teeth (Keyes and Jordan, 1963). Although this disease has been reported from representatives of many mammalian orders (Colyer, 1936), it appears to have a differential incidence in nature. Among the Chiroptera, dental caries possibly is uncommon, although gross identification of carious lesions in teeth of museum specimens does not necessarily provide an accurate picture of what happens in nature. In 1508 specimens from the families Emballonuridae, Noctilionidae, and Mormoopidae, Phillips and Jones (1969) found only one individual (a specimen of *Mormoops megalophylla*) in which carious teeth could be recognized at the relatively low magnification (20 ×) used for the examination.

The spear-nosed bat, *Phyllostomus hastatus*, is clearly an exception because in this species dental caries is extremely common (Phillips and Jones, 1970). A 40 per cent incidence of caries was found in 52 specimens; additionally, an unexplained significant ($P \geqslant 0.99$) difference in incidence was found between males (75 per cent) and females (19 per cent). Specimens of *P. hastatus* were compared to a series of 103 specimens of *P. discolor*, in which gross carious lesions were lacking, in an effort to isolate some of the possible endogenous and exogenous factors involved. Certain specific differences between these species could be correlated in a general way with the surprisingly high incidence of caries in *P. hastatus*. For example, in this species the large and robust teeth frequently exhibited stained fissures within which lesions usually were located. Additionally, the structure of the oral mucous membrane and gingivum at the posterior end of the toothrow was such that debris tended to accumulate there.

The significance of a high incidence of dental caries in *P. hastatus* is as yet unclear but two possible interpretations have been offered (Phillips and Jones, 1970): 1) one or more genetic factors that result in a high incidence of dental caries are associated with some characteristics, for example large size, that are of significant survival value; 2) some exogenous factors, such as an evolutionarily recent shift in food habits, are of considerable cariogenic importance, and selection has not yet produced a phenotype capable of ameliorating these environmentally produced conditions, or that the adaptive value of exploitation of a new food source is of far greater benefit to the species than is prevention of dental caries. The study of positive allometry between body size and width of teeth discussed in the section on evolutionary mechanisms (Pilbeam and Gould, 1974) can be applied to this particular problem. Selection for large size clearly has occurred in the evolution of *P. hastatus*. The large and robust teeth in this species probably are the result of positive allometry. An essentially "automatic" increase in tooth size in absence of modification of morphogenetic patterns, changes in mineralization, or even modifications of rate of development could well account for the absence of an effective system for modulating incidence of dental caries.

Carious lesions also have been reported in teeth of several species of glossophagine bats (Fig. 26) but are regarded as rare in incidence (Phillips, 1971). It is especially important to remember, however, that the teeth in these bats are so small that recognition of dental caries is limited to relatively severe lesions. Survey of specimens of glossophagines by means of the SEM would lead us to be extremely cautious about determination of rarity of this form of pathology. For example, carious lesions were not found in examination of several hundred specimens of *Leptonycteris nivalis* and *L. sanborni* by means of a dissecting microscope (Phillips, 1971), but in three specimens of *L. nivalis* examined with the SEM, carious lesions were readily visible in molars of each individual. The lesions always were within basins and were characterized by loss of enamel and exposure of a surface of primary dentin (Fig. 27). Examination at $1500 \times$ revealed a general absence of dentinal tubules although in at least one lesion a group of tubules could in fact be seen. The overall appearance of the dentin exposed in these lesions was remarkably similar to that exposed by either of the components of bimodal attrition. A wide variety of materials, some of which could not be identified with certainty, were found within carious lesions. Small spherical objects, measuring approximately one micrometer, were found in large numbers within the carious lesions. These had the size and appearance of coccus type micro organisms (Fig. 27). Two configurations are shown in Fig. 27; several fairly large clusters are clearly visible as well as several pairs of organisms. The presence of coccus type bacteria at sites of carious activity is not surprising. Several kinds of acidophilic microorganisms, including lactobacilli and streptococci have been shown to have cariogenic potential (Orland *et al.*, 1955; Fitzgerald and Keyes, 1960; Keyes and Jordan, 1963) in primates and rodents. Nothing is known about the microflora of the oral cavity of glossophagine bats and, therefore, identification of the microorganisms must await an opportunity for preparation of cultures.

The paucity of exposed dentinal tubules in the carious lesions probably reflects the fact that calcium salts are deposited around exposed, degenerating odontoblastic processes resulting in obliteration of the tubules (Sicher and Bhaskar, 1972). Obliteration of tubules is of clear-cut functional significance; the tubules not only can become packed with microorganisms (Johansen, 1963) but, more importantly, they communicate directly with the dental pulp.

Periodontal Disease

Periodontal disease involves inflammation of the gingivum and periodontal membrane and often leads to destruction of alveolar bone and dental tissue. This form of pathology probably is the major cause of loss of teeth in mammals (Colyer, 1936; Fullmer, 1966; Glickman, 1972). A wide variety of etiological factors have been associated with periodontal disease: these include microorganisms, calculus, oral hygiene, vitamin insufficiencies, irregular teeth, and salivary gland secretions (Fullmer, 1966; Klinkhamer, 1968). Protein deprivation and certain enzymes (kallikrein, for example) also apparently play roles as etiological factors or mediators of periodontal disease but are as yet only poorly known (Sweeny, 1966; Narrod and Braunberg, 1966; Fullmer, 1966).
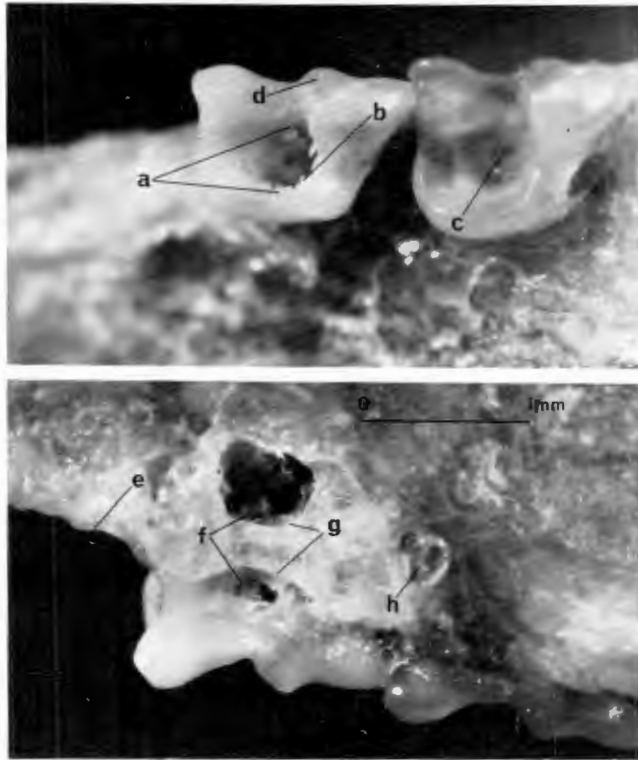
FIG. 26.—Occlusal and labial views of dental caries in a glossophagine bat (*Anoura geoffroyi*) Symbols are: a, carious lesion; b, exposed carious dentin; c, normal (noncarious) molar; d, wear facet; e, edentulous maxillary; f, exposed, partially resorbed root; g, h, areas of bone resorption. From Phillips (1971).

Among the phyllostomatids, only the glossophagines have been surveyed for periodontal disease (Phillips, 1971). Aside from a common localized rarefying osteitis, typical periodontal pathology is relatively rare in these bats, at least insofar as can be determined by examination of cleaned skulls in museum collections (Phillips, 1971).

An unusual periodontal disease, thus far known only in glossophagine bats, has been reported and studied previously in some detail (Phillips *et al.*, 1969; Phillips, 1971; Radovsky *et al.*, 1971). In this disease, the major etiological factor is the presence of protonymphs of mites of the genus *Radfordiella* (Macronyssidae), which become embedded in lesions in the oral mucosa and gingivum (Figs. 28, 29). The resultant pathological condition, which includes destruction of soft and hard oral tissues, frequently leads to exfoliation of teeth in life. The mites are highly host specific and consequently the presence or absence of pathology can actually be used as an unusual taxonomic character in separating *Leptonycteris nivalis* from *L. sanborni*. In *Monophyllus*, which is endemic to the Antilles, oral mites are found in *M. redmani* but have not been reported from *M. plethodon*. In contrast to *Leptonycteris nivalis*, however, the incidence of in-
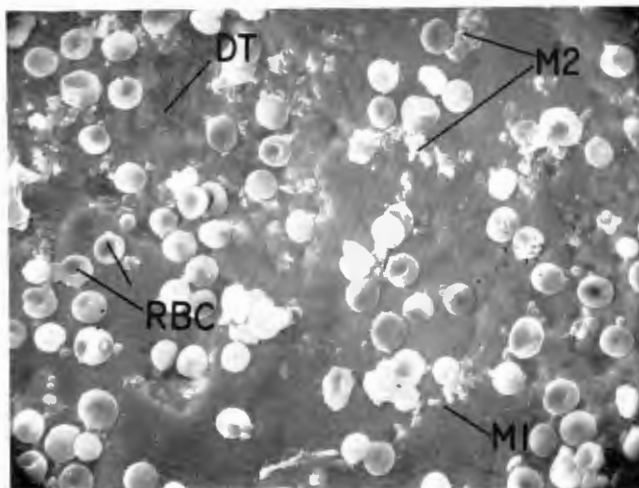
FIG. 27.—Scanning electron micrograph of a carious lesion in a molar from a Mexican long-nosed bat, *Leptonycteris nivalis*. Abbreviations are: RBC, red blood cells; DT, dentinal tubules; M1, paired microorganisms; M2, clusters of microorganisms. 1140×.

festation in *M. redmani* apparently is geographically variable (Phillips, 1971). *Anoura* is the third genus in which *Radfordiella* infests the oral cavity; once again the mites (both *Radfordiella oricola* and *R. anourae*) are found only in one species (*A. geoffroyi*) but seem to have geographically variable incidence (Phillips, 1971).

The reasons for species-specific and geographically variable incidences of infestation are as yet unclear. The long-tongued bats of the genus *Leptonycteris* have been examined most closely in this regard. As of this writing, no ecological factors or distributional characteristics provide good candidates for explanation of why only *L. nivalis* is infested. The two species are partially sympatric and apparently have similar feeding habits (see chapter by Gardner, this volume). Many mammalogists have had difficulty distinguishing between the species, as is reflected by confusing and inadequate taxonomic arrangements suggested over the past 30 years (Martinez and Villa-R., 1940; Hoffmeister, 1957; Villa-R., 1967; Alvarez, 1966). In point of fact, however, the three currently recognized species not only are distinctly different in several phenotypic characters, but also are relatively easy to identify (Davis and Carter, 1962; Phillips, 1971). Superficial similarities between *L. nivalis* and *L. sanborni* belie some apparently noteworthy differences in their oral anatomy and, indeed, their oral environments. For example, light-level microscopic comparisons of their salivary glands has revealed structural differences, particularly in the parotid gland (see section on salivary glands). These differences are far from minor and carry through to the ultrastructural level (B. Wilder, personal communication). It is reasonable to assume, of course, that differences in subcellular structure and in structural characteristics of secretory granules suggests in turn that the oral cavities in these two species are bathed by a considerably different saliva. The role of saliva in miti-
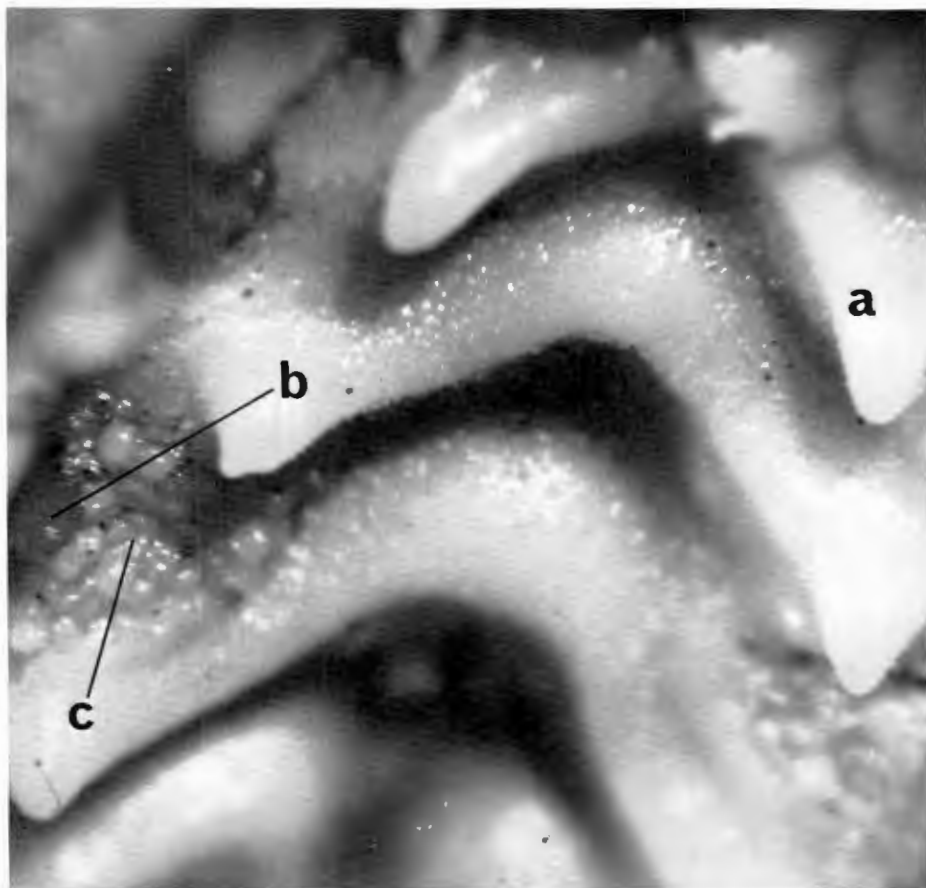
FIG. 28.—*Radfordiella oricola* in the mouth of a Mexican long-nosed bat, *Leptonycteris nivalis.* Symbols are: a, palatal ridge; b, upper premolar; c, mites. From Phillips (1971).

gating disease and controlling both inflammation and microflora is well established and currently attracting considerable attention from dental researchers (For instance, see Klinkhamer, 1968). Most striking, perhaps, was the finding of Greenbaum and Phillips (1974) that the tongue of *L. sanborni*, which species lacks oral mites, is characterized by highly keratinized, recurved hooks positioned so as to scrape the lingual gingivum and adjacent oral mucosa (see section on tongues and associated musculature). Anatomical and environmental differences such as these do not explain apparent geographic differences in incidence of infestation within species, even though they certainly provide a basis for explaining species specificity of the oral mites.

Tissue responses to infestations of oral mites are of special interest because of a general paucity of data on effect of parasites (Lavoipierre *et al.*, 1967; Lavoipierre and Rajamanickam, 1968) and the potential, in this instance, for studying specific responses of periodontal and hard dental tissue. The results of initial

FIG. 29.—Scanning electron micrograph of *Radfordiella oricola* in the mouth of a Mexican long-nosed bat, *Leptonycteris nivalis*. Abbreviations are: B, red blood cells; C, connective tissue: F, foreign (plant) material; L, lymphocytes; G, gnathostome of mite. 533×.

studies of periodontal pathology associated with infestations of *Radfordiella oricola* in *Leptonycteris nivalis* have been published (Phillips *et al.*, 1969; Phillips, 1971). In the following paragraphs we have reviewed these findings and have included new, unpublished information based on both general histological analysis and studies with the scanning electron microscope.

Macronyssid oral mites most frequently enter the oral mucosa adjacent to the first and second upper premolars. Occasionally, especially in cases of severe infestation, the protonymphs also are found adjacent to other upper teeth or even along the midline of the palate. The resultant lesions (Figs. 28, 29) can contain up to at least 200 individual mites. Oral epithelium around the lesions is characterized by destruction of the orthokeratotic outer layer as well as the granular, prickle-cell, and basal layers. At the same time, however, the size of the lesions apparently is in some way limited and does not continue to increase even in unusually severe infestations. It is possible, of course, that size of lesions is limited by the mites themselves in response to some density-dependent factor(s). Average palatal and alveolar lesions are approximately 1.0 millimeters in length and width and 0.5 in depth. The edges of lesions grossly appear rounded; histologically it can be demonstrated that oral epithelium grows inward and, thus, provides a partial lining for the walls of the lesion. Oral submucosa or periodontal membrane (depending on the position of the lesion) or both are exposed in the bottom of the lesion. The mites do not burrow into the connective tissue; instead they become packed into the lesion with their gnathosomes and first pair of legs penetrating the mass of connective tissue remanents and free cells at the bottom of the lesion (Figs. 29, 30). These parasites appear to be highly mobile and it is likely that they transfer from one lesion to another within the oral cavity. Indeed, when the mouth of a living specimen of *Leptonycteris nivalis* is forced open, it is possible to observe the mites as they move about with considerable agility.

Histologically, the lesions typically are packed with large numbers of lymphocytes and necrotic cells (Figs. 29, 30). Relatively few plasma cells occur within or adjacent to these lesions. Staining with azure-A and eosin-B also has revealed coccus-type bacteria within adjacent oral epithelium and within the epithelial cuff of teeth adjacent to lesions. Additionally, microscopic plant materials (possibly spines from agave flowers) become embedded in the connective tissue at the base of most lesions (Figs. 28, 31). These materials have offered an excellent opportunity to study multinucleate foreign-body giant cells within the lesions. These large masses of cells have been studied with general histology and the SEM (Fig. 31). With azure-A and eosin-B, the cytoplasm around foreign plant material stains bright pink, whereas the basal cytoplasm is somewhat basophilic. Careful comparison of histological preparations with critical-point-dried SEM materials from only a few micrometers (~ 10) away, has enabled identification of this cytoplasmic difference with the latter instrument (Fig. 31). By comparison of SEM photographs with adjacent histological materials, it is possible to determine the three-dimensional appearance of these cells. It is interesting that at the apical surface (adjacent to foreign material) the cell membrane conforms to the shape of the plant material and that the surface appears smooth and unbroken (at 5000 to 10,000 ×).

It also is noteworthy that foreign-body giant cells can be found in association with sites of alveolar and palatal bone resorption (Fig. 30) in a way similar to that reported by Irving and Handelman (1963). Resorption of palatal and alveolar bone might also result from localized circulatory disturbances. Increase in amount
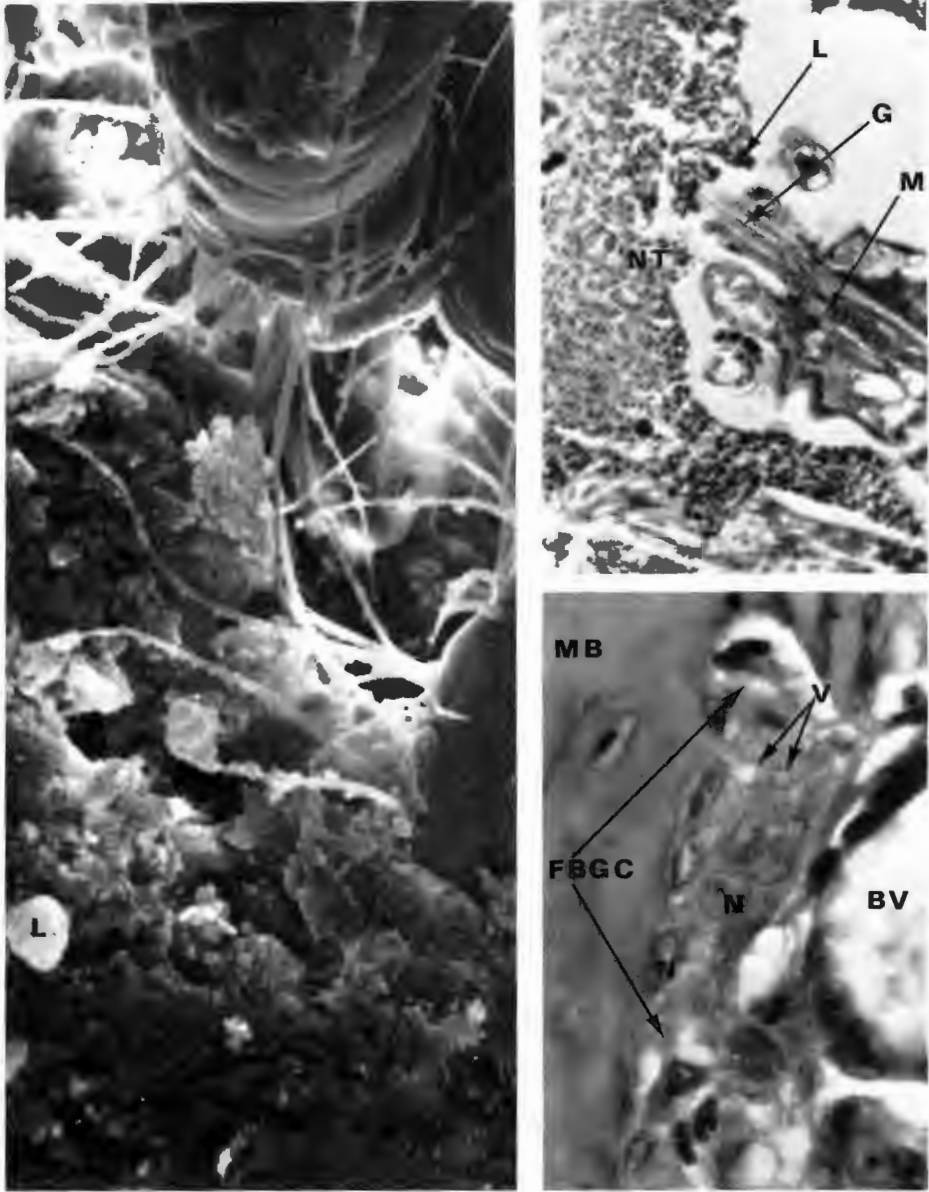
Fig. 30.—*Left*: Scanning electron micrograph of necrotic cell remnants, lymphocytes (L), and legs (LG) of a mite within an oral lesion. 1034×. *Upper right*: histological view of a typical lesion. Abbreviations are: G, gnathostome; L, lymphocytes; M, body of mite; NT, necrotic tissue. Hematoxylin and eosin-Y. 167×. *Lower right*: A multinucleated foreign-body giant cell (FBGC) adjacent to an area of palatal bone resorption. Abbreviations are: BV, blood vessel; MB, maxillary (palate) bone; N, nuclei; V, cytoplasmic vesicles character-istic of these cells. Hematoxylin and eosin-Y. 1900×.
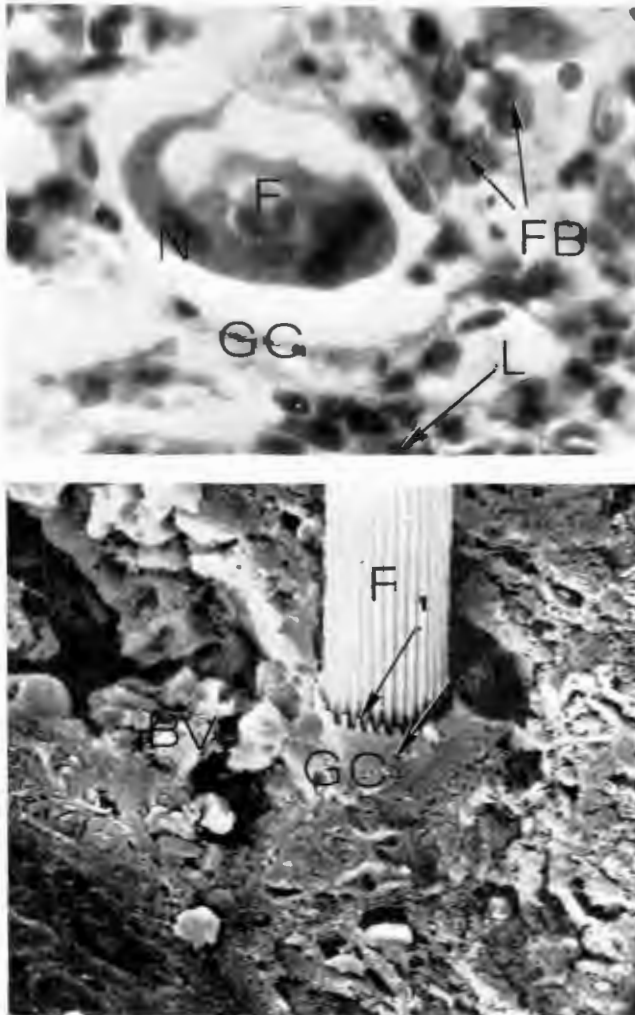
FIG. 31.—Comparative histological (top) and scanning electron microscope views (bottom) of foreign plant material (F) and a multinucleated foreign-body giant cell (GC). These two views represent sections through the same cell separated by approximately 10 micrometers. Abbreviations and symbols are: BV, blood vessel; FB, fibroblasts; L, lymphocytes; N, nucleus; arrow, apical cytoplasm of giant cell; arrow 1, conformation of apical cell surface to surface of plant material. Hematoxylin and eosin-Y; top, 1600×; bottom, 2000×.

of blood transported to the site of periodontal infection alters the level and quality of transudate supplied to bone, a condition that can lead to resorption (Reich-born-Kjennerud, 1963). In histological preparations, it can be seen that venules at sites of infestations are considerably dilated.

Response of the various types and stages of fibers (periodontal ligaments, reticular fibers, elastic and oxytalan fibers) also has been studied with both general histological techniques and the SEM. Except for remanents, or relatively

short lengths, fibers essentially are lacking from within the inflammatory sites. Collagenous fibers and reticular fibers (distinguishable with silver impregnation, after Lillie, 1965) generally are found at the periphery of lesions but are not as dense as elsewhere (in healthy areas). Elastic fibers have not been demonstrated in either healthy or infected areas of oral submucosa in these bats. Oxytalan fibers, which have been studied extensively by Fullmer (1959, 1960a, 1960b, 1967) appear to be of special interest. First, it has not been possible to demonstrate these fibers in the periodontium of *Leptonycteris* or other species of bats (see section on dental microanatomy). At the same time, however, in materials stained with aldehyde fuchsin following oxidation with peracetic acid, a dense, dark purple layer of oxytalan fibers sometimes can be found around the border of an inflammatory lesion. A possible role of these fibers in various types of fibrous pathology has been studied previously by others (see Fullmer, 1960a). Their relationship to inflammatory responses in the oral submucosa in bats with oral mites is as yet uncertain.

Attrition and Erosion

Aside from dental caries and periodontal disease, there are at least three other causes of destruction of dental hard tissue (Sognnaes, 1963): abrasion; resorption from external causes; and erosion caused by both exogenous and endogenous chemical agents, mechanical factors, and idiopathic conditions. Abrasion is but one form of bimodal attrition (following Every and Kühne, 1971; MacIntyre, 1966) and generally can not be regarded as pathological although specimens of glossophagines sometimes are seen in which the degree of abrasion suggests abnormal occlusion. It has been pointed out that particular teeth and specific coronal surfaces are especially prone to abrasion in this subfamily (Phillips, 1971). For example, in *Leptonycteris*, the metaconid of the first lower molar commonly is worn more greatly than are elements of other teeth within an individual.

Resorption of secondary teeth is not common in the phyllostomatids, with exception of teeth found adjacent to lesions caused by oral mites in *Leptonycteris*, *Monophyllus*, and *Anoura*. The mechanisms of this resorption are unknown but can be regarded as an aspect of periodontal disease rather than some agent external to the teeth and oral cavity.

In contrast to pathological abrasion and resorption due to external causes, dental erosion (Figs. 32, 33) apparently is common in many species of phyllostomatids. To date, this pathology has been surveyed only in the Glossophaginae (Phillips, 1971), but a cursory examination of museum specimens, particularly of frugivorous genera such as *Artibeus*, suggests that erosion is an important and common form of dental pathology among phyllostomatids. In the glossophagines, erosion is characterized by a generalized area of dissolution (Figs. 32, 33) often beginning at sites of wear facets (Phillips, 1971). In these species, which are characterized by small teeth, dental erosion frequently results in fracturing and loss of crowns. It is possible with the scanning electron microscope to study closely the characteristics of initial lesions representing
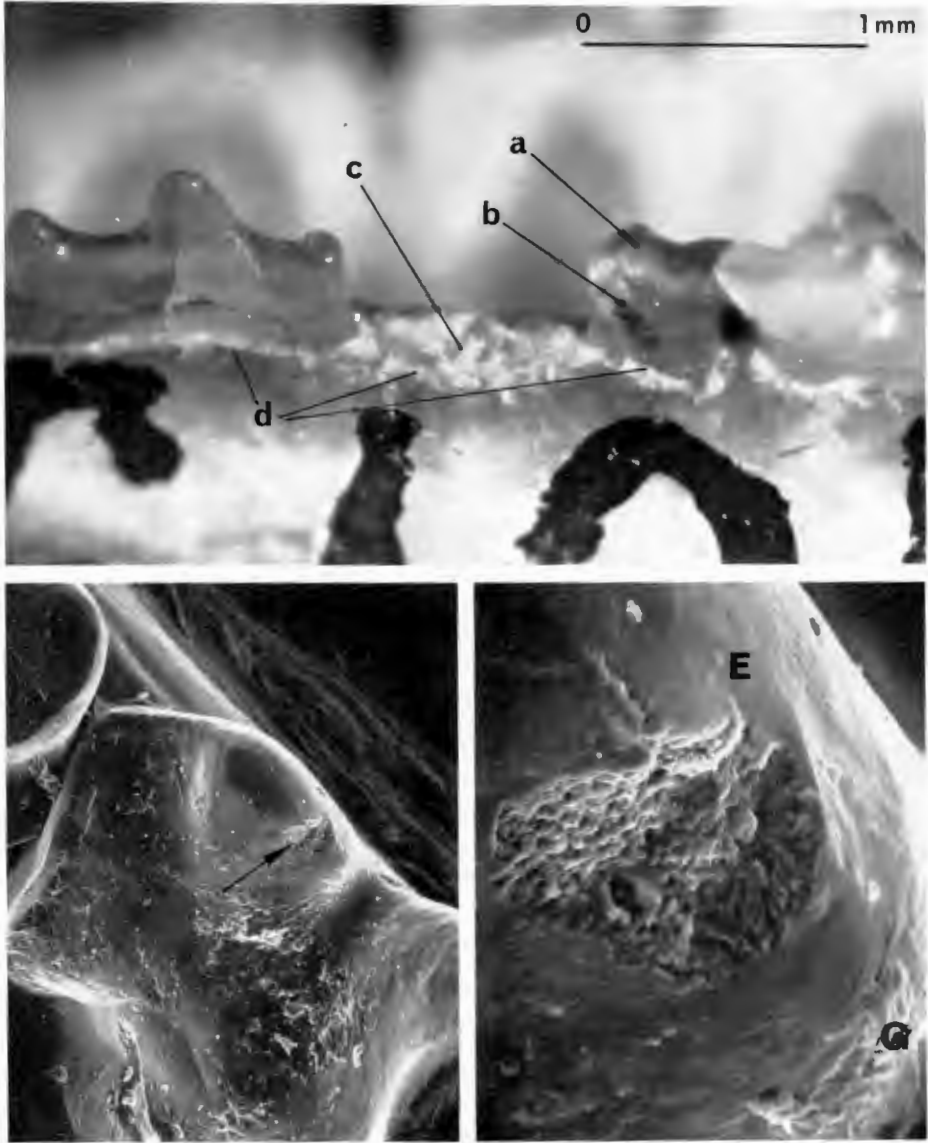
FIG. 32.—Dental erosion in the last lower premolar in a specimen of *Anoura geoffroyi*. Abbreviations are: a, occlusal surface of remaining portion of tooth; b, exposed dentin; c, healed alveolar socket; d, normal dentary bone at dental cervix. From Phillips (1971).

FIG. 33.—Scanning electron micrographs of dental erosion (arrow) on a lower molar of *Glossophaga soricina*. Abbreviations are: E, enamel surface; G, globular dental plaque. $350 \times$ (left) and $700 \times$ (right).

dental erosion (Fig. 33). Such lesions differ from those of dental caries in that the former are not found in basins. In the example illustrated, which is a lower molar from an adult specimen of *Glossophaga soricina*, the outer enamel cuticle

is absent and the inner portion of the enamel layer has a rough, rugose appearance (Fig. 33).

Tongues and Associated Musculature

The gross anatomy of phyllostomatid tongues, except for the structure and distribution of papillae and for the tongues of glossophagines and desmodontines, is similar to that for other groups of microchiropterans. The tongues of *Artibeus*, *Carollia*, and *Phyllostomus*, as described or figured by several authors, are broad and usually rounded at the apex (Park and Hall, 1951; Lautenschlager, 1935). In many species, the distal portion of the tongue is progressively dorsoventrally compressed. Robin (1881) suggested that the tongue of *Macrotus* usually is somewhat more pointed and tapered than that of the others mentioned above and also noted that the tongue of *Aritibeus* ("*perspicillatus*") is substantially different in relative length and topography from that of megachiropterans despite the general similarity in food habits.

Dorsal grooves generally seem to be lacking in tongues of fruit-eating phyllostomatids; however, a shallow depression has been described on the posterior surface in *Carollia* and *Macrotus* (Park and Hall, 1951).

Gross features of glossophagine tongues differ from those of other groups of phyllostomatids. The tongues of these nectar feeders are highly specialized for withdrawing liquid from elongate flower corollas. They are narrow, extremely elongate, highly extensible, and often have a pointed apex (Fig. 34).

Winkelmann (1971) examined numerous adaptations for nectar feeding in glossophagines and identified two types of tongues, each of which has substantially different specializations for drinking nectar. The first group, which consists of *Lonchophylla robusta*, *L. mordax*, *Lionycteris spurrelli*, and *Platalina genovensium*, possesses deep laterally placed longitudinal grooves, one on each side. These grooves probably enlarge to fill with nectar during extension. The ventral surfaces of the grooves in *Lonchophylla robusta* have numerous elongate papillae that are directed laterally. Other species in this group lack papillae in the grooves. The second group consists of *Glossophaga soricina*, *Anoura geoffroyi*, *A. caudifer*, *Monophyllus redmani*, *Leptonycteris nivalis*, *L. sanborni*, *Choeronycteris mexicana*, and *Musonycteris harrisoni*. The tongues of these lack lateral grooves. A dorsal trough widens posteriorly in the tongues of *Leptonycteris* (Greenbaum and Phillips, 1974), *Choeronycteris mexicana*, and *Glossophaga soricina* (Park and Hall, 1951).

Most investigations of phyllostomatid tongues have focused upon the numerous, and sometimes highly specialized and elaborate papillae, which principally adorn the dorsal or, in some cases, the lateral surfaces (Fig. 34). Many species of the subfamily Glossophaginae are highly unusual with respect to papillae, and these specializations will be considered separately.

Two large vallate papillae (Figs. 34, 35) are found on the posterodorsal surface of the tongue in most microchiropterans (Grassé, 1955), and thus their absence in *Choeronycteris* and *Desmodus*, among phyllostomatids, is noteworthy. Papillae are otherwise highly variable in frequency, distribution, and shape among the
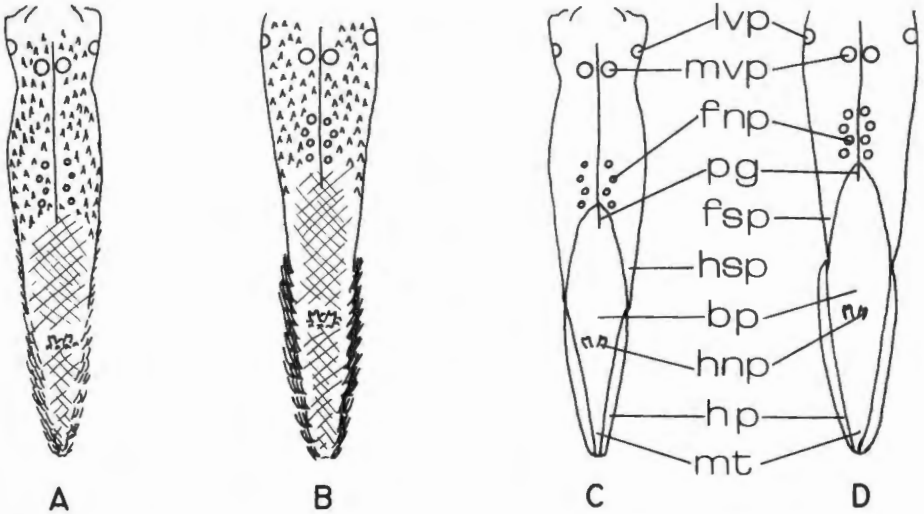
FIG. 34.—Diagrammatic overview of tongues from *Leptonycteris sanborni* (A, C) and *L. nivalis* (B, D). Abbreviations are: mt, median trough; hp, hairlike papillae; hnp, horny papillae; bp, bifid papillae; hsp, hooklike singly pointed papillae; fsp, fleshy singly pointed papillae; pg, posterior groove; fnp, fungiform papillae; mvp, median vallate papillae; lvp, lateral vallate papillae. From Greenbaum and Phillips (1974).

few phyllostomatids that have been examined in detail. One species of *Artibeus*, as examined by Lautenschlager (1935) and Park and Hall (1951), has many large, broad, flattened papillae within the posterior region that are unusual in being directed anteriorly. In *Carollia perspicillata*, however, the large, posterior papillae are elongate and assume a basketlike appearance. Those of equivalent location in *Macrotus californicus* and *Desmodus rotundus* are soft and flattened, but often terminate in a hairlike apex. In *Phyllostomus*, Robin (1881) noted an abundance of conical papillae, which are largest in the midregion of the tongue.

Fungiform papillae are found relatively infrequently on the tongues of most phyllostomatids. Park and Hall (1951) described the presence of a few scattered ones in *Carollia* (also described as rare by Robin), *Desmodus*, and *Leptonycteris* but reported their absence in *Macrotus*, *Choeronycteris*, *Glossophaga*, and *Artibeus*. Intraspecific variability in distribution of these papillae is possible judging from the fact that Fishman (1963) described the innervation of fungiform kinds in his study of gustatory response in *Aritbeus jamaicensis*. Greenbaum and Phillips (1974) noted differences between two species of *Leptonycteris* with regard to fungiform papillae. *Leptonycteris nivalis* has a few large ones on each side of the posterior groove of the tongue, whereas in *L. sanborni* they are more abundant, but smaller.

Variations of papillae that are most adaptive for particular foods are found on the tongues of glossophagines. The distal portion of the *Lonchophylla*-type tongue of five of the glossophagines described by Winkelmann (1971) is covered with approximately two dozen papillae that decrease in size posteriorly. Most of the remaining surface in this species group is covered with small, nodulelike fili-
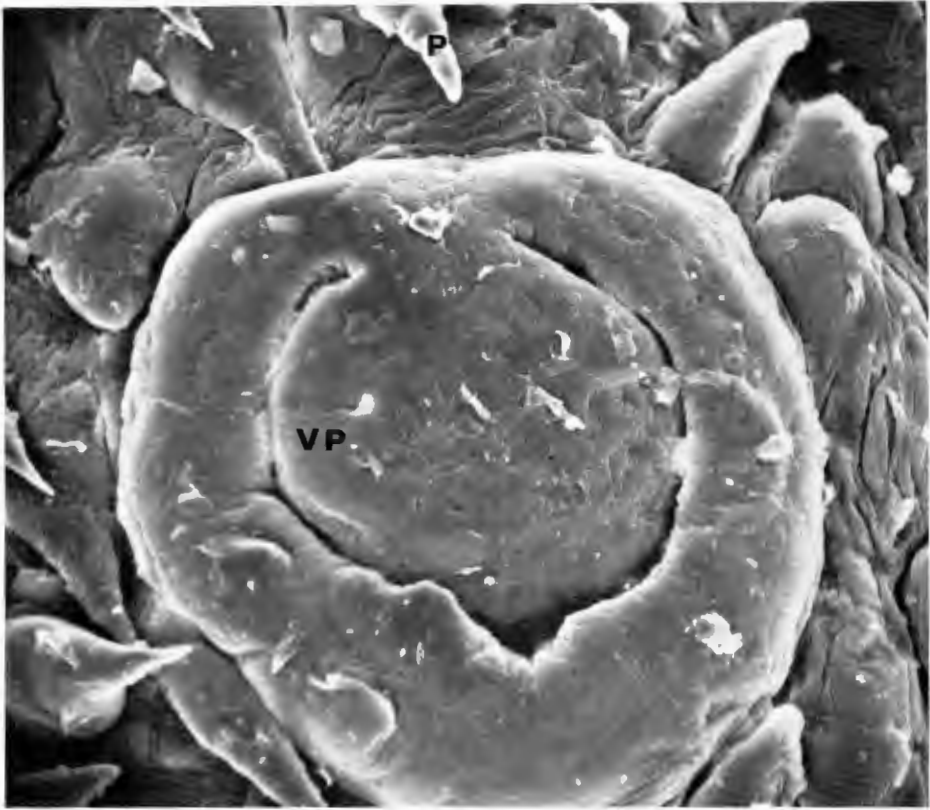
Fig. 35.—Scanning electron micrograph of a vallate papilla (VP) and singly pointed papilla (P) in a specimen of *Leptonycteris sanborni.* 870 × .

form papillae. There are four or five bifid horny papillae (Fig. 36) within the midline about one-third of the way back from the tip of the tongue.

Along the dorsolateral edge on each side of the anterior third of the *Glossophaga*-type tongue (after Winklemann), are rows of long hairlike vertical papillae. The number and size of these are highly variable among the species of *Glossophaga, Anoura, Monophyllus, Leptonycteris, Choeronycteris*, and *Musonycteris*, and those of *G. sorcina* have been described by several workers as especially coarse. These elongate papillae probably load nectar by capillary action following extension of the tongue. Horny papillae, similar in shape and location to those in the *Lonchophylla*-type tongue, are present in this second group of species. The remainder of the tongue is covered with smaller hairlike papillae.

Of related interest are the studies of differences in tongue structure in relation to the presence of an unusual periodontal disease (see section on pathology) in only one of two extremely similar and sympatric species of *Leptonycteris* (Phillips, 1971; Greenbaum and Phillips, 1974). The macronyssid mite *Radfordiella oricola* produces lesions in the palate and alveolar bone only in *L. nivalis*. Dorsal and lateral filiform papillae on the posterior portion of the tongue in *L. sanborni*
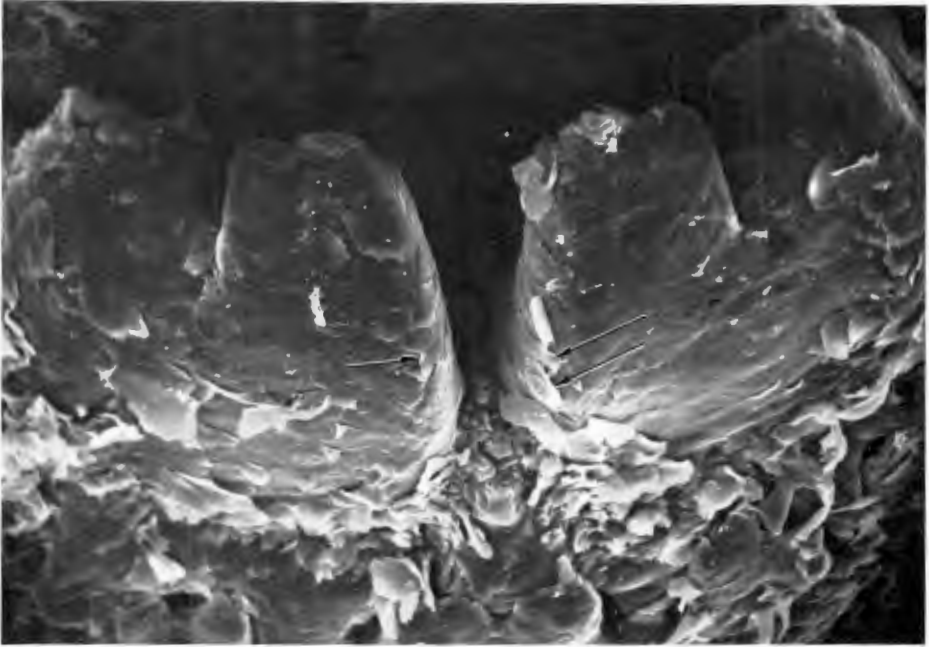
FIG. 36.—Scanning electron micrograph of a pair of bifid papillae on the tongue of a specimen of *Leptonycteris sanborni*. Scalelike keratinized epithelial cells can be seen sloughing off from the surface (arrows). 1020 ×.

(Fig. 37) might prevent attachment of the mites in this species by way of a brushing action against the oral and gingival mucosa.

The tongue musculature, both extrinsic and intrinsic, has been studied in few leaf-nosed bats. Because some glossophagines probably feed almost exclusively with the tongue, they are of particular interest, and their tongue musculature has been the most thoroughly studied among phyllostomatids. The tongue musculature of glossophagines and other phyllostomatids is qualitatively like that of other mammals. However, Wille (1954) described some noteworthy specializations of origins and insertions of muscles in glossophagines that are highly contributive to the great extensibility and mobility of their tongues. Wille (1954) observed that the genioglossus is highly developed into a leaflike form in *Leptonycteris*, *Anoura*, *Lonchophylla*, and *Choeronycteris* and contributes to the great protrusibility of the tongue. The sternohyoideus has its origin on the sternum, but inserts into the base of the tongue to permit improved retractility. Also, the point of origin of this muscle shifts posteriorly from the manubrium of the sternum to the xiphoid process thereby increasing the length and force of tongue retractility. This, along with particularly deep insertion of the sternohyoideus into the tongue, and insertion of the stylohyoideus on the lateral edges results in improved efficiency of manipulation. Intrinsic muscle fibers form a complex system of longitudinal, vertical, and transverse bundles that serves to reduce depth and diameter of the tongue, resulting in its elongation (Fig. 38).
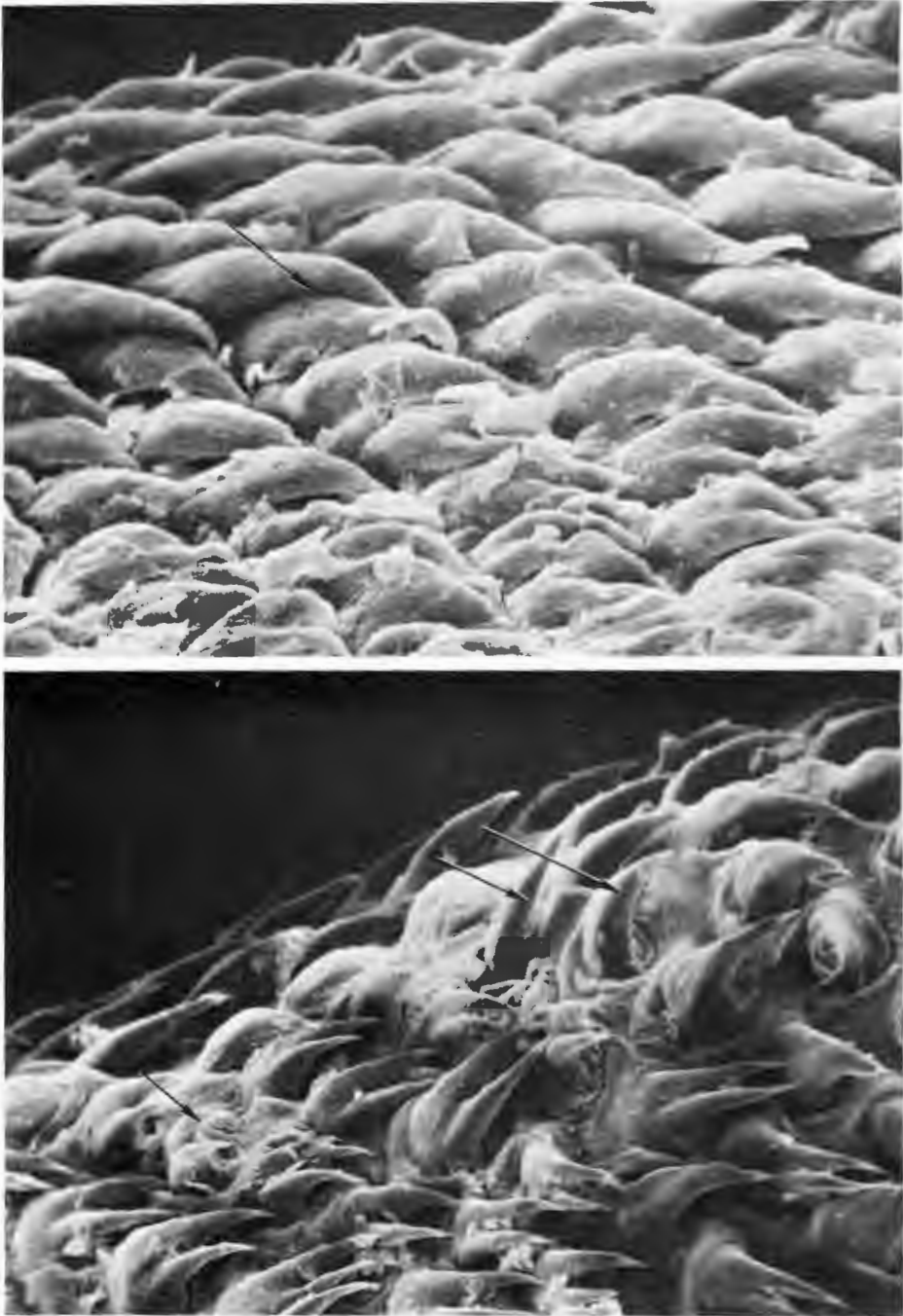
FIG. 37.—Scanning electron micrograph of flat, fleshy papillae (top; arrow) in *Leptonycteris nivalis* in comparison to the well-keratinized, hooklike papillae in *L. sanborni* (bottom; arrows). Both views 140×.

Winkelmann (1971) developed a model for tongue movement in glossophagines. The great extensibility of the tongue results from a combination of elongation through contraction of intrinsic muscles and protraction of the base of the tongue by the action of the extrinsic muscles. Protraction is effected by relaxation of the sternohyoids (retractors), thus providing increased reach to the base of flowers. The mechanism of unloading of the tongue is unknown in any of the glossophagines but Winkelmann (1971) assumed that shortening of the tongue proceeds from proximal to distal to prevent unloading until the tongue is in the mouth.

The tongues of vampire bats are structurally and functionally specialized to permit consumption of large quantities of blood. The tongue of the common vampire, *Desmodus rotundus*, is rounded and has a deep dorsal fissure within the posterior half and a groove along the ventrolateral border on each side. The change in orientation of the blood grooves from front to back and the anatomy of associated papillae have been described by Glass (1970). During feeding, the tongue has been observed to move very rapidly in and out of the mouth; blood is visible only on the dorsal surface at the rear. Consequently, blood is thought to move along the ventrolateral grooves by peristalsis and emerge dorsolaterally on the tongue at the back of the mouth.

A complex system of abundant motor endplates has been observed by Field and Holbrook (1969) in the tongues of *Artibeus lituratus* and *Desmodus rotundus*, as well as in two species of vespertilionids. Three to four individual fibers combine to form each endplate, each of which then splits into seven or eight terminal branches. No features of motor of sensory fibers or associated structures in the tongue were cited as unique to *Desmodus* or *Artibeus*.

Suthers (1970) reviewed what is known about taste in bats, including data on experimental gustatory responses in *Artibeus jamaicensis* (Fishman, 1963) and *Desmodus rotundus*. Application of dilute acid to the dorsal surface of the tongue yields greater responses in *D. rotundus* than it does in several other bats for which data are available, including, and especially, *A. jamaicensis*. In contrast, *A. jamaicensis* apparently is relatively sensitive to NaCl concentrations greater than that required for minimum responses and is unusual among the few bats that have been examined because its response to salt is greater than that for the other three principle taste categories.

SALIVARY GLANDS

Salivary glands are an integral and important component of the oral biology in all mammals. Although the general impression often is that these glands are

FIG. 38.—Diagrammatic presentation of tongue masculature in long-nosed bats (*Leptonycteris*). *Top*: anterior musculature in the region of the horny papillae. *Bottom*: peripheral musculature in detail (box labeled *X* in top drawing). Abbreviations not explained in Fig. 34 are: 1m, longitudinal muscle; hm, horizontal muscle; vm, vertical muscle; 1v, lingual vein; la, lingual artery; 11, lingual ligament; de, dorsal epithelium; lp, lamina propria; cc, central muscle core. From Greenbaum and Phillips (1974).
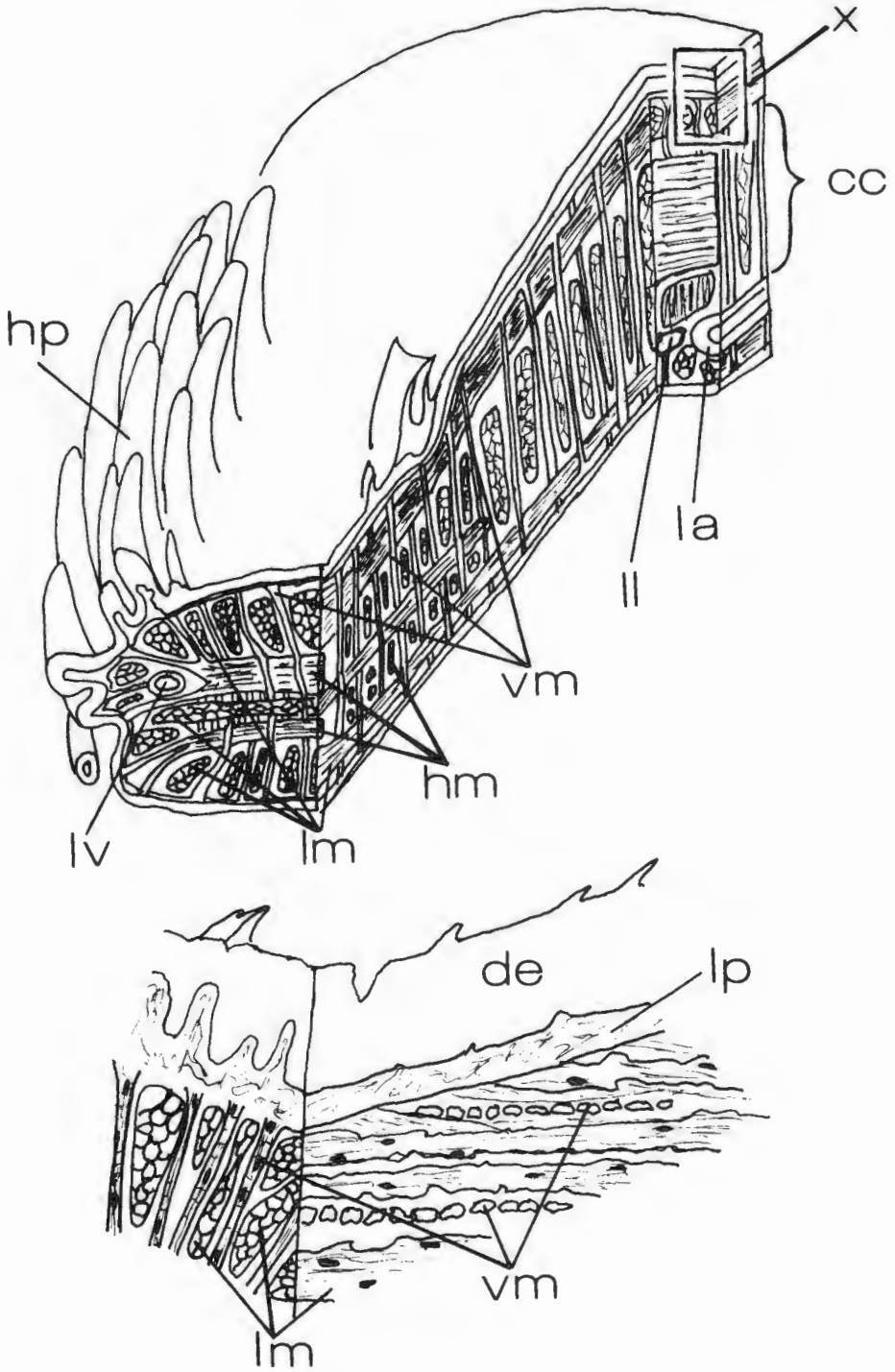
only involved with the initial stages of digestive processes, in fact they have a wide variety of functions that include provision of a protective coating for the teeth; production of antibacterial agents, toxic substances, and anticoagulants; maintenance of salt and water balance; and production of one or more hormones (Klinkhamer, 1968; Pearson, 1950; Rutberg, 1961; DiSanto, 1960; Ito, 1960).

The major salivary glands, particularly the submandibular, have been studied in considerable detail in man and in certain laboratory species (Leeson and Jacoby, 1959; Luzzato *et al.*, 1968; Parks, 1962; Scott and Pease, 1959; Tamarin and Sreebny, 1965; Tandler, 1962, 1963, 1965). Interest in this particular gland partly is due to its tendency toward noteworthy specialization in many species. For example, it is the submandibular of the short-tailed shrew (*Blarina brevicauda* that produces a toxin (Pearson, 1950); the submandivular of the house mouse (*Mus musculus*) and Norway rat (*Rattus norvegicus*) that displays sexual dimorphism (Junqueira *et al.*, 1951; Lacassagne, 1940; Caramia, 1966); the submandibular of the hamster (*Mesocricetus auratus*) that produces a sexually dimorphic mucin (Shackleford and Klapper, 1962); and the submandibular of the common vampire bat (*Desmodus rotundus*) that produces an anticoagulant (DiSanto, 1960).

Investigational techniques employed in studies of salivary glands have progressed from general gross anatomical and histological procedures to experimental cytological and physiological methods (Caldwell and Shackleford, 1967; Amsterdam *et al.*, 1969; Bressler, 1974; Scott and Pease, 1964; Castle *et al.*, 1972, 1975). The abundant literature on mammalian salivary glands shows wide variation in quantity and quality of information about all aspects of these glands in wild and domestic species. Indeed, most wild species are almost unknown. The most notable exceptions are provided by a series of excellent papers by Shackleford and his co-workers on such species as the opossum (Wilborn and Shackleford, 1969), kangaroo rat and antelope ground squirrel (Shackleford and Schneyer, 1964), nine-banded armadillo (Shackleford, 1963), and squirrel monkey (Cowley and Shackleford, 1970a, 1970b). The general paucity of studies on wild mammals is somewhat surprising, especially in view of the striking structural and histochemical diversity apparent in salivary glands of mammals (see Shackleford and Wilborn, 1968, for a review).

The variety of functions attributed to salivary glands notwithstanding, it is reasonable that bats (particularly the phyllostomatids) could be an extremely important model for comparative studies of these structures. The impressive array of feeding habits that mark the evolutionary history of the Phyllostomatidae provides an excellent opportunity for investigations of cellular evolution and, in the long run, could prove valuable to biosystematic interpretations. Systematic and evolutionary implications of differences and similarities in salivary glands generally have not been presented because the species previously studied often were only distantly related (Andrew, 1964) or, sometimes, because basic taxonomic misconceptions caused confusion and considerable analytic difficulty for the investigators. For example, rabbits (*Oryctolagus*) were regarded as rodents as recently as 1960 by Quintarelli and Chauncey (1960) who compared meta-

chromatic tinctorial characteristics of salivary glands of these animals to those of albinistic Norway rats (*Rattus norvegicus*) and house mice (*Mus musculus*). Comparisons of even highly detailed features of salivary glands of a few species of rodents with data from lagomorphs, man, dogs, and cats have been inadequate for development of an understanding of the evolutionary process insofar as these organs are concerned.

The salivary glands of phyllostomatid bats, aside from two important exceptions, are poorly known. Robin (1881) apparently was the first, and for many years the only worker, to describe salivary glands of various species of megachiropteran and microchiropteran bats. His descriptions included 41 recognized species. *Glossophaga soricina*, one of the phyllostomatid species studied by us, was included in his report. More recently, Dalquest and Werner (1951) reported on what they incorrectly termed "interscapular glandular adipose tissue" in *Artibeus jamaicensis*. A series of other studies (Werner *et al.*, 1950; Werner and Dalquest, 1952; Dalquest *et al.*, 1952; Dalquest and Werner, 1951, 1954) also dealt with certain general histological aspects of salivary glands in a variety of microchiropteran bats. Grassé (1955) briefly described the salivary glands of bats, with particular reference to production of an anticoagulant by the salivary glands of the common vampire bat, *Desmodus rotundus*. The best, and most recent, studies of salivary glands of phyllostomatids are those by Wimsatt (1955, 1956) and DiSanto (1960). It was Wimsatt (1955) who pointed out that Dalquest and Werner (1951) had mistakenly identified a portion of the parotid gland of *Artibeus* as brown fat; later, he (Wimsatt, 1956) provided an excellent, complete histological and histochemical analysis of the salivary glands of this frugivorous species. Likewise, DiSanto (1960) has undertaken a complete study of the anatomy, histology, and histochemistry of the salivary glands of *Desmodus* and provided a partial comparison with *Artibeus*. In *Artibeus jamaicensis*, the parotid secretory cells were judged by Wimsatt (1956) to be serous even though they were found to be morphologically more like mucous cells, at least when viewed with the light microscope. These secretory cells are negative to mucopolysaccharide techniques such as PAS, Alcian blue, and mucicarmine, apparently do not produce amylase, and are not serozymogenic (Wimsatt, 1956). Both the intercalated duct cells and striated cells of the striated duct are PAS positive, suggesting a secretory role in this species (Wimsatt, 1956). In *Desmodus*, the parotid secretory cells were regarded as seromuccoid based on their histochemical responses, even though they appear to be serous cells from a morphological standpoint (DiSanto, 1960). In this species, the secretory cells showed prominent reactivity to five of six carbohydrate reactions and also revealed beta and gamma metachromasia to toludine blue (DiSanto, 1960). The secretory cells in parotids of vampire bats lack both acid and alkaline phosphatase activity, even though both enzymes apparently are present in the saliva (DiSanto, 1960). The fact that extracts of parotid glands from this species do not cause dissipation of blood clots suggests that they do not play a role in anticoagulation (DiSanto, 1960).

Although the classical submandibular gland is characterized by mucous cells with a cap or demilune of serous cells (Sicher and Bhaskar, 1972), the opposite

is true in both *A. jamaicensis* and *Desmodus rotundus* (Wimsatt, 1956; DiSanto, 1960). Additionally, it is the submandibular of *Desmodus* that apparently produces an anticlotting agent. This salivary component does not act as a true anticoagulant because it does not prevent formation of fibrin; instead, it acts directly on formed fibrin by dissolving it (DiSanto, 1960).

The sublingual gland of *Artibeus jamaicensis* is morphogically and, generally speaking, histochemically similar to that of other mammals (Wimsatt, 1956). The sublingual gland of *Desmodus*, on the other hand, is unusual in that the secretory acini are composed of both mucous cells and metachromatic cells, which exhibit extensive metachromasia through a broad pH range. The metachromatic cells might produce an unusual polysaccharide of low pH and could, according to histochemical data presented by DiSanto (1960), produce an anticoagulant such as heparin. At the same time, however, extracts from the sublingual do not prevent coagulation of blood.

The lack of basic histological information about salivary glands in most phyllostomatids has led us to describe in following paragraphs the gross anatomy and general histology of the three major salivary glands of five additional phyllostomatid species. The following accounts, which are intended to serve as a basis for more detailed and sophisticated study, are preceded by brief, generalized overviews of both gross anatomy and cellular morophology.

General Gross Anatomy

Gross dissection and examination of the three major salivary glands (parotid, submandibular, sublingual) in *Glossophaga soricina*, *Leptonycteris nivalis*, *L. sanborni*, *Anoura geoffroyi*, and *Sturnira ludovici*, revealed considerable differences in size and shape of the glands (Fig. 39). General findings about the gross anatomy of the major salivary glands are presented in the following paragraphs.

The parotid gland varies in appearance, being either soft and loose or distinct and compact, and in size, ranging from extremely small to strikingly large (Fig. 39). It is found at the base of the auricle and is enclosed in a strong and tightly adherent capsule of connective tissue. Stenson's duct can be traced from the anterior edge of the gland (having originated on the inferior surface) anteriorly, across the masseter muscle.

A submandibular gland is found in all five species studied by us. Although it varies greatly in number of lobes, size, and appearance (Fig. 39), in all of the species it is encased in a capsule of dense connective tissue that appears to be continuous with that of the parotid gland. The position of the submandibular varies somewhat, but generally the lobes are located in the mastoid region of the skull and are separated from the parotid by the external jugular. With exception of *Anoura geoffroyi*, the submandibular possesses a single duct, to which all of the lobes are joined. This duct typically passes anteriorly, under the digastric muscle, and along the lingual surface of the ascending mandibular ramus. In *Anoura* the anterior lobe of the principle submaxillary has its own duct, which is described in detail in the account of this species.
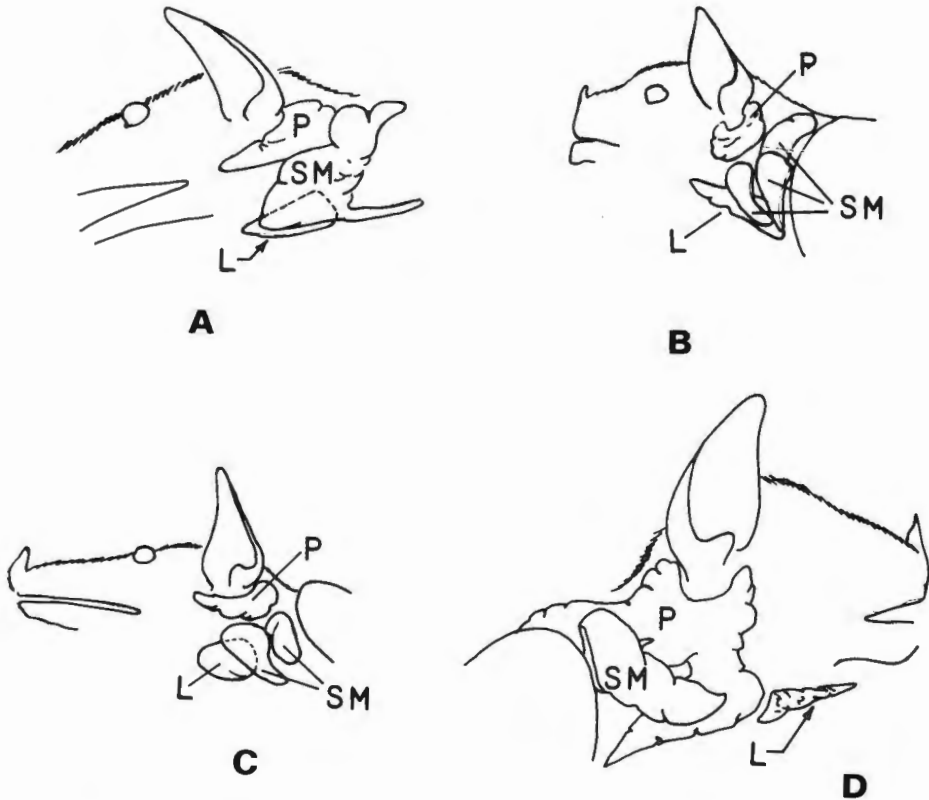
FIG. 39.—Diagrammatic presentation of the gross anatomy of major salivary glands in A) *Leptonycteris nivalis*; B) *Sturnira ludovici*; C) *Anoura geoffroyi*; and D) *Artibeus jamaicensis*. Abbreviations are: P, parotid; SM, submandibular; L, sublingual.

The sublingual salivary gland is a delicate, soft, loosely encapsulated mass of tissue located in a triangular-shaped depression bounded by the digastricus, sternohyoideus, and sternomastoideus and positioned directly ventral to the thyroid glands and larynx. The size and shape of the sublingual, as well as the size of the depression in which it rests and the depth at which it is located, varies greatly from species to species (Fig. 39). In all five species this gland has a single duct that originates on the dorsal surface of the gland and enters the oral cavity at the base of the tongue, from which point it travels anteriorly to the tip of the sublingual flap.

General Microanatomy

Diagrammatic representations of salivary glands of five species are presented in Figs. 40 and 41. The basic microanatomy is fairly consistent even though the cellular details and functions vary widely from species to species.

Terminal portions.—The terminal portions of the salivary ducts are characterized by groups of secretory cells (acini) clustered around a narrow lumen

(Figs. 40, 41, 42). In phyllostomatids, the parotid secretory acini typically are comprised of a single type of secretory cell, which is either serous or seromucoid in morphology. The parotid acini usually are relatively small and somewhat round in shape and can be termed compound acinus. The typical phyllostomatid submandibular gland consists of elongate and often branched secretory acini comprised of at least two types of secretory cells (Fig. 41). In most species one type of secretory cell forms a cap, or demilune, at the distal end of the acinus. The submandibular secretory cells are a combination of serous, seromucoid, or mucous-type cells. The secretory acini of the sublingual gland are elongate (sometimes extremely so), branched, and comprised exclusively of mucous cells.

Dramatic overviews of salivary gland microanatomy are provided by the scanning electron microscope (Figs. 42, 43). In Fig. 42 and 43, which show the sublingual gland from a dwarf fruit-eating bat, *Artibeus phaeotis*, the branched, elongate secretory acini are clearly visible. The exposed cytoplasm of the mucous cells is rough and trabecular in appearance, except at the basal margins where it is smooth (Figs. 42, 43). Certain other microanatomical features associated with the terminal portion of the duct system also are well illustrated by these SEM photographs. For example, in Fig. 42, one can easily distinguish a large capillary adjacent to an acinus; a major nerve bundle as well as smaller nerves that connect separate acini; and the basal lamina covering the secretory acini. In Fig. 43, the basal lamina can be compared to the connective tissue capsule, which is considerably thicker.

The microanatomy of the acinar lumen also can be analyzed with the SEM. In Fig. 44, secretory granules about to be extruded into the lumen can be seen to cover the apical surfaces of the secretory cells. This view, which is from the submandibular gland of *Macrotus waterhousii*, is characteristic of acinar lumina lined by secretory cells of the serous type. An interesting comparison can be made between SEM microanatomy and transmission electron microscopy. Although the TEM photograph shown here is from the submandibular gland of a specimen of *Phyllonycteris*, moderately electron dense serous granules can be seen at the cell apex, adjacent to the acinar lumen. These granules are still covered by a membrane, which appears as a thin, dark line (Fig. 44).

Ducts.—The duct system leading away from the secretory acini can be divided into three segments; in order, they are intercalated ducts, striated ducts, and excretory ducts. Certain microanatomical features allow for relatively easy recognition of each type of duct. The intercalated ducts vary in length and degree of branching but typically have a narrow lumen and flattened appearance (Fig. 43). The transition between these ducts and the so-called striated ducts is abrupt (Fig. 43); the latter are considerably thicker, although the lumen still is narrow relative

FIG. 40.—Diagrammatic presentation of basic microanatomy of the parotid salivary gland in A) *Glossophaga soricina*; B) *Leptonycteris sanborni*; C) *L. nivalis*; D) *Anoura geoffroyi*; and E) *Sturnira ludovici*.

FIG. 41.—Diagrammatic presentation of basic microanatomy of the submandibular salivary gland in the same species as shown in Fig. 40.
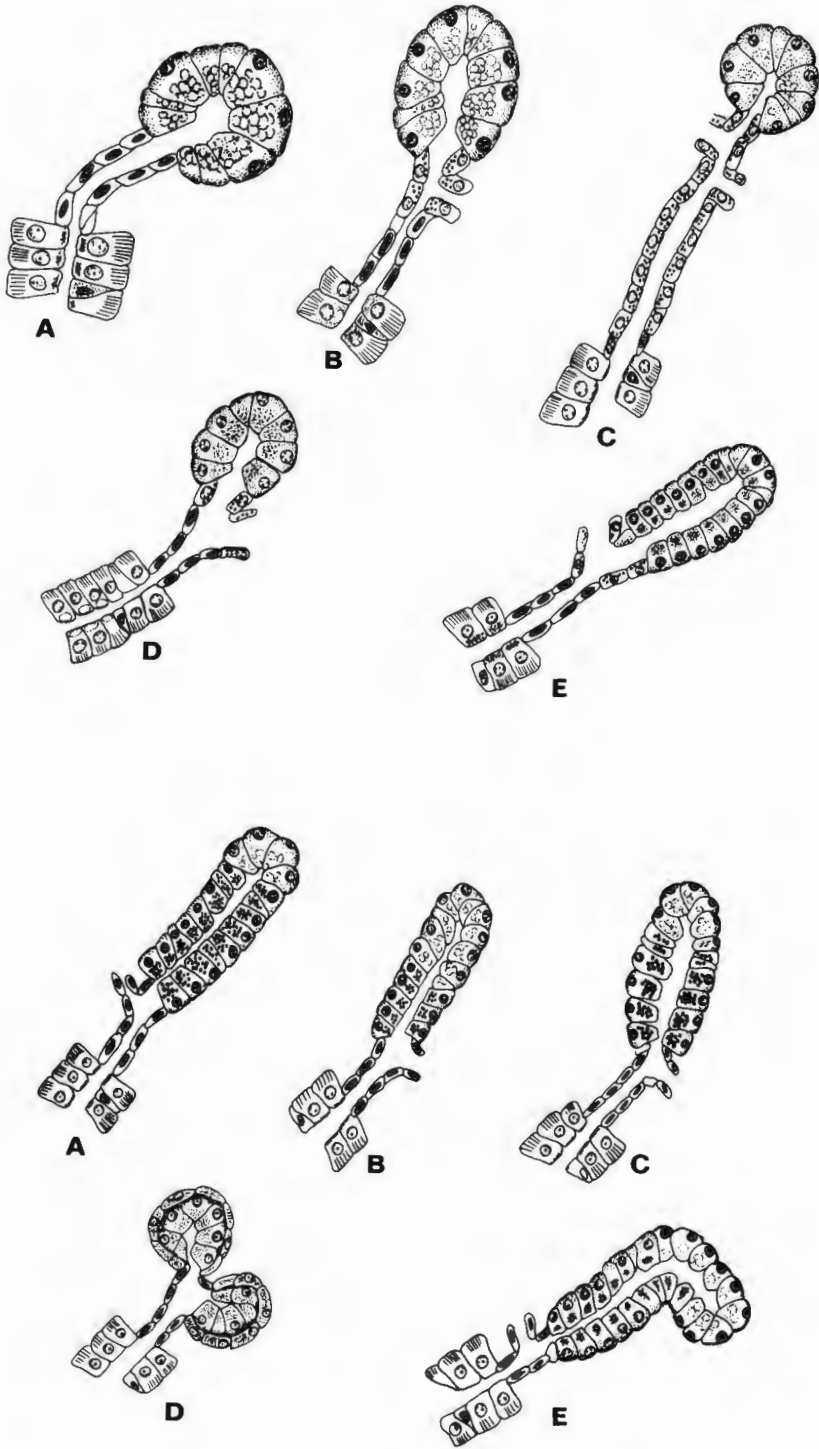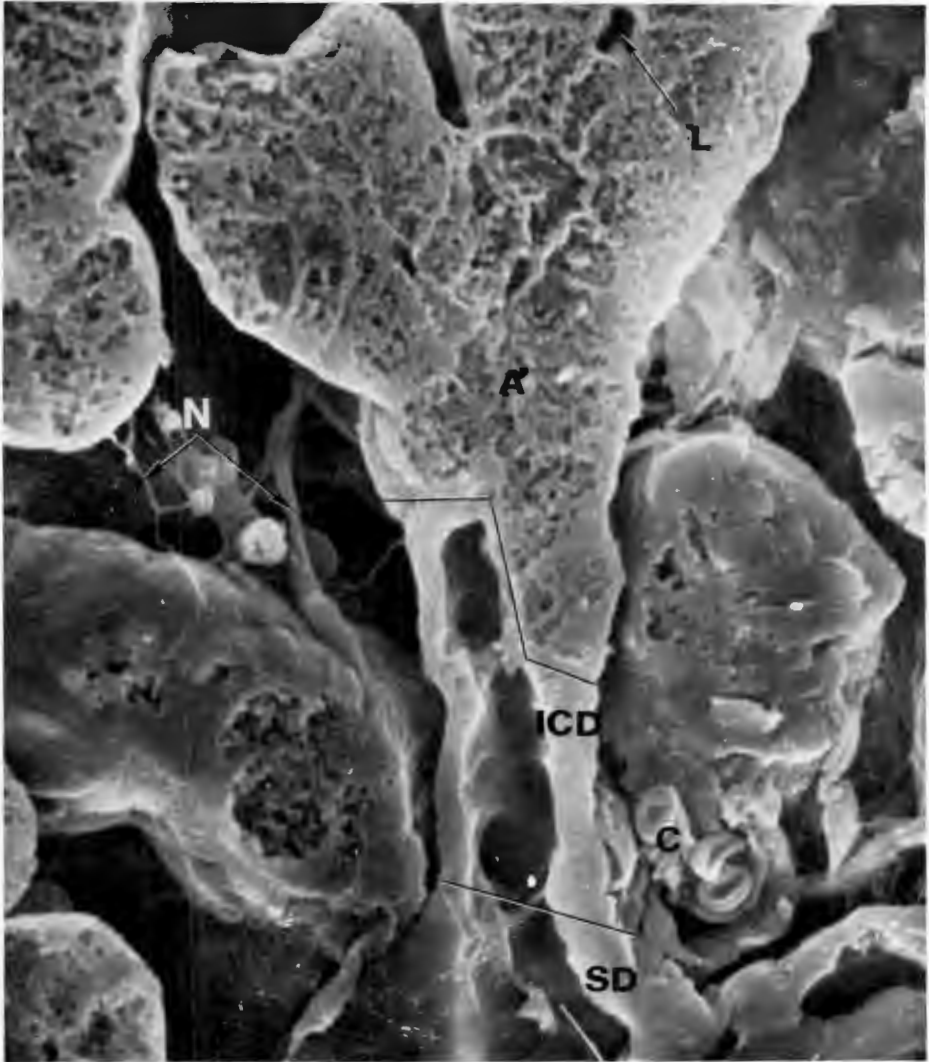
FIG. 42.—Scanning electron micrograph of a secretory acinus (A), intercalated duct (ICD), and striated (intralobular) duct (SD) in the sublingual salivary gland of *Artibeus phaeotis*. Abbreviations are: C, capillary; L, acinar lumen; N, nerves. 1170×.

to the overall (outside) diameter. The luminal surfaces of these ducts vary considerably; they can be smooth, covered by microvilli, or even covered by microvilli so long and densely packed that they resemble a brush border. An example of luminal microvilli is presented in Fig. 45, which is an SEM photograph from the submanibular of *Macrotus*. In this view, it is apparent that many of the microvilli are interconnected by narrow bridges of cytoplasm. Such bridges have not been reported previously in salivary glands, and their significance here is unknown. Excretory ducts, which carry saliva away from the lobes of the gland, are charac-
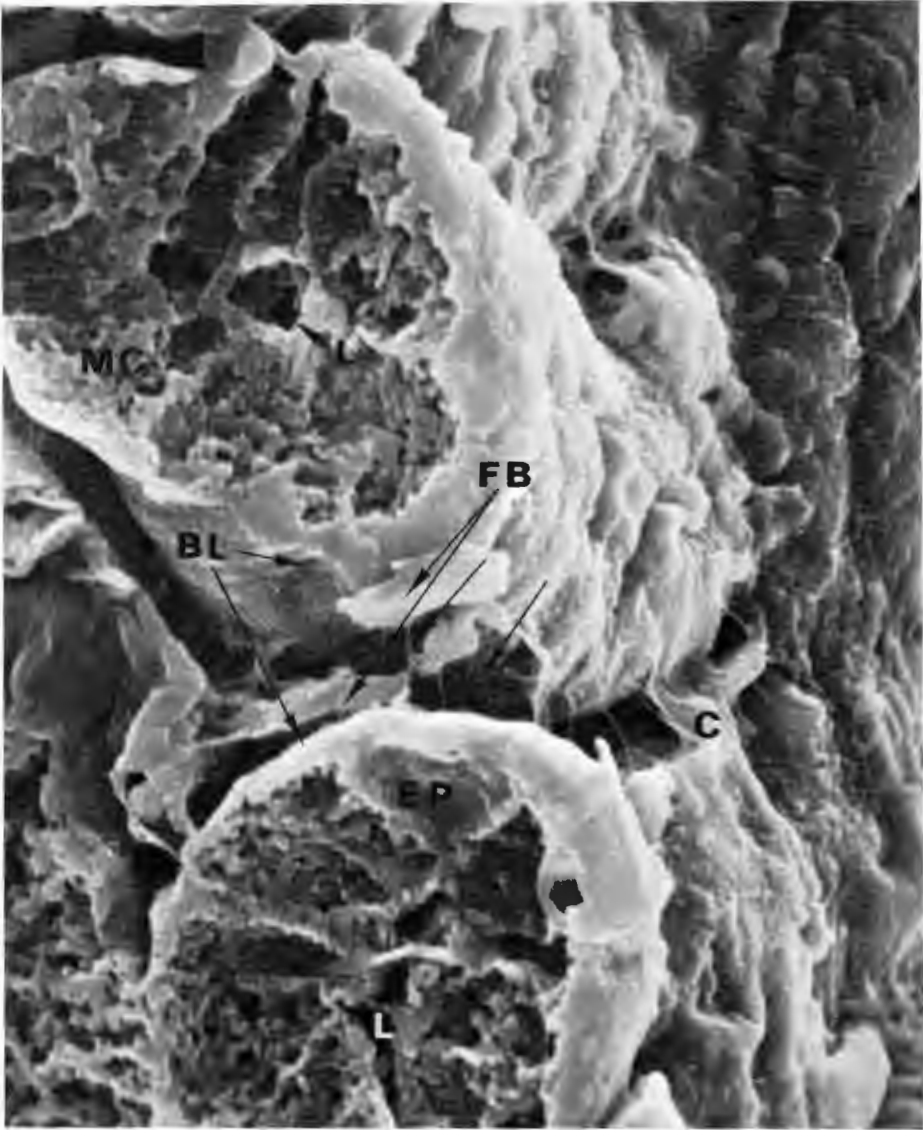
Fɪɢ. 43.—Scanning electron micrograph showing mucous secretory cells (MC) and extra-acinar space in the sublingual gland of *Artibeus phaeotis*. Abbreviations and symbols are: BL, basal lamina; C, connective tissue; EP, ergastoplasm; FB, fibroblast; arrows, fibrils (presumably collagenous). 1206×.

terized by a wide lumen and narrow wall, the latter reflecting the low, almost cuboidal nature of the cells.

Detailed Descriptions

Details of gross anatomy and general histology of five phyllostomatid species are provided for the first time in the following paragraphs.
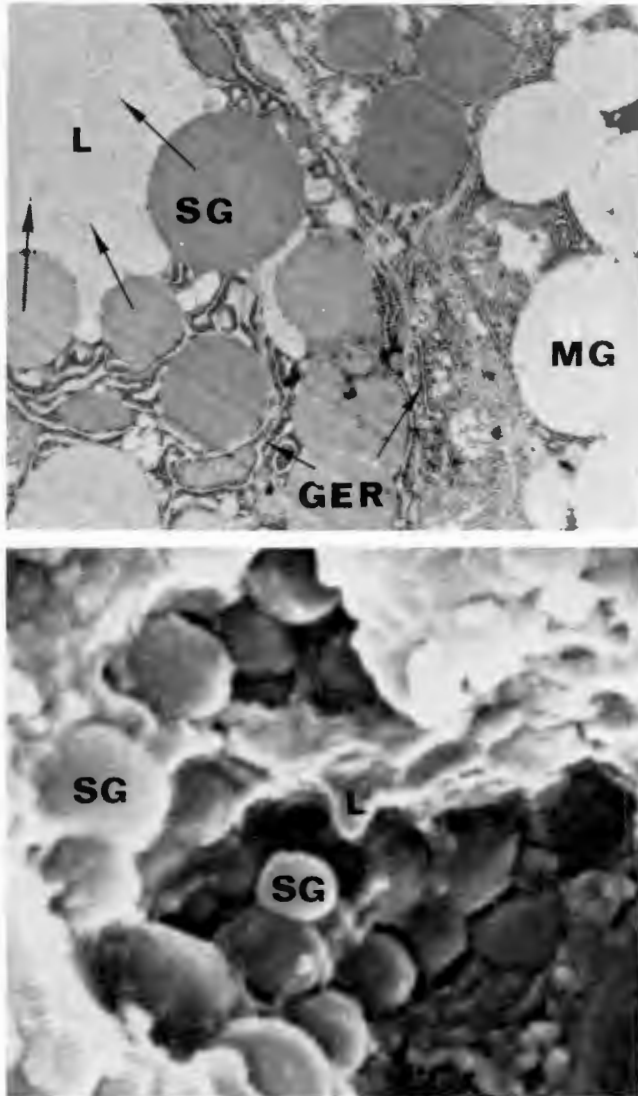
FIG. 44.—Comparative transmission (top; *Phyllonycteris*) and scanning (bottom; *Macrotus*) electron micrographs of exocytosis of serous secretory product (SG) into the acinar lumen (L). Abbreviations and symbols are: GER, granular endoplasmic reticulum; MG, mucous secretory granule; arrows, direction of export into lumen. Both approximately 9750×.

Glossophaga soricina

Gross Anatomy

Parotid.—A moderate-sized gland extending from the lambdoidal region to the auricle (Fig. 39). A small lobe of the gland extends ventrally, over the masseter and digastricus muscles and lateral margin of the sublingual gland. Stenson's duct
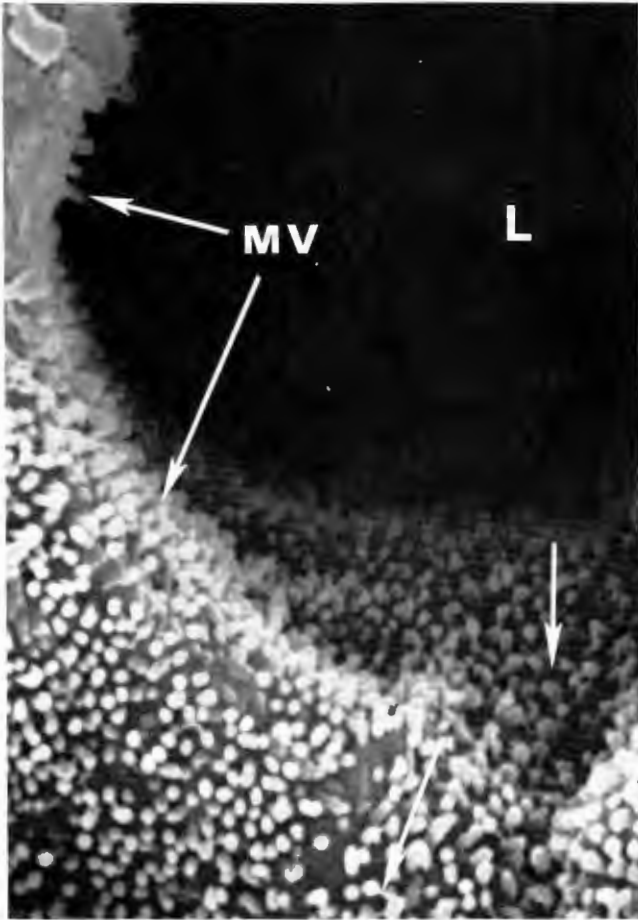
FIG. 45.—Scanning electron micrograph showing microvilli (MV) at apical membranes (luminal surface; L, lumen) of cells in a striated duct in the submandibular salivary gland of *Macrotus*. Note the interconnections between microvilli (arrows). Approximately 7600×.

originates on the inferior surface, near the anterior border, and follows the external jugular along the base of the masseter to the anterior border, where it enters the connective tissue of the upper lip in the area of the canines.

Submandibular.—A large gland consisting of four distinct lobes, each being ovoid and flat (Fig. 39). The two anterior lobes, which are slightly smaller than the remaining two, lie directly over the sublingual. The third and fourth lobes are located ventrally to the parotid and over the sternomastoideus. The main ducts of the four lobes join and pass over the digastricus before turning mediodorsad to meet the main duct of the sublingual near the inferior surface of the angle of the mandible. The two ducts enter the anterior portion of the oral cavity together.

Sublingual.—A relatively large, triangular gland consisting of three finely subdivided lobes (Fig. 39). It is located at the angular process of the mandible and
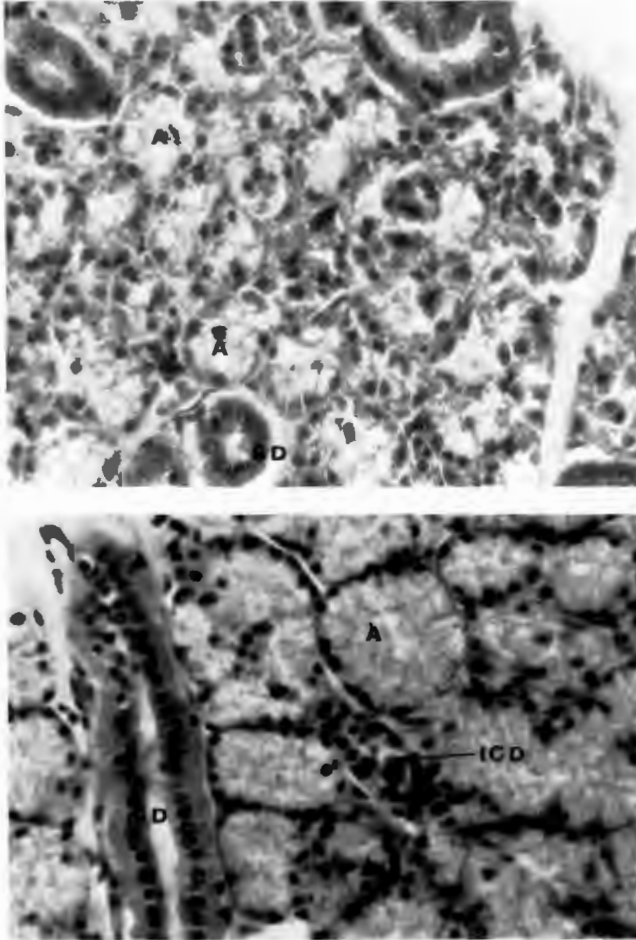
FIG. 46.—*Top*: Secretory acini and striated ducts in the parotid of *Glossophaga soricina*. Abbreviations are: A, acini; SD, striated duct. Masson's trichrome. 222×. *Bottom*: Secretory acini and striated duct in the sublingual of *Glossophaga soricina*. Abbreviation not defined above is: ICD, intercalated duct. Hematoxylin and eosin-Y. 370×.

covered by the mylohyoideus muscle. The lateral edge of the gland extends from the digastricus to the mastoid region, passing under the sternomastoideus. Medially, this gland extends to the ventral surface of the throat, under the lateral margin of the sternohyoideus. The main duct arises on the anterior margin of the sublingual and joins the main duct from the submandibular (see above).

Histology

Parotid.—The lobules of the parotid are densely packed with small, generally round, secretory acini (Figs. 40, 46). The secretory cells are seromucoid when stained with H&E. The small, round nucleus is positioned basally and heterochromatic. The cytoplasm, which is most dense in the basal area around the nu-

cleus, is intensely basophilic (Fig. 46). The secretory cells appear to have large, irregularly shaped vacuoles between the nuclei and acinar lumina. These vacuoles appear to be empty (even at $1800 \times$) in secretory cells stained with H&E, Masson's trichrome, or PAS. The cytoplasm around the vacuoles, which forms a distinct network throughout the apical portion of the cell, is intensely reactive to PAS. In some cells PAS-positive material can be seen adjacent to the vacuoles.

The numerous lobules of the parotid gland have a moderately extensive duct system. The short, intercalated ducts are comprised of medium-sized cuboidal cells, each having a round, heterochromatic nucleus and faintly acidophilic cytoplasm that nearly is obscured by the nucleus. PAS-positive granules are lacking in the intercalated ducts.

The transition from intercalated to striated ducts is abrupt (Fig. 40). The centrally placed nuclei of striated cells are large and euchromatic (Fig. 46). When stained with Masson's trichrome, the striated portion of the cell is rust colored, whereas the apical cytoplasm around the nucleus is gray and that directly adjacent to the lumen of the duct is pale greenish gray. This region of the cytoplasm also is strongly PAS positive. The transition from the typical striated ducts to the interlobular ducts is gradual. It is characterized by a gradual increase in luminal diameter and a change in cell morphology. The nucleus becomes more centrally positioned and the cytoplasm adjacent to the lumen becomes only faintly acidophilic. This pale area is clearly visible in cells stained with Masson's trichrome and is even more intensely reactive to the PAS technique than it is in the typical striated cells.

This PAS-positive response suggests the presence of mucosubstance and possibly indicates a secretory role for this portion of the duct system. Additionally, Mallory triple connective tissue stain reveals that the cells of this transitory region contain large, red granules. In comparison, only a few granules are found in the basal (striated) cytoplasm of the striated cells. Approximately 30 per cent of the cells comprising the striated duct system lack basal striations, are totally PAS negative, and have small, heterochromatic nuclei. These cells correspond to the "dark cells" that have been described by electron microscopy (see section on ultrastructure).

The interlobular ducts are characterized by an increased luminal diameter and a decrease in cell volume. The cells of these ducts are nearly cuboidal and have a centrally placed, moderately heterochromatic nucleus. The cytoplasm is strongly acidophilic (with H&E), nonreactive to PAS, and uniformly brown with Masson's trichrome. When stained with Mallory triple, the cytoplasm is pale gray and contains numerous large, round, red granules.

Submandibular.—The lobules of the submandibular gland are densely packed with compound tubular secretory acini of moderate size (Figs. 41, 47). Most of the acini are comprised of serous cells with a mucous demilune, but some acini appear to be entirely mucous. These latter acini comprise approximately five to 10 per cent of the total acinar population. The relatively small, round nuclei of the serous cells are heterochromatic and basally restricted (Fig. 47). The small nuclei of the mucous cells are more euchromatic and basally restricted.
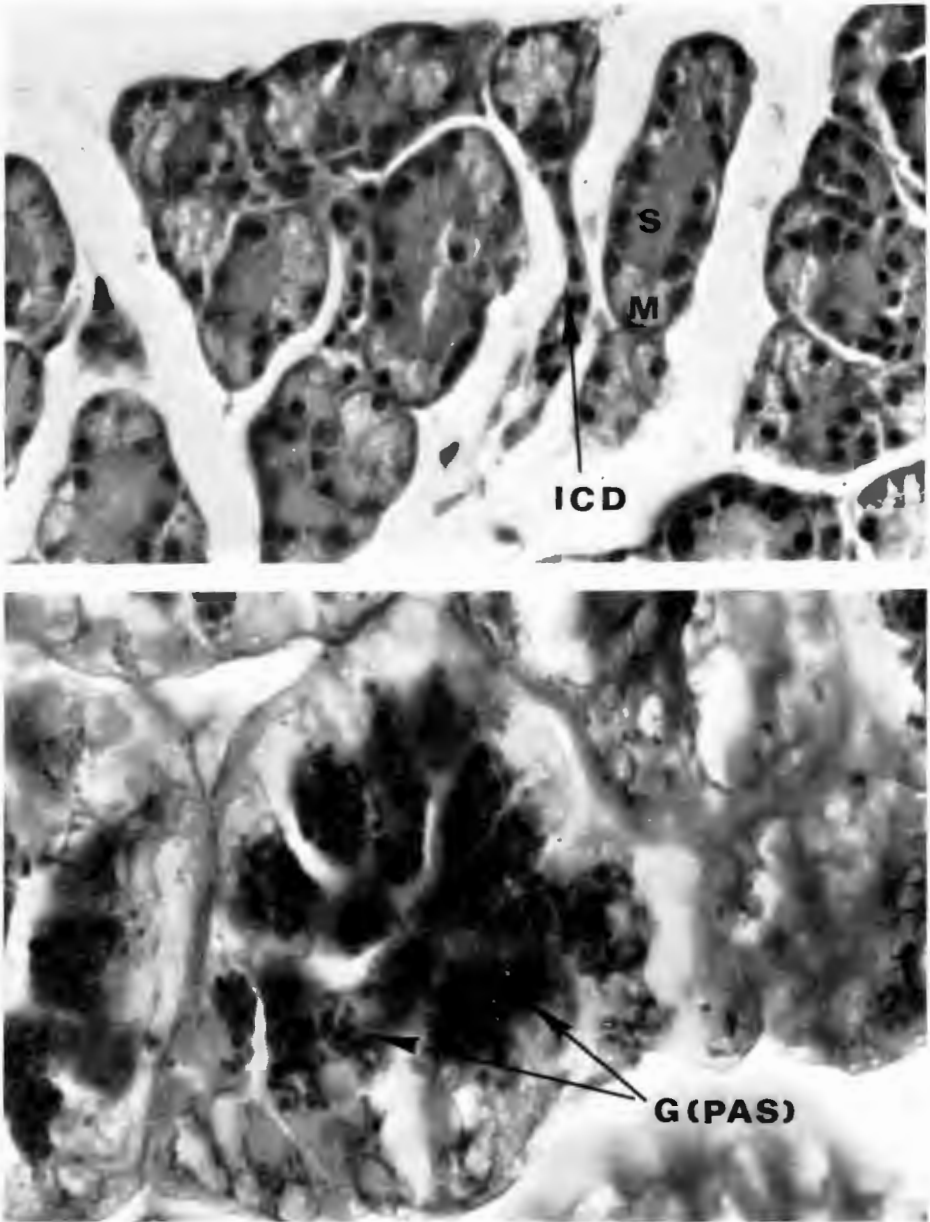
FIG. 47.—*Top*: Mixed serous (S) and mucous (M) secretory acini and intercalated duct (ICD) in the submandibular of *Glossophaga soricina.* Hematoxylin and eosin-Y. 580×. *Bottom*: PAS-positive secretory granules (G) in serous cells of the submandibular of *Glossophaga soricina.* 1972×.

When stained with H&E, the cytoplasm of these latter cells is pale gray, almost achromatic, whereas that of the serous cells is dense and strongly basophilic. When the PAS technique is employed, the serous cells are packed with large, strongly reactive, round granules (Fig. 47). The cytoplasm of the demilunar cells, on the other hand, is characterized by irregularly shaped clear areas outlined by a fine, reticular network that is moderately PAS positive. This network stains dark purple when oxidized prior to staining with aldehyde-fuchsin (this staining reaction is the only overlap with PAS in the submandibular). When Mallory triple is used, the serous cells are pale pink and contain from one to four large, red granules each. The mucous cells, on the other hand, are essentially nonreactive. With Masson's trichrome, the cytoplasm of the serous cells is pale green and that of the demilunar cells is nonreactive.

All four main lobes of this gland are histologically identical. The lobules of each lobe are characterized by an extensive system of ducts. The branched intercalated ducts are comprised of medium-sized cuboidal cells with ovoid nuclei; the reduced cytoplasm is strongly acidophilic (Fig. 47). The system of intercalated ducts is extensive and the ducts are relatively long; in many small sections of lobules, only a few striated but many intercalated ducts are found.

The transition from intercalated to striated ducts is abrupt (Fig. 40). The striated cells have large, round, apically displaced nuclei that are relatively euchromatic. The striated portion of the cytoplasm is intensely acidophilic, whereas that of the apical region usually is somewhat paler in cells stained with H&E. A narrow band of apical cytoplasm adjacent to the lumen of the duct is PAS positive. Additionally, when these cells are oxidized and stained with aldehyde-fuchsin, this area of the cytoplasm is pale purple. With Masson's trichrome the cytoplasm is green in the striated region and pale green in the apical region adjacent to the lumen. The striated cells are essentially nonreactive with Mallory triple connective tissue stains. The transition from striated to interlobular ducts is gradual; the nuclei become more centrally located and the basal striations are lost. The cells remain columnar but become slightly smaller; the luminal diameter increases slightly. As in the parotid, about 30 per cent of the cells comprising the striated ducts can be identified as dark cells with the light microscope. They have small, heterochromatic nuclei and are PAS negative.

The cells of the interlobular ducts are nearly cuboidal; the nuclei are more heterochromatic than are the nuclei of the striated cells and are centrally located. The cytoplasm is strongly acidophilic, nonreactive to PAS, and pale green with Masson's trichrome. The luminal diameter of the ducts is considerably greater than that of the striated ducts.

Sublingual.—The secretory acini of the sublingual are of the compound tubular type and are comprised of cells that have the classical mucous characteristics when stained with hematoxylin and eosin-Y. The small, round, heterochromatic nuclei are basally restricted (Fig. 46). In our formalin-fixed materials, these secretory cells were found to contain small, irregularly shaped, PAS positive granules. With Masson's trichrome, the secretory cells have dark brown cytoplasm, which is restricted to the area of the nucleus; the remainder of the cytoplasm of

these cells has small, dark granules and a faint reticular network. The sublingual gland is essentially nonreactive when oxidized with peracetic acid and stained with aldehyde-fuchsin.

All lobules of this gland are histologically identical. The duct system is only moderately developed. The branched intercalated ducts, which are not easily seen, are comprised of small, cuboidal cells with heterochromatic, round, centrally placed nuclei (Fig. 46). The limited cytoplasm is only moderately acidophilic. Small PAS-positive granules are found in the intercalated duct cells adjacent to the secretory acini. The transition between intercalated and striated ducts is abrupt. Within each lobule, the majority of the ducts can be classified as striated. The moderately heterochromatic nuclei are located adjacent to the lumen in the large, columnar, striated cells; the basal striated portion of the cytoplasm is strongly acidophilic (Fig. 46). The striated cells are nonreactive to PAS and are uniformly dark brown when stained with Masson's trichrome. Approximately 30 per cent of the cells in these ducts are small, somewhat cuboidal, lack basal striations, and have heterochromatic nuclei. The transition from the striated ducts to the interlobular (excretory) ducts is gradual and marked only by an increase in luminal diameter and slight decrease in cell height. The nuclei of cells of the interlobular ducts are slightly smaller and more heterochromatic than those of the striated cells. The tinctorial properties, however, are essentially the same for these cells as for the striated cells, at least with the procedures employed by us. Additionally, the basement membrane of the interlobular ducts is consistently thicker and more fibrous than that of the striated ducts.

Leptonycteris sanborni

Gross Anatomy

Parotid.—This is a moderate-sized gland that extends from the lambdoidal region of the skull around the auricle, and anteriorly until it overlies the posterior margin of the masseter (Fig. 39). Stenson's duct arises from the anterior border of the gland, passes across the masseter and anteriorly enters the connective tissue of the upper lip before entering the oral cavity near the upper canines.

Submandibular.—This is a moderate-sized gland consisting of three to four compact lobes (Fig. 39). The posterior most lobe is the largest; it lies between the sternomastoideus and the external jugular vein. The anterior lobes of this gland are flattened and ovoid and cover the sublingual gland. Wharton's duct arises from the posterior most lobe and passes along the inferior surface of the anterior lobes receiving branches from each. From the anterior margin of the gland, the duct passes over the dorsal surface of the digastricus and joins with the duct from the sublingual gland in the region of the angle of the mandible. These two ducts run together along the floor of the oral cavity and enter the mouth at a point directly posterior to the mandibular symphasis, under the sublingual flap.

Sublingual.—In *Leptonycteris sanborni*, the sublingual is a moderate-sized gland that is triangular in outline (Fig. 39). It is located at the angular process of the mandible; the lateral edge lies against the digastricus, and the medial side

extends under the lateral margin of the sternohyoideus. The anterior half of the gland is covered by the mylohyoideus. Posteriorly, the gland extends to the mastoid region of the skull and is covered there by the relatively wide sterno-mastoideus. The duct arises from the anterior margin of the gland and joins Wharton's duct of the submandibular, as described above.   ·

Histology

Parotid.—In this species, the parotid is a compound acinar gland; the secre-tory acini are relatively small but numerous and, thus, densely packed (Fig. 40). The secretory cells best approximate the seromucoid type. They contain large, round, basally positioned nuclei that are moderately heterochromatic (Figs. 48, 49). The nuclei are surrounded by dense, basophilic cytoplasm; the remainder of each cell is characterized by achromatic vacuoles of varying sizes. These are outlined by basophilic trabeculae that also are PAS positive (Fig. 48). The secretory cells are essentially nonreactive to Masson's trichrome and Mallory triple connective tissue stains. Round, PAS-positive granules are found in many secretory acini at the junction with the intercalated ducts. Although myoepithe-lial cells presumably are found in all salivary glands, they are especially obvious in the parotid of this species (Fig. 50).

The lobules of the parotid are characterized by an extensive duct system com-prised of relatively complex cells. The intercalated ducts are long and highly branched. The distal cells (adjacent to the acini) are large, elongate or rectangu-lar, and have large, ovoid, moderately euchromatic nuclei. The cytoplasm ap-pears to be only slightly acidophilic with hematoxylin and eosin-Y; small, round PAS-positive granules often are found in the apical cytoplasm (Fig. 40). Ad-ditionally, some granules also are visible within the lumen. After oxidation with peracetic acid, these granules stain dark purple with aldehyde-fuchsin (Fig. 50). The majority of cells in the intercalated ducts are flat, have heterochromatic nuclei, and are PAS negative.

The transition from intercalated to intralobular ducts is abrupt (Fig. 40). The distal segment of the latter is comprised of large, columnar cells and has a narrow lumen that generally contains PAS-positive material (Figs. 48, 49). The cytoplasm is only slightly acidophilic (with hematoxylin and eosin-Y); large, round, euchromatic nuclei are apically positioned and the basal one-half of the cells have the characteristic striations. The striated cells are only weakly reactive to Masson's trichrome; the cytoplasm has a pale rust-brown color. With Mal-lory triple the cytoplasm is pale pink, and with peracetic acid and aldehyde-fuchsin it is achromatic. The apical cytoplasm has an achromatic vacuole that is readily apparent when stained with hematoxylin and eosin-Y (Fig. 49). When examined with oil immersion optics, following staining with hematoxylin, eosin-Y, and PAS, extremely fine trabecular PAS-positive network within the vacuole is observed. When stained with Masson's trichrome, only the basal (striated) portion of the cytoplasm is reactive, being pale rust-brown. This same area of the cytoplasm is weakly acidophilic with hematoxylin and eosin-Y. Cells comprising the proximal portion of the duct system lack the apical vesicle;
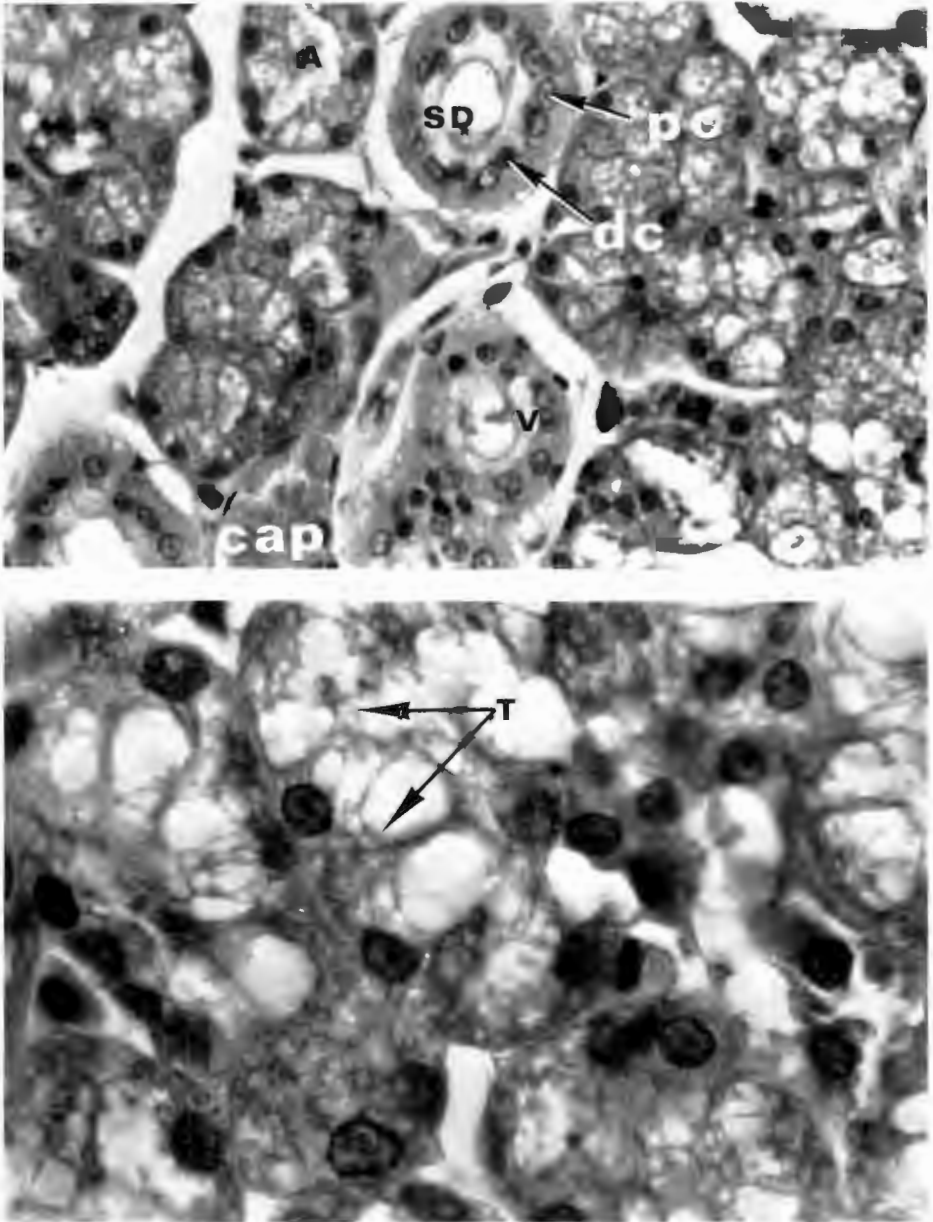
FIG. 48.—Seromucoid secretory acini and striated ducts in the parotid of *Leptonycteris sanborni*. Abbreviations are: A, acinus; cap, capillary; dc, dark cell; SD, striated duct; T, trabeculae of cytoplasm. Hematoxylin and eosin-Y. Top, 610×; bottom, 2140×.
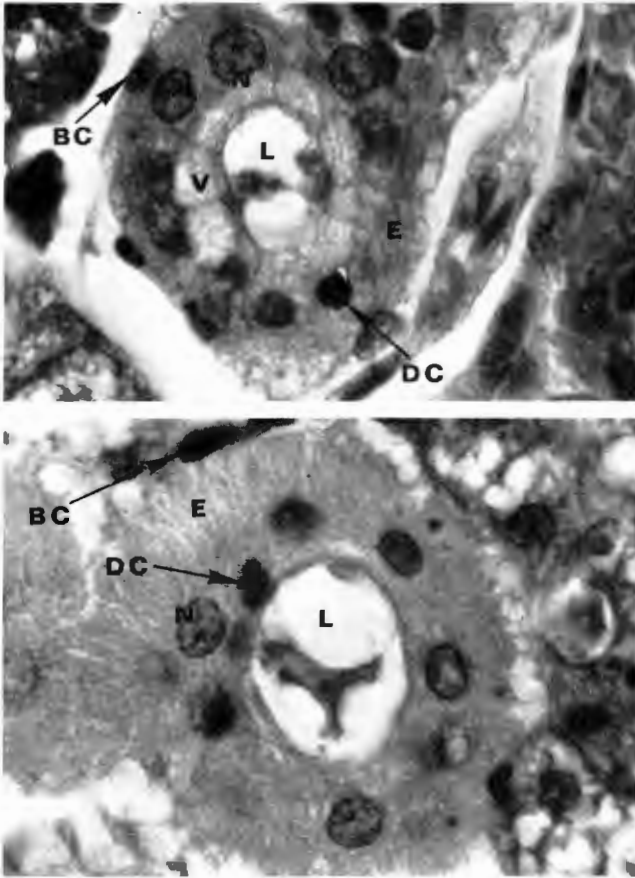
FIG. 49.—*Top*: Distal segment of striated duct in parotid of *Leptonycteris sanborni*. *Bottom*: Proximal segment of the same duct as shown above. Abbreviations are: BC, basal cell; DC, dark cell; E, ergastoplasm; L, lumen; N, nucleus; V, apical vesicle. Hematoxylin and eosin-Y. Both are 1720×.

their nuclei are somewhat more apical in position (Fig. 49). Approximately 30 per cent of the cells comprising the striated ducts can be identified as dark cells (Figs. 48, 49). They are somewhat smaller than the striated cells, have heterochromatic nuclei, and are PAS negative.

In the gradual transition to the more typical excretory ducts, the cells become less and less columnar (until they nearly are cuboidal) and consequently the luminal diameter increases considerably. The basal striations are lost, as is the apical achromatic vacuole, and the nuclei become more nearly ovoid. The staining reactions of the cells generally are the same as those of the striated cells, at least with the procedures used in this study.

Submandibular.—The submandibular is a mixed compound acinar gland; the secretory acini are complex, numerous, and densely packed (Fig. 41). Two types of secretory cells are found; one, a serous type, is uncommon, representing
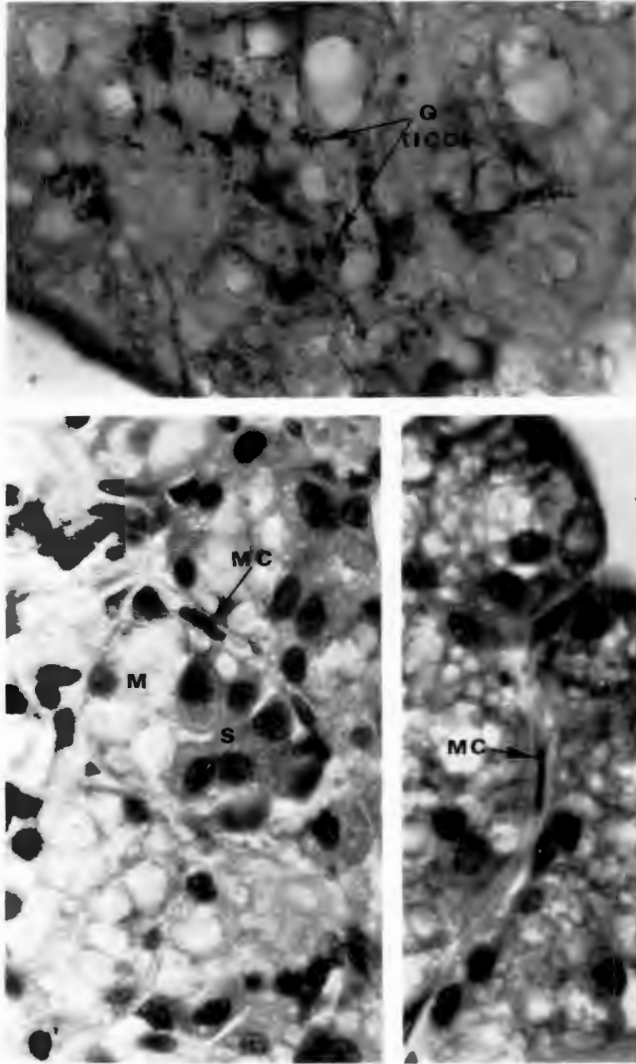
Fig. 50.—*Top*: Reactive secretory granules (G ICD) in the distal portion of the inter-calated duct in a parotid of *Leptonycteris sanborni*. Peracetic acid and aldehyde fuchsin. 888×. *Lower left*: Mixed secretory acini in the submandibular of *L. sanborni*. Abbreviations are: M, mucous cells; S, serous cells; MC, myoepithelial cell nucleus. Hematoxylin and eosin-Y. 1184× *Lower right*: A myoepithelial cell (MC) covering the surface of a secretory acinus in *L. sanborni*. Hematoxylin and eosin-Y. 1184×.

only about 10 per cent of the total number of secretory cells and is lacking from most secretory acini. Generally, these cells are clearly columnar and have large, heterochromatic nuclei that are basally restricted. These cells can best be de-scribed as serous when stained with hematoxylin and eosin-Y or azure-A and eosin-B (Fig. 50). The cytoplasm appears to be uniformly and densely baso-

philic with hematoxylin and eosin-Y, but with azure-A and eosin-B, the basal region is more distinctly basophilic than the apical cytoplasm. The latter contains numerous PAS-positive granules that are nonreactive to aldehyde-fuchsin after oxidation with peracetic acid. Additionally, the cytoplasm of these secretory cells stains rust-brown with Masson's trichrome and is nonreactive with Mallory triple. The remainder (about 90 per cent) of the secretory cells have round, basally restricted nuclei surrounded by a small amount of basophilic cytoplasm (hematoxylin and eosin-Y and azure-A and eosin-B). Most of the cytoplasm contains large vacuoles outlined by basophilic trabeculae and is thus similar in appearance to the almost achromatic mucous cells (Fig. 50). The trabeculae are PAS positive and also stain dark purple with aldehyde-fuchsin following oxidation with peracetic acid. The mucous cells are nonreactive to Masson's trichrome and Mallory triple.

Submandibular lobules are characterized by an extensive system of ducts. Generally, however, the cells of each portion of the duct system are relatively simple. The intercalated ducts are short, branched, and comprised of small, cuboidal cells with round, heterochromatic nuclei. The limited cytoplasm is weakly basophilic with hematoxylin and eosin-Y and lacks PAS-positive granules. Peracetic acid aldehyde-fuchsin, Masson's trichrome, and Mallory triple also are nonreactive.

The intercalated ducts open abruptly into the striated ducts, which are comprised of large, columnar and moderately acidophilic (with hematoxylin and eosin-Y) cells. These cells have large, apical, euchromatic nuclei, and basal striations. The striated cells are nonreactive to PAS, with exception of a narrow band of apical cytoplasm. The cytoplasm of the striated cells is rust-brown with Masson's trichrome and pale red with Mallory triple. After oxidation with peracetic acid, small, round granules that stain dark purple with aldehyde-fuschsin are found in the apical portion of many striated cells. Approximately 20 per cent of the cells comprising this portion of the duct system can be classified as dark cells. They have small, heterochromatic nuclei and are positioned adjacent to the lumen. The transition between striated and excretory ducts is gradual, being characterized only by a decrease in cell height and increase in luminal diameter. The excretory duct cells are cuboidal and have more nearly ovoid nuclei than are present in the striated cells. The general staining reactions of the cells of the excretory ducts are the same as those of the striated cells, at least with the techniques used by us.

Sublingual.—The secretory acini of the sublingual are compound tubular. They are relatively large, branched, and loosely packed and are comprised completely of mucous cells (Figs. 51, 52). The secretory cells have small, round or sometimes flattened nuclei that are heterochromatic and restricted to the basal portion of the cells (Fig. 51). The nucleus generally is surrounded by a small amount of basophilic cytoplasm (Fig. 52), whereas the remainder of the cell is pale, almost clear. Examination with oil immersion (1500×) reveals a dense but fine trabecular network (hematoxylin and eosin-Y) that probably represents the restricted cytoplasm between secretory vacuoles (Fig. 52). With
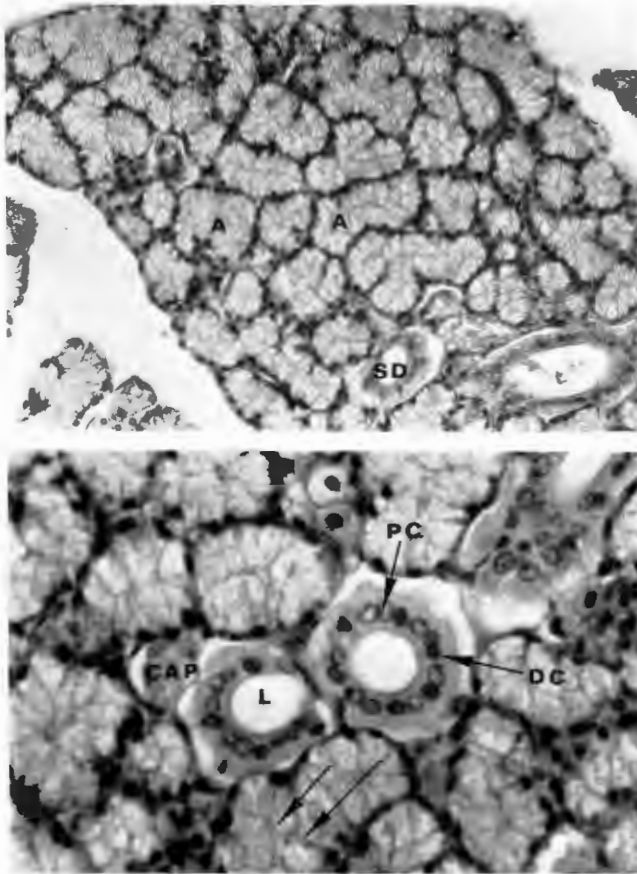
FIG. 51.—*Top*: General histology of mucous sublingual gland of *Leptonycteris sanborni*. *Bottom*: Striated ducts and well-defined lumina (arrows) in secretory acini in the same gland as shown above. Abbreviations are: A, acini; cap, capillary; L, lumen of striated duct; dc, dark cell; pc, pale striated cell; SD, striated duct. Hematoxylin and eosin-Y. Top, 170×, bottom, 481×.

PAS, the basal cytoplasm of these cells is strongly reactive, whereas the remainder has a moderately reactive granular appearance and strongly reactive trabeculae. Aldehyde-fuchsin following oxidation with peracetic acid produces essentially the same staining reaction. The secretory cells are nonreactive to Masson's trichrome and Mallory triple connective tissue stains. The sublingual gland has a moderately extensive, but relatively simple, duct system. The intercalated ducts are long, branched, and comprised of elongate or rectangular cells that have large, ovoid, nearly euchromatic nuclei (Fig. 52). The limited cytoplasm of these cells is only slightly acidophilic (hematoxylin and eosin-Y); the apical cytoplasm varies from slightly to strongly PAS reactive. The cells are nonreactive to aldehyde fuchsin following oxidation with peracetic acid, as well as Masson's trichrome and Mallory triple connective tissue stains.
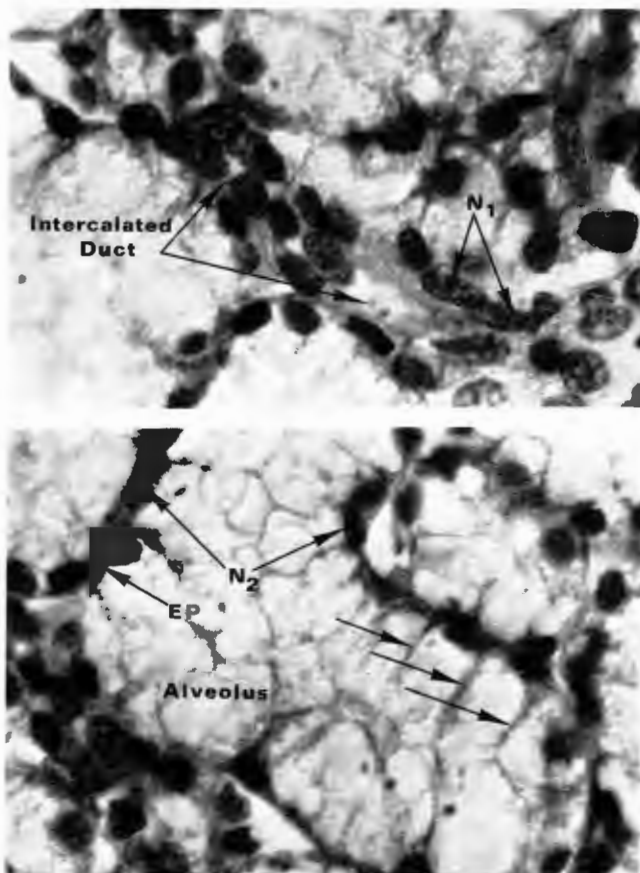
FIG. 52.—Composite histological views of a sublingual gland in *Leptonycteris sanborni*. The large, euchromatic nuclei (N_1) of intercalated duct cells can be compared with the smaller, heterochromatic nuclei (N_2) of the mucous cells. The basal cytoplasm of the mucous cells is characterized by a distinct ergastoplasm (EP), whereas the remainder of the cytoplasm is dense (arrows) but greatly restricted by secretory granules and is, therefore, trabecular in appearance. Hematoxylin and eosin-Y. Both figures are 1184×.

The intercalated ducts open abruptly into striated ducts comprised mainly of large, relatively narrow, columnar cells with round, euchromatic, apically displaced nuclei (Fig. 51). The cytoplasm is only weakly acidophilic with hematoxylin and eosin-Y and nonreactive with the PAS technique. These cells stain pale green with Masson's trichrome and pale pink with Mallory triple. They are nonreactive to peracetic acid aldehyde-fuchsin. The transition to interlobular ducts is gradual and characterized by a decrease in cell height and increase in luminal diameter. Although the nuclei become more nearly ovoid, the basal striations are not lost. Indeed, the striations are found even in the cuboidal cells comprising the interlobular ducts.

Leptonycteris nivalis

Gross Anatomy

Parotid.—This is a moderate-sized, elongate gland extending from the angle of the jaw to the posterior side of the ear. The parotid is separated from the main mass of the submandibular by the external jugular. Stenson's duct arises from the inferior surface of the anterior end of the parotid and runs across the masseter into the connective tissue of the upper lip. It enters the oral cavity in the region of the upper canines.

Submandibular.—This is a large gland, consisting of a series of six or seven main lobes, each of which is extensively subdivided. All but one of these ovoid, flat lobes are arranged, one behind the other, along the external jugular. The most posterior lobe is located dorsally to the external jugular, directly posterior to the parotid. The submandibular extends from the base of the neck anteriorly to the angle of the jaw; it covers portions of the sternomastoideus muscle and the sublingual gland. The main ducts of the various lobes join and leave the submandibular gland on the inferior surface of the most anterior lobe. Wharton's duct passes dorsal to the digastricus, in the region of the angle of the mandible, and is joined by the main duct from the sublingual. The two ducts together enter the anterior portion of the oral cavity.

Sublingual.—This gland is large, triangular, and unilobular but finely subdivided. It is located at the angle of the jaw, bordered laterally by the digastricus. Medially, the gland extends to the lateral margin of the sternohyoideus muscle. The posterolateral edge of the sublingual extends to the mastoid region of the skull, where it is covered by the sternomastoideus muscle. The main duct from this gland joins with that of the submandibular (see above).

Histology

Parotid.—The parotid is a compound acinar gland that is characterized by small, round secretory acini (Fig. 40). As in *Leptonycteris sanborni*, the secretory cells are of the seromucoid type. They are triangular in shape and have moderate-sized, somewhat ovoid, heterochromatic nuclei that are basally positioned. The nuclei are surrounded by dense, basophilic cytoplasm; the remainder of the cytoplasm is trabeculated, although basophilic granules can be distinguished with oil immersion (1500 ×, stained with hematoxylin and eosin). The trabeculae are intensely PAS positive but are essentially nonreactive to both Masson's trichrome and Mallory triple connective tissue stain.

The lobules of this gland are characterized by an extremely extensive and complex system of ducts. The intercalated ducts, which are unusally long and branched (Fig. 53), are difficult to distinguish in sections stained only with hematoxylin and eosin. The intercalated duct cells are large and rectangular and have large, round, centrally placed nuclei that are euchromatic. The size of the nuclei in conjunction with the limited amount of cytoplasm and its almost achromatic appearance with H&E account for this difficulty. With PAS or aldehyde-fuchsin following oxidation with peracetic acid, the extensive, winding
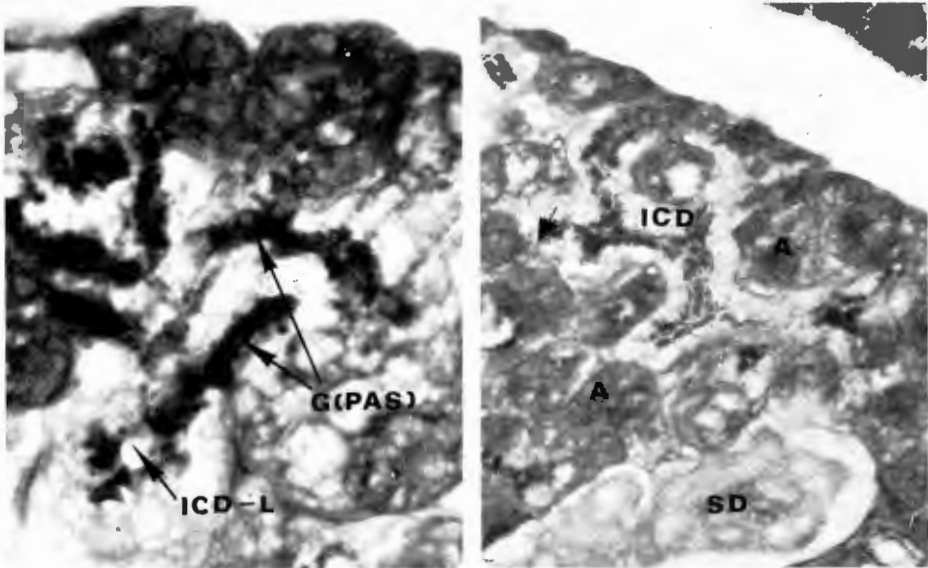
FIG. 53.—Two histological views of the highly developed, branched, secretory intercalated duct system in the parotid of *Leptonycteris nivalis*. Large numbers of PAS-positive granules can be seen in the apical cytoplasm of these cells. Abbreviations and symbols are: A, acinus; ICD, intercalated duct; ICD-L, lumen of intercalated duct in cross-section; G(PAS), PAS-positive granules; SD, striated duct; arrow, junction between ICD and acinus. Periodic-acid Schiff's. Right, 1044×, left, 392×.

course of the intercalated ducts can be recognized because of the presence of positive staining granules in both the apical cytoplasm and lumen of the duct (Fig. 53). One to three cells are positioned between the secretory intercalated ducts cells and the abrupt beginning of the striated ducts. The former cells are PAS negative, have heterochromatic nuclei, and are more nearly cuboidal than rectangular.

The striated cells are large and columnar; they are slightly basophilic and only weakly acidophilic (hematoxylin and eosin-Y). The nuclei are centrally placed, large, round, and euchromatic. With PAS, the cytoplasm reacts faintly, giving the cell a pinkish cast. The only exception is a narrow band along the apical membrane, which is moderately reactive. The striated ducts are comprised of approximately 30 per cent dark cells, which can be recognized by their small heterochromatic nuclei and proximity to the lumen. The striated ducts give way gradually to interlobular ducts, which are characterized by reduced cell size, loss of basal striations, increased luminal diameter and decrease in number of dark cells.

Submandibular.—The submandibular is a compound tubuloacinar gland; the secretory acini are relatively large and densely packed within the lobules of the gland (Fig. 41). The acini are comprised of two types of secretory cells; the most abundant type has a dense, basophilic (hematoxylin and eosin-Y) cytoplasm, whereas the second type, which forms a demilune, has a pale, almost achromatic
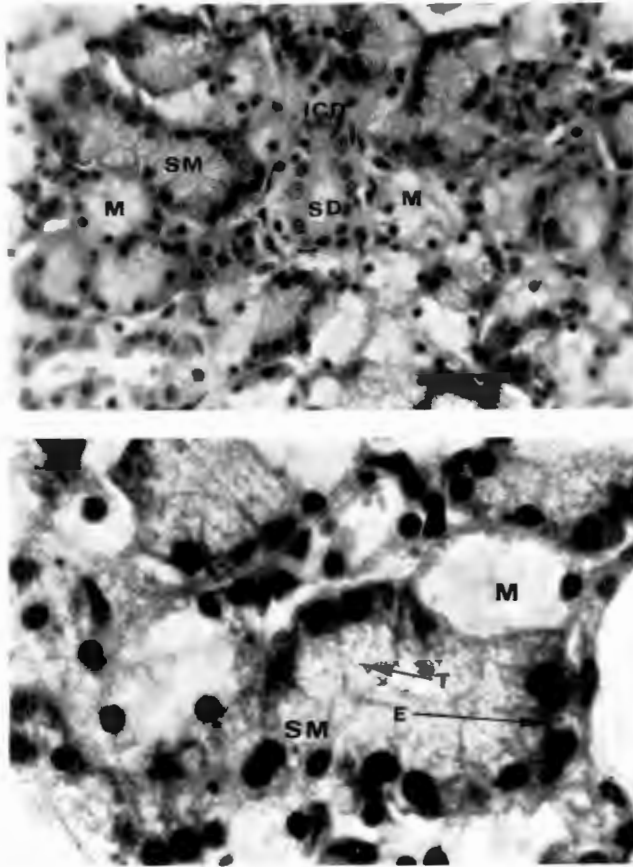
FIG. 54.—*Top*: Histological overview of submandibular in *Leptonycteris nivalis*, showing mixed secretory acini. Abbreviations are: ICD, intercalated duct; M, mucous cells; SD, striated duct; SM, seromucoid cells; Hematoxylin and eosin-Y. 494×. *Bottom*: Detail of seromucoid and mucous cells; note the trabeculae (T) and dense ergastoplasm (E) in the seromucoid cells. Hematoxylin and eosin-Y. 1140×.

cytoplasm (Fig. 54). The first type of cell approximates the classical serous cell and the demilunar kind is essentially a mucous type. The basophilic serous cells have a moderate-sized, round, basally located nucleus that is fairly hetero-chromatic. The cytoplasm, when stained with hematoxylin and eosin-Y and observed with oil immersion optics (1500×), is uniformly stained but appears to contain many small vacuoles (or pale granules) of varying size. With PAS, these granules are essentially nonreactive, although the cytoplasm is faintly pink and coarsely granular in appearance (Fig. 54). The mucous cells have smaller, more hererochromatic nuclei that are basally positioned and surrounded by a small amount of basophilic cytoplasm. The cytoplasm of the mucous cells contains a trabecular network that is intensely PAS positive. With Masson's trichrome the cytoplasm of the serous cells is pale gray and that of the mucous cells is essentially achromatic.

The submandibular duct system is moderately extensive and comprised of relatively simple cells. The intercalated ducts are long and branched; the cells are cuboidal and have round, heterochromatic nuclei that are centrally placed (Fig. 54). The limited cytoplasm is only moderately acidophilic (hematoxylin and eosin-Y) and nonreactive to PAS. The lumina of these ducts also lack PAS-positive material. Aldehyde-fuchsin following oxidation with peracetic acid also is nonreactive. The cells of the intercalated ducts are only slightly stained (pale gray) with Masson's trichrome and are nonreactive with Mallory triple connective tissue stain.

The intercalated ducts open abruptly into striated ducts (Fig. 54). The latter are comprised of large, columnar, striated cells that have large, round, centrally-placed euchromatic nuclei. The cytoplasm is only moderately acidophilic, staining pale pink with hematoxylin and eosin-Y only after prolonged immersion in eosin-Y. A narrow band of apical cytoplasm is moderately reactive to PAS in the striated cells. The same region stains purple with aldehyde-fuchsin after oxidation with peracetic acid. The striated cells are only slightly stained (pale gray) with Masson's trichrome; the basal (striated) portion of these cells stains deep red with Mallory triple connective tissue stains. Approximately 20 per cent of the cells comprising the striated ducts can be classified as dark cells. They have heterochromatic nuclei and are PAS negative and are adjacent to the lumen. The transition from striated to interlobular ducts is gradual and characterized mainly by a decrease in cell height and an increase in luminal diameter. The nuclei become slightly more ovoid, and the basal striations are lost. The apical reactivity to PAS and peracetic acid aldehyde-fuchsin found in the striated cells is lost in the transition. With Masson's trichrome, the cells of the interlobular ducts are pale gray, and, unlike the striated cells, the basal portion of these cells is nonreactive with Mallory triple connective tissue stains. Both kinds of cells are nonreactive to the peracetic acid aldehyde-fuchsin procedure.

Sublingual.—The general histology of the sublingual in this species is essentially the same as that of the same gland in *Leptonycteris sanborni.* The reader thus is referred to the description given in that account.

Anoura geoffroyi

Gross Anatomy

Parotid.—This is a moderate-sized gland located at the base of the auricle. It extends from the angle of the jaw, over a portion of the masseter muscle, to the auricle and, ventrally, to the mastoid region of the skull. This gland is separated from the submandibular by the external jugular vein. Stenson's duct arises from the anterior part of the parotid and runs anteriorly into the connective tissue of the upper jaw and enters the oral cavity at the level of the first premolar.

Submandibular.—This is a moderate-sized gland consisting of two main lobes, each of which is extensively subdivided. The gland lies on the mastoid region of the skull and is positioned in the cervical fossa along with two lobes of the sublingual. The anterior lobe of the submandibular is elongate in shape; it ex-

tends medially from near the external jugular and mastoid region and covers a portion of the sternomastoideus muscle. The posterior lobe, to which the anterior one is attached, extends from the lambdoidal region and covers the sternomastoideus and external jugular. Wharton's duct passes dorsally to the digastricus, posterior to the angle of the jaw, and joins the main duct of the sublingual. Together, these ducts pass anteriorly into the muscle and connective tissue of the floor of the mouth and open into the region of the mandibular symphasis.

Sublingual.—A relatively large gland that consists of three major lobes. One lobe occupies the typical site for this gland; it is positioned in a depression bordered by the sternohyoideus, sternomastoideus, and digastricus. This lobe is ovoid and flat and is overlain by two more lobes. The anterior one of these latter lobes is the largest; it is somewhat triangular in shape and has a convex anterior margin and a concave posterior margin. It is bordered by the parotid dorsally and the sternohyoideus ventrally. Posteriorly, within the concave margin, lies the last main lobe of the sublingual. It is elongate in shape and is bordered posteriorly by the submandibular gland. A short duct joins the posterior and anterior lobes and then passes anteriorly, ventral to the digastricus, and joins the main duct from the lobe first described. The common excretory duct has been described above.

Histology

Parotid.—The secretory acini are densely packed and of the compound acinar type (Fig. 40). When stained with hematoxylin and eosin-Y, the cells have a classical serous appearance. They have small, round, heterochromatic nuclei usually located basally and surrounded by a strongly basophilic cytoplasm (Fig. 55). These cells contain numerous small granules that can be seen easily when stained with H&E (formalin-fixed). The secretory cells are PAS negative and stain pale gray-brown with Masson's trichrome.

The numerous lobules of the parotid are connected by an extensive, complex system of ducts. The short, nonbranched intercalated ducts are comprised primarily of cuboidal cells with heterochromatic, round or slightly ovoid nuclei. The relatively small amount of cytoplasm is moderately acidophilic. The intercalated ducts are difficult to locate in any given section because of their short length, which does not exceed three or four cells at most. PAS-positive granules are lacking from these cells, although in many sections the most distal cells (at the junction with the secretory acinus) do appear to contain some PAS-positive material and also have euchromatic nuclei.

The transition between the intercalated and striated ducts is abrupt. The striated cells of the distal portion are typical in that the large round nucleus is euchromatic and located near the apical membrane of these large, columnar cells (Fig. 55). The cytoplasm is uniformly acidophilic and the lumen of this portion of the duct system is narrow. In sections stained with Masson's trichrome, the cytoplasm is pale green, and in those stained with the PAS technique, the cells are nonreactive. Staining with aldehyde-fuchsin following oxidation with peracetic acid also is negative. Relatively small, dark cells having hetero-
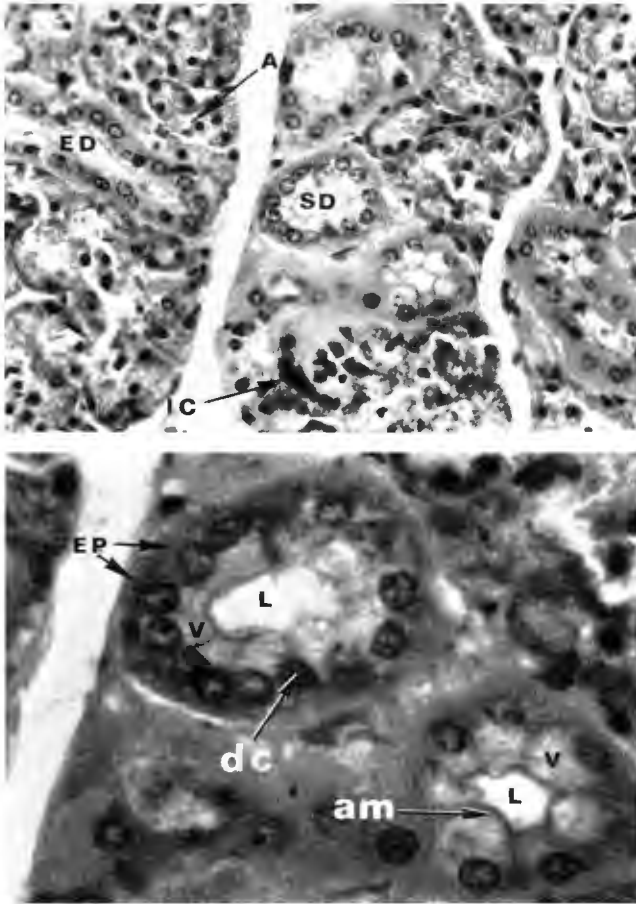
FIG. 55.—*Top*: Histological overview of the parotid in *Anoura geoffroyi*. Abbreviations are: A, acinus; ED, excretory duct; IC, intercalated duct; SD, striated duct. Masson's trichrome. 494×. *Bottom*: Portion of the striated duct apparently having a secretory function. Abbreviations are: am, apical membrane and adjacent cytoplasm; dc, dark cell; ep, ergastoplasm; l, lumen; v, apical "vesicle." Hematoxylin and eosin-Y. 1140×.

chromatic nuclei are found throughout the striated duct system and comprise as many as 30 per cent of the total number of cells. The proximal portion of the striated duct is characterized by striated cells that apparently are secretory. These large, columnar cells have large, round euchromatic nuclei that are centrally positioned (Fig. 55). The basal cytoplasm around the nucleus is strongly acidophilic and striated, whereas the apical cytoplasm is slightly basophilic (H&E). Although easily distinguished, the pale basophilic portion of the cytoplasm does not form a distinct vesicle (Fig. 55). In sections stained with Masson's trichrome, the basal cytoplasm is green, whereas the apical cytoplasm is pale, nearly achromatic. The entire cell is, however, nonreactive to PAS.

The cells of the excretory ducts are nearly cuboidal, have round, centrally placed, somewhat heterochromatic nuclei, and lack basal striations. The cyto-

plasm is strongly acidophilic when stained with hematoxylin and eosin-Y and pale green when stained with Masson's trichrome. Additionally, these cells are nonreactive to PAS. On the other hand, a considerable amount of PAS-positive material typically is found in the lumen of this portion of the duct system.

Submandibular.—The submandibular is a compound tubuloacinar gland that is densely packed with small, round secretory acini (Fig.41). Two types of secretory cells can be distinguished easily with standard stains. Both have the appearance of being serous cells when stained with hematoxylin and eosin-Y. The secretory cells (Fig. 56) that surround the acinar lumen are large, essentially rectangular or slightly triangular, and have nearly euchromatic nuclei. The cytoplasm has a uniform, finely granular appearance (H&E). These granules are moderately PAS positive. The second type of secretory cell is relatively small and flat but numerous enough to form a cap over the entire secretory acinus (Fig. 56). These cells are basophilic and generally resemble the special serous cells described elsewhere by Wilborn and Shackleford (1969). The nuclei are small, round, basally positioned, and heterochromatic. When stained with the PAS technique, the cytoplasm is generally reactive and appears to contain large numbers of small secretory granules. The outer layer of special serous cells stains uniformly green with Masson's trichrome, whereas the inner secretory cells are green, but distinctly paler.

The duct system of the submandibular is of moderate length and of relatively simple morphology. The intercalated ducts are of moderate length, branched, and comprised of small cuboidal cells with round, centrally placed heterochromatic nuclei. The cytoplasm is restricted but clearly acidophilic with hematoxylin and eosin-Y. These cells are PAS negative and essentially nonreactive to Masson's trichrome.

The transition between intercalated and striated ducts is characteristically abrupt. Judging from the relative paucity of striated ducts in any given section, this portion of the duct system apparently is short. The major type of cell is large and columnar and has a large, round, centrally placed euchromatic nucleus (Fig. 56). Basal striations are easily discernible; the cytoplasm is typically acidophilic with hematoxylin and eosin-Y. The striated cells are nonreactive to PAS and stain pale green with Masson's trichrome. Approximately 10 per cent of the cells in the striated portion of the duct can be classified as dark cells, judging from their small and heterochromatic nuclei and proximity to the duct lumen. The transition from striated to interlobular (excretory) ducts is gradual and characterized by an increase in luminal diameter, a decrease in cell height, and eventual loss of basal striations.

Sublingual.—The numerous lobules of this gland have a moderate duct system comprised of relatively simple cells. The short, branched, intercalated ducts are easily seen. The cells comprising these ducts are nearly rectangular and narrow except near the junction with the striated ducts where they appear to be somewhat more cuboidal. The heterochromatic nucleus is ovoid and occupies most of the cell. The small amount of cytoplasm is only moderately acidophilic (hematoxylin and eosin-Y) and nonreactive to PAS, Masson's trichrome, and Mallory
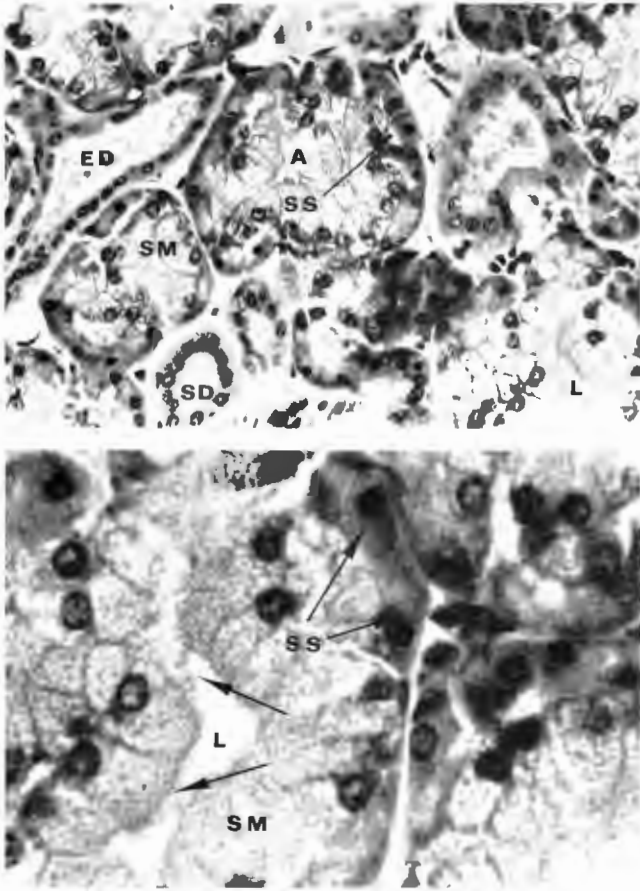
FIG. 56.—*Top*: Histological overview of submandibular of *Anoura geoffroyi.* Masson's trichrome. 481×. *Bottom*: Detail of a secretory acinus; note the extruded materials (arrows) at the apical membranes of the seromucoid cells. Abbreviations are: A, acinus; ED, excretory duct; L, lumen; SD, striated duct; SM, seromucoid cells; SS, special serous cells. Masson's trichrome. 1258×.

triple connective tissue stains. PAS-positive granules were not found in the lumina of intercalated ducts.

The secretory acini are of moderate density and compound tubular in nature. The secretory cells, when stained with hematoxylin and eosin-Y, have the classical mucous appearance; the cytoplasm is relatively clear although a fine trabecular network can be distinguished. The nuclei are small, round, and heterochromatic. They are basally located and typically surrounded by a small amount of basophilic (with hematoxylin and eosin-Y) cytoplasm. The trabeculae of the cytoplasm of these cells are intensely PAS positive. Furthermore, they stain dark purple with aldehyde-fuchsin following oxidation with peracetic acid. The cells are essentially nonreactive with Masson's trichrome and Mallory triple connective tissue stains.

The transition between the intercalated and striated ducts is abrupt. The striated cells of the latter are large and columnar and have large slightly ovoid euchromatic nuclei that are apically displaced. The cytoplasm is strongly acidophilic with hematoxylin and eosin-Y, nonreactive to PAS, and pale green with Masson's trichrome. Additionally, these cells stain intensely red with Mallory triple connective tissue stains. The transition from the striated to interlobular ducts is gradual and characterized by a decrease in cell height concomitant with an increase in luminal diameter and slight decrease in size of the nucleus. The basal striations are lost. The staining reactions of the cells of the interlobular ducts, with the techniques used in this study, were the same as those of the striated cells.

Sturnira ludovici

Gross Anatomy

Parotid.—The parotid is extremely large (Fig. 39), its ventral margin extends to the ventral midline of the throat and overlies the posterior half of the sublingual gland. Dorsally, the parotid extends around the cervical region and covers the area where the digastricus and sternomastoideus cross, posterior to the masseter. A small portion of the gland extends anteriorly between the auricle and masseter. The remainder of the glandular mass lies over the mastoid, lambdoidal, and occipital regions of the skull and extends into the cervical fossa where it is partially covered by the posterior half of the submandibular. Stenson's duct arises from the anterior edge of the parotid and runs along the ventrolateral surface of the masseter in a groove between the masseter and digastricus, following the contour of the masseter anteriorly and dorsally. The duct continues anteriorly in the connective tissue and muscle of the upper lip and enters the oral cavity at the level of the posterior side of the canines.

Submandibular.—This is a large gland that fills the cervical fossa from the lateral midline to the ventral midline of the throat in the region of the sternomastoideus (Fig. 39). The gland is triangular in cross section; its posterior surface lies against pectoral muscles and the inferior surface lies against the parotid gland. Wharton's duct arises from the center of the inferior surface, passes under the ventral margin of the parotid, over the dorsal surface of the digastricus in the region of the angle of the mandible. The duct runs along the floor of the oral cavity in the region of the ventrolateral margin of the tongue. It is joined by the main duct from the sublingual gland at the base of the tongue and together they enter the anterior part of the oral cavity, opening near the first lower premolar.

Sublingual.—This is a moderate-sized gland that is triangular in shape and soft and loosely encapsulated in thin sheets of connective tissue (Fig. 39). This gland is unilobular but its numerous fine subdivisions can be seen clearly. The anterior half of the gland is covered by the posterior margin of the mylohyoideus; the medial edge lies against the sternohyoideus and the lateral edge is in contact with the medial surface of the digastricus. The duct arises on the inferior surface and joins the main excretory duct of the submandibular near the base of the tongue (see above).

Histology

Parotid.—The parotid is a compound acinar gland that is densely packed with elongate secretory acini comprised of typical serous cells (Figs. 40, 57). These cells are basophilic with hematoxylin and eosin-Y; the cytoplasm appears to be finely granular when observed with oil immersion (Fig. 57). The nuclei of the secretory cells are basally positioned, small and round, and heterochromatic. Small, densely packed secretory granules can be distinguished in the apical cytoplasm when stained with the PAS technique (Fig. 58). At the same time, however, these granules are not stained with aldehyde-fuchsin following oxidation with peracetic acid. With Mallory triple connective tissue stain the cytoplasm contains relatively large red granules that apparently are not secretory product, judging from their size.

The parotid is characterized by an extensive system of ducts. The intercalated ducts are of moderate length, branched, and comprised of two distinct segments. Adjacent to the secretory acini, the intercalated duct cells are large and rectangular; the nuclei are euchromatic and the cytoplasm contains relatively large, intensely PAS-positive granules (Fig. 58). The remainder of the intercalated duct is comprised of rectangular or cuboidal cells with heterochromatic nuclei, restricted cytoplasm, and no trace of PAS-positive materials.

The transition from intercalated to striated ducts is abrupt (Fig. 57). The latter portion of the duct system is comprised of large columnar cells with centrally positioned euchromatic nuclei. The cytoplasm is acidophilic when stained with hematoxylin and eosin-Y. Intensely stained, PAS-positive granules are found in the apical cytoplasm of these cells. These granules also stain with aldehyde-fuchsin following oxidation with peracetic acid. Approximately 10 per cent of the cells in the striated ducts can be classified as dark cells based on their small and heterochromatic nuclei and absence of PAS-positive staining. The transition from striated to typical interlobular ducts is gradual and characterized by a decrease in cell height and eventual loss of basal striations.

Submandibular.—The submandibular is a compound tubuloacinar gland with large and densely packed secretory acini (Fig. 41). The majority of each acinus is comprised of narrow columnar serous cells with basally positioned and somewhat heterochromatic nuclei. The cytoplasm of these cells has a distinctly dense, basophilic basal region and a slightly paler but basophilic middle and apical portion (Fig. 59). The apical cytoplasm contains densely packed, small PAS-positive granules that also stain with aldehyde-fuchsin following oxidation with peracetic acid (Fig. 59). The demilunar secretory cells are of the mucous type; the nuclei are basally restricted and heterochromatic. The cytoplasm, with exception of a distinct basal ergastoplasm, is pale and somewhat trabecular when viewed with oil immersion (1500 $\times$). The vacuoles in the cytoplasm are PAS negative but the trabecular network, which presumably represents restricted cytoplasm between secretory granules, is PAS positive and reactive to aldehyde fuchsin peracetic acid (Fig. 59).

The duct system of the submandibular is relatively simple. The intercalated ducts are short and branched but are difficult to locate in any given section.
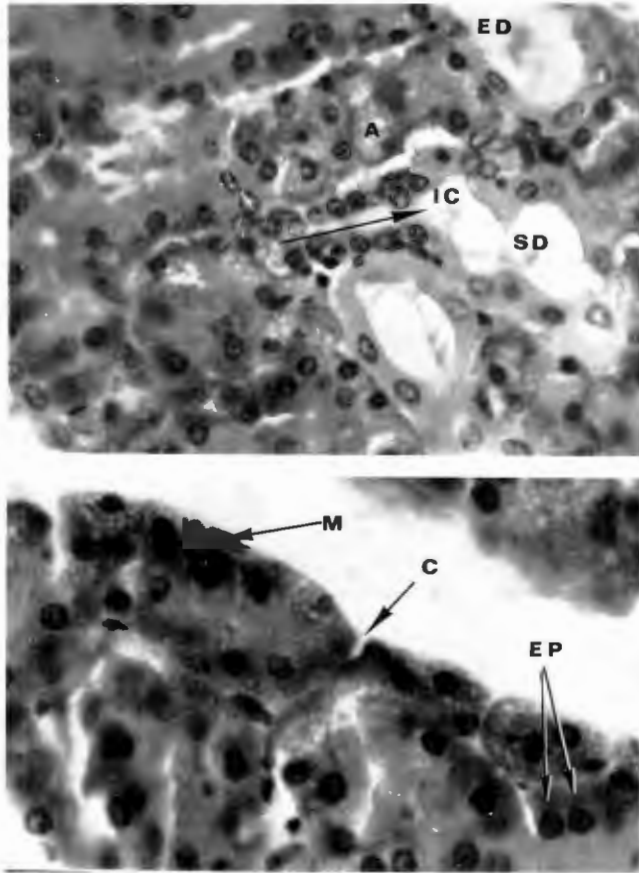
FIG. 57.—*Top*: Parotid salivary gland of *Sturnira ludovici*; the arrow shows direction of flow of formative saliva from an acinus (A) to the striated duct (SD) via the intercalated duct (IC). The other abbreviation is: ED, excretory duct. Hematoxylin and eosin-Y. 900×. *Bottom*: Parotid acini showing a myoepithelial cell (M), the thin connective tissue capsule (C), and distinct ergastoplasm (EP) of the secretory cells. Hematoxylin and eosin-Y. 1125×.

The cells are rectangular and have ovoid, heterochromatic nuclei and a limited amount of slightly acidophilic cytoplasm. The intercalated ducts are generally PAS negative although some of the cells occasionally have a slightly pinkish cast.

The transition to striated ducts is abrupt. The striated cells are columnar, have a centrally positioned, large, round, and euchromatic nucleus, and are PAS negative. These ducts are comprised of approximately 20 per cent dark cells characterized by heterochromatic nuclei. The interlobular duct can be recognized by the decrease in cell height, loss of basal striations in the major cell type, and an increase in luminal diameter.

Sublingual.—The sublingual is a compound tubuloacinar gland comprised of mucous cells. The secretory cells have basally restricted, irregularly shaped,
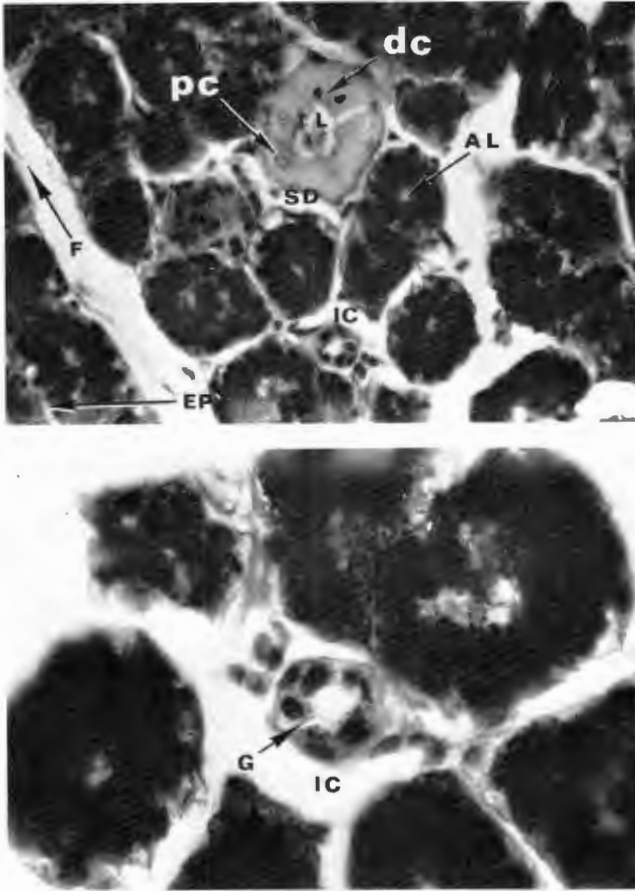
FIG. 58.—*Top*: PAS reactivity in the secretory acini of a parotid gland from *Sturnira ludovici*. Note the nonreactive ergastoplasm (EP) and striated duct (SD). Other abbreviations are: AL, acinar lumen; dc, dark cell; F, fibroblast; IC, intercalated duct; pc, pale striated cell. Periodic-acid Schiff's and hematoxylin and eosin-Y. 481×. *Bottom*: PAS-positive granules (G) in intercalated duct cells (IC). Periodic-acid Schiff's. 814×.

heterochromatic nuclei. The adjacent basal cytoplasm is fairly dense and baso-philic. The bulk of the cytoplasm is pale when stained with hematoxylin and eosin-Y and is highly vesiculated when viewed with oil immersion optics (1500×). The trabeculae are intensely PAS positive and also reactive to alde-hyde-fuchsin following oxidation with peracetic acid.

The duct system of the sublingual is relatively simple. The intercalated ducts are long and branched and comprised of flat or rectangular cells having little cytoplasm and ovoid or round heterochromatic nuclei. These cells show only slight reactivity to the PAS procedure. The junction between intercalated and striated portion of the duct system is abrupt. The latter is comprised of large, columnar cells with apically positioned, large, round and euchromatic nuclei. The cytoplasm is acidophilic (H&E) and PAS negative.
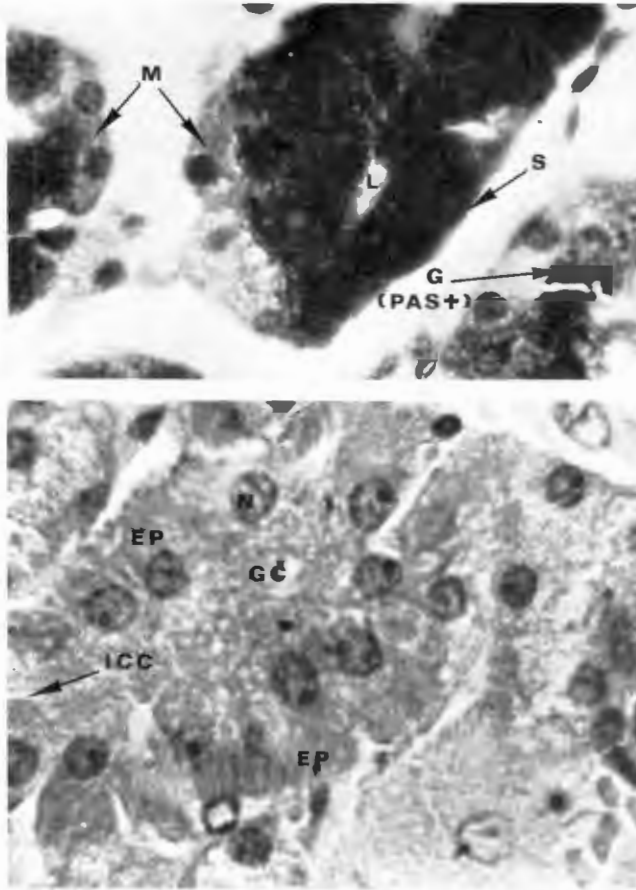
FIG. 59.—*Top*: PAS reactivity (G PAS+) in the serous cell (S) in the submandibular gland from *Sturnira ludovici*. Note the nonreactivity of the mucous cells (M) and the wide acinar lumen (L). Periodic-acid Schiff's and hematoxylin and eosin-Y. 988×. *Bottom*: Serous secretory cells, showing the granular apical cytoplasm (GC), euchromatic nucleus (N), striated basal ergastoplasm (EP). Note the distinct intercellular canaliculus (ICC). Hematoxylin and eosin-Y. 1596×.

Comparisons

Parotid and submandibular salivary glands are compared in the following paragraphs. We have not included the sublingual because of its conservative character. Our summary statements are based partly on our own observations and partly on Wimsatt (1955, 1956) and DiSanto (1960). Additionally, for ease of presentation we have compared species gland by gland rather than species by species.

Parotid.—As pointed out in the general results of gross anatomical examinations, the parotid gland varies considerably in size, degree of compactness, and, to a certain extent, in position in the aural region. None of these features was found to be related to the general histological characteristics of the gland. In

comparison to the other species, this gland is relatively large in *Artibeus*, where it extends into the interscapular region, and relatively small in *Desmodus*. Comparisons of size or appearance, or both, do not reveal any relationship with taxonomic grouping, at least insofar as we could determine.

The general histological features of the parotid vary as greatly as does the gross anatomy. The phyllostomatids studied thus far can be grouped relatively easily on basis of structural and tinctorial characteristics of the secretory acinar cells. In all seven species the parotid can be described best as compound acinar although the shape and size, as well as number, of secretory acini vary considerably. For example, in *Artibeus* and *Sturnira* the acini are elongated and nearly tubular, whereas in *Leptonycteris nivalis*, *L. sanborni*, and *Glossophaga* they are relatively small and nearly bulblike. In the other species, the parotid secretory acini are irregularly shaped, of moderate size, and more typically compound acinar.

As we have pointed out in the section on Materials and Methods, the terms serous, mucous, and seromucoid are used by us only guardedly and for purposes of description rather than on the basis of knowledge about chemistry of secretory product. In four species (*Glossophaga* sp., *Leptonycteris nivalis*, *L. sanborni*, and *Artibeus* sp.), the secretory cells have been described as seromucoid based on their relatively achromatic cytoplasm (when stained with either hematoxylin and eosin-Y or azure-A and eosin-B) and morphologically intermediate position. In the remaining species, the secretory cells have dense basophilic cytoplasm and are fairly representative of typical serous cells.

On the basis of characteristics discernible as a result of the methods used by us, comparisons allow for the following groupings. Three glossophagine species (*Glossophaga soricina*, *Leptonycteris nivalis*, and *L. sanborni*) are notably similar in both morphology (Fig. 40) and tinctorial characteristics. In each kind, the apical cytoplasm of the large, somewhat triangular secretory cells contain vacuoles of variable sizes that with the light microscope appear to be outlined by a PAS-positive trabecular network. The notable differences within this group are: 1) in *Glossophaga*, the PAS reaction is slightly more intense; and 2) the number (in terms of density) and size of the secretory alveoli are by far the greatest in *Glossophaga* and the least in *L. nivalis*. The parotid secretory acini of the fourth glossophagine species, *Anoura geoffroyi*, differ considerably from those of the others. The acini in this species are comprised of secretory cells that best can be described, as seen through the light microscope, as serous.

A second grouping includes *Sturnira* and *Desmodus*, in which the parotid secretory cells are notably similar. In both species the acini are irregularly shaped and somewhat tubular and the secretory cells have dense, generally basophilic cytoplasm that stains blue pink with hematoxylin and eosin-Y and azure-A and eosin-B. With PAS, the cytoplasm of these cells can be seen to contain small, evenly distributed granules.

The remaining species, *Artibeus jamaicensis*, is distinctly different from the others. The secretory cells morphologically are most similar to the seromucoid type, but the cytoplasm is relatively achromatic, lacks vesicles or trabeculae

such as those found in the glossophagines having seromucoid parotid secretory cells, and are PAS negative. Additionally, histochemical analysis suggests that they should be classified as serous cells (Wimsatt, 1956).

The intercalated segment of the duct system also varies greatly. In *Anoura*, it is relatively short, usually being only three or four cells in length, whereas in most species it is long (sometimes extremely so) and highly branched. In addition to differences in length and degree of branching, the intercalated ducts also differ notably in cellular composition as revealed with the light microscope. Each of the four. glossophagines studied are different, even at the congeneric level (Fig. 40). In *Glossophaga soricina*, the somewhat flattened cells apparently are nonsecretory or, at least, essentially PAS negative. In the closely related *Leptonycteris sanborni*, the initial segment of intercalated duct is comprised of secretory cells (PAS positive), whereas the proximal-most segment resembles the intercalated duct of *Glossophaga*. In *L. nivalis*, on the other hand, the extremely long intercalated ducts are almost entirely secretory. Only the last one or two cells separating this segment from the striated duct are nonsecretory (Fig. 40). *Anoura geoffroyi*, the other glossophagine studied, is characterized by one or two secretory intercalated duct cells adjacent to the secretory acinus, but the remainder of the short duct is comprised of nonsecretory cells (Fig. 40). This pattern also is found in *Sturnira*. In *Artibeus* and *Desmodus*, the intercalated ducts contain PAS-positive material and the cells possibly are secretory, but their morphology at the light microscope level of magnification is slightly different from that of the secretory intercalated duct cells at least in the glossophagines.

The striated portion of the duct system in all seven phyllostomatid species is characterized by a narrow lumen and large, columnar cells with basal striations (mitochondria and basal infoldings of the cell membrane) interspersed with smaller cells distinguishable with the light microscope by their small and heterochromatic nuclei. A PAS-positive apical staining reaction of granules of various sizes suggests strongly that the striated cells in the parotids of *Glossophaga*, *Leptonycteris nivalis*, *Sturnira*, and *Desmodus* are secretory and thus add directly to the formative saliva. The absence of PAS-positive granules (or materials detectable by the other stains and histochemical procedures used by us and by Wimsatt, 1955, 1956) in the striated cells in *Artibeus jamaicensis* implies that these cells are nonsecretory in this species. *Leptonycteris sanborni* and *Anoura geoffroyi* differ from the other species in that the striated cells are PAS negative, but, nevertheless, the apical cytoplasm stains differently from that of the remainder of the cell, suggesting a specialized function. The role of this somewhat vesicular-appearing region will be undetermined until ultrastructural or special histochemical studies are undertaken.

Submandibular.—As is the case with the parotid, the submandibular varies considerably in gross anatomical characteristics. The variable features (size, position, appearance, and number of lobes) can not be used for meaningful taxonomic groupings or for groupings reflective of apparent food habits or general histology.

Two basically different types of secretory acini are found in the submandibular of the species studied. In all of the species except *Anoura geoffroyi*, the

acini are both mixed and tubular in morphology. The glossophagines other than *Anoura* differ from each other but display a definite pattern. In *Glossophaga*, the secretory acini include a large number of serous cells (Fig. 41) that contain large-sized, PAS-positive granules. The acini are capped with demilunes of mucous cells. In basic light microscope morphology and proportion of serous to mucous cells, the secretory acini of *Leptonycteris nivalis* are similar to those in *Glossophaga* (Fig. 41). However, some of the tinctorial reactions, especially that to PAS, are quite different; in *L. nivalis*, the serous cells are not densely packed with large-sized PAS-positive granules. Instead, the cytoplasm typically is packed with extremely small, evenly distributed PAS-positive granules. *Leptonycteris sanborni* differs greatly from the other two species in that there are far fewer serous cells and far more demilunar mucous cells per acinus (Fig. 41). At the same time, however, the PAS granules in the serous cells are more like those found in the homologous serous cells of *Glossophaga* than they are like those of its congener, *L. nivalis*. The other glossophagine, *Anoura*, is extremely different. In this species, the secretory acini are small and bulbous. Although mixed, both types of cells appear to be of the serous type. Most striking is the fact that the inner layer of secretory cells is covered completely by a layer of small, flat cells (Fig. 41). This "demilune" is histologically and morphologically similar to the "special serous" cells found in the submandibular of the opposum, *Didelphis* (Wilborn and Shackleford, 1969). The degree of difference between the secretory acini of both the submandibular and parotid of *Anoura* and those of other glossophagines described here is striking, at least at the light microscope level. These notable differences, considered in view of dental, serological, karyological, and digestive tract differences (Phillips, 1971; Gerber and Leone, 1971; Baker, 1967, 1970; Forman, 1971, 1972), suggest that salivary gland histology might be useful in systematic analysis.

Artibeus, *Sturnira*, and *Desmodus* have tubular mixed secretory acini comprised of serous cells containing PAS-positive granules and a demilune of mucous cells. The serous granules differ from those in comparable cells in *Glossophaga* and *Leptonycteris sanborni* by being smaller and more densely packed. Overall, however, the submandibular secretory acini of the phyllostomatids thus far studied, excepting *Anoura*, show a considerable degree of conservatism in general histology at the light microscopic level.

The intercalated ducts of the submandibular vary somewhat in length but are similar in all of these species. In *Artibeus*, the cells adjacent to the secretory acini apparently contain PAS-positive granules within their cytoplasm, but in all of the others the intercalated duct cells are histologically simple and PAS negative.

The striated ducts also are relatively simple and similar in each of the species studied. Three species (*Glossophaga soricina*, *Leptonycteris nivalis* and *L. sanborni*) can be grouped on the basis of PAS-positive staining reaction in the apical-most cytoplasm (distinct granules can not be discerned), whereas in all of the others the striated cells are PAS negative.

Ultrastructure

General histological studies such as those described in the preceding paragraphs provide an overview of microanatomy but fall short of answering the most intriguing questions. Histochemical analysis, which can provide considerably different kinds of information about cellular activities and secretory products have to date been applied to only two species, *Artibeus jamaicensis* and *Desmodus rotundus*. Both of these techniques suggest, however, that salivary glands of bats in general, and phyllostomatids in particular, will provide a fertile source of data on evolutionary biology and systematics. A third approach, comparative ultrastructure, is clearly warranted; the histological differences observable with the light microscope illustrate an opportunity for analysis of evolutionary changes at the ultrastructural level.

Although the parotid and submandibular salivary glands of a reasonably wide range of mammalian species have been investigated, and to some extent compared, at the ultrastructural level, to date, none of the Chiroptera has been described. We recently have had an opportunity to study the ultrastructure of the parotid secretory acini and ducts and the submandibular secretory acini of the dwarf fruit-eating bat, *Artibeus phaeotis*. Our findings, which are presented in the following paragraphs, are intended to serve as an example of phyllostomatid salivary gland ultrastructure and as a basis for future comparative studies.

Parotid.—The parotid salivary gland of *Artibeus phaeotis* is a compound acinar gland with tightly packed, slightly elongate secretory acini. From an ultrastructural standpoint, the parotid acinar cells are best described morphologically as seromucoid (Fig. 60). The basal plasmalemma is delicately infolded and lacks concentrations of free ribosomes (RNP) and granular endoplasmic reticulum (GER). Consequently, there is a distinct margin that continues along the base of the cell and extends along nearly two-thirds of the lateral cell surfaces. The apical one-third of the lateral margin is either smooth or slightly infolded or has narrow intercellular canaliculi lined with microvilli. Each acinus in surrounded by a typical basal lamina; myoepithelial cells typically overlay the secretory acini. The nuclei of the secretory cells are basally displaced, considerably heterochromatic, and have a moderate-sized nucleolus. The outer margins of the nuclei frequently have a scalloped appearance, possibly as a response to pressure from adjacent membrane-bound secretory vesicles and organelles. Elongate mitochondria are found throughout the cytoplasm but most often are positioned along the cell margins, just internal to the infolded plasma membrane. Stacks of GER are found in the basal portion of the secretory cell, usually cradling the nucleus. Short segments of GER also are distributed throughout the remaining cytoplasm. Densely packed free ribosomes also are numerous, particularly in the cytoplasm between secretory vesicles. Golgi complexes are located in the basal half of the cell frequently but not necessarily adjacent to the nucleus. Typically, they have only a few flattened lamellae, but numerous swollen cisternae containing pale, flocculent material and electron dense particles. Relatively large saccules containing these materials can be observed adjacent to cisternae and secretory vesicles. The presence of membrane-bound saccules of secretory ma-
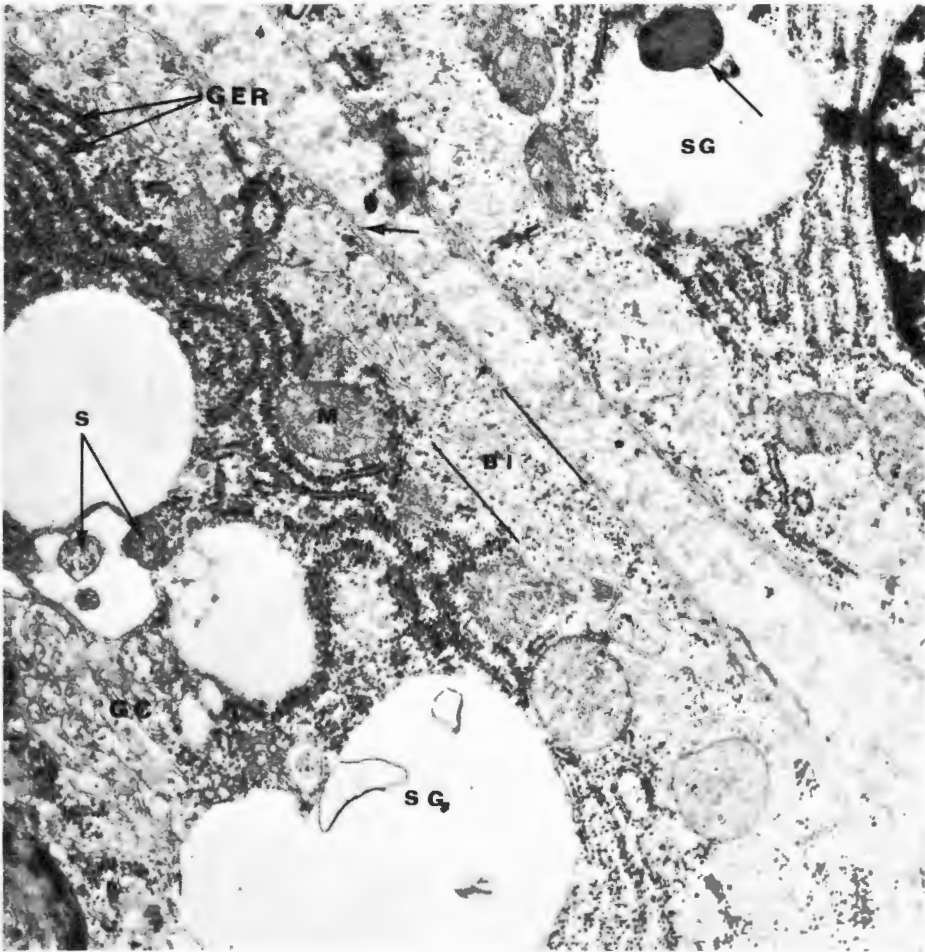
FIG. 60.—Transmission electron micrograph (TEM) of parotid secretory cells in *Artibeus phaeotis*. Abbreviations and symbols are: arrow, basal lamina; BI, basal infoldings of the plasma membrane; GC, Golgi complex; GER, granular endoplasmic reticulum; M, mitochondria; SG, secretory granules (note the electron dense material indicated by an arrow); S, saccules forming an immature secretory granule, 20,625 ×.

terials within some of these vesicles, as well as at their boundaries, probably reflects the method by which the secretory vesicles are filled. When the contents of saccules are released, their membranes apparently become part of the limiting membrane of the secretory vesicle. The mature secretory vesicles usually contain a relatively small accumulation of electron dense material as well as barely visible flocculent material, at least under the conditions of fixation used by us. Generally, however, most of the area within a secretory vesicle is essentially electron transparent; it is possible, of course, that some components of the secretory product were solubilized in the extensive fixation employed. The secretory granules are negative to both toluidine blue (1-micrometer epoxy sections)
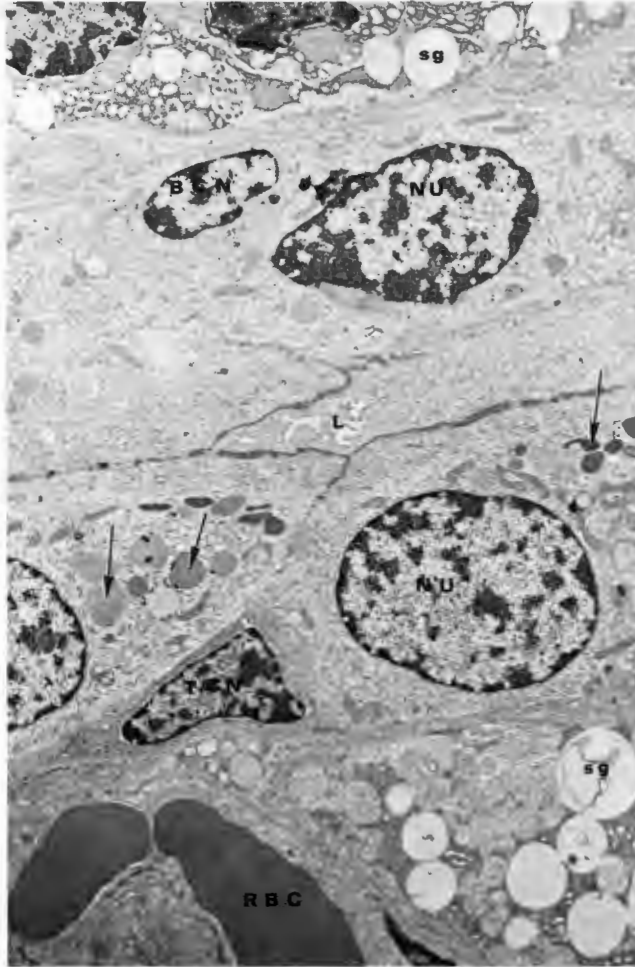
FIG. 61.—TEM of parotid intercalated duct showing cytoplasmic granules (arrows) in the pale duct cells. Abbreviations not explained in Fig. 60 are: NU, nucleus; BCN, basal cell nucleus; TCN, triangular dark cell nucleus; RBC, red blood cell. 4760×.

and PAS (7-micrometer paraffin sections). The apical membrane of the sero-mucoid parotid secretory cell is relatively smooth. We found no indication of microvilli in available examples of the acinar lumen.

The branched parotid intercalated ducts are comprised of at least two types of cells (Figs. 61, 62). The most prominent type is rectangular and has a relative-ly clear cytoplasm and a large, centrally located nucleus (Fig. 61). The short strands of GER are not regularly arranged, instead being found throughout the cytoplasm; the cisternae are greatly swollen, giving the short strands a round, vesicular appearance (Fig. 63). At higher magnifications the cisternae can be seen to be filled with moderately electron dense, flocculent material. Free RNP particles are found in considerable numbers most often in the juxtanuclear re-
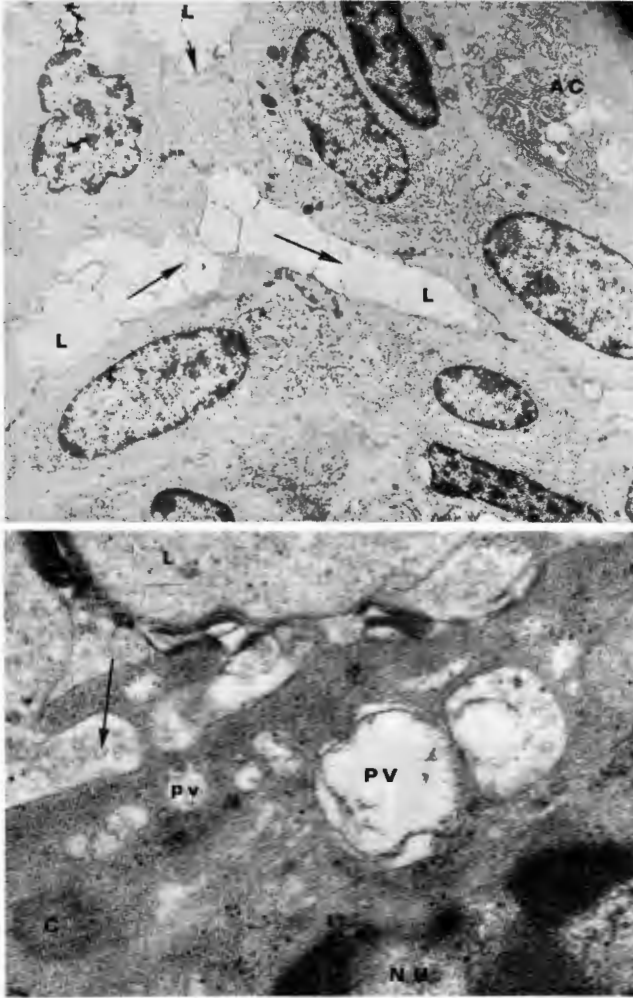
FIG. 62.—TEM views. *Top*: Branched parotid intercalated duct, showing the lumen (L) and direction of flow of formative saliva. Abbreviation not explained in Fig. 60 is: AC, acinar cell. 2800×. *Bottom*: Detail of apical membrane and cytoplasm of a striated duct dark cell. Note the flocculent material (arrow) in the lumen (L) and the micropinocytotic vesicle (PV). Abbreviation not explained in Fig. 60 is: C, centriole, 25,200×.

gion. The marginal cytoplasm in these intercalated duct cells is characterized by large numbers of oriented filaments, particularly in areas adjacent to the zone of contact with other cells of the same type (Fig. 63). Additionally, the zones of contact between these cells are characterized by relatively flat plasma membranes with extensive desmosomes (Figs. 61-63). By way of contrast, the junctions between these intercalated duct cells and the two other peripheral cell types, always lack desmosomes and tend to be moderately interdigitated (Figs. 61, 63). The pale cells have relatively small, elongate, branched mitochondria, which
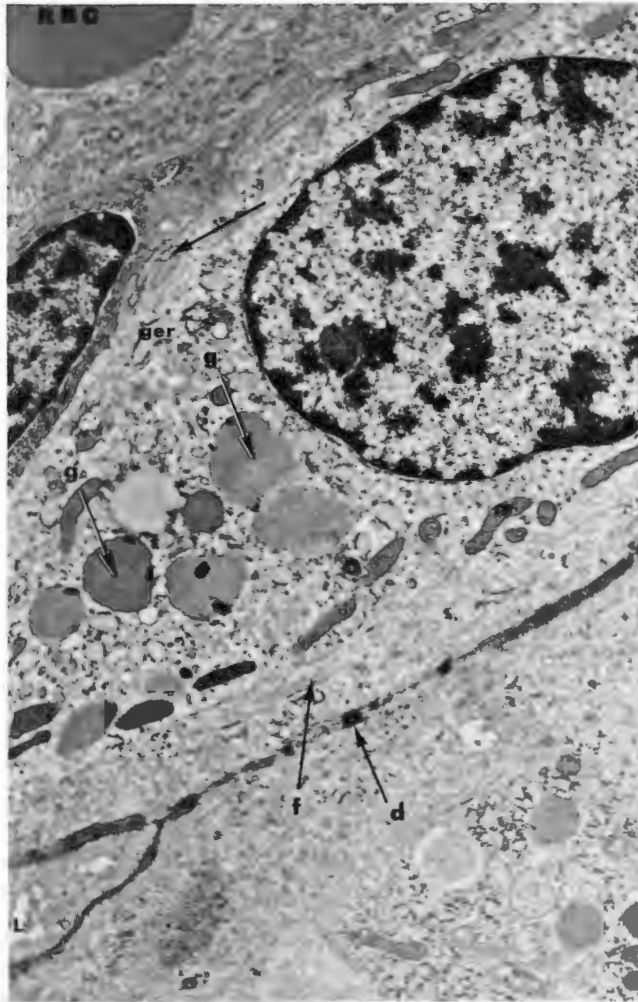
FIG. 63.—TEM of intercalated duct cell showing detail of cytoplasmic granules (g). Note the desmosome (d) at junction between pale cells, and the infolded membrane (arrow) at junction with dark cell. Abbreviation not explained in Fig. 60 is: f, fibrils. 9520×.

are found throughout the cytoplasm. A variety of granules, usually grouped in one area, also are present in the cytoplasm. The shape appears to vary from flat to spherical or elongate, but this might be an artifact of cutting (these granules were not serially sectioned). The material also varies from moderate to dense and in some cases seems to be somewhat flocculent, whereas in other instances it is essentially uniform.

In addition to pale cells, which comprise most of the parotid intercalated duct, small dark cells and pale basal cells are found at the outer margins of the ducts (Figs. 61, 63). The dark cells have a limited amount of extremely dense cytoplasm and a large, irregularly shaped, heterochromatic nucleus (Figs. 61, 62). A few

small mitochondria and scattered free ribosomes characterize the cytoplasm. The pale basal cells also have little cytoplasm and few organelles but differ in that the nucleus is much less heterochromatic and the cytoplasm is almost clear.

The striated, or intralobular, ducts are comprised of three distinctly different kinds of cells (Figs. 64, 65). The most prominent type is a pale, columnar cell with extensive and complex infolding of the basal plasma membrane. These "striated" cells, which are the basis for the term often applied to this portion of the duct system, have large, round or slightly ovoid euchromatic nuclei that are apically displaced (Fig. 64). The basal plasma membrane is characterized by deep and moderately dense infoldings whereas the lateral cell membranes either are complexly interdigitated or are tightly adherent but slightly infolded where in contact with dark cells, other pale striated cells, or basal cells (Figs. 64, 65). The apical membrane of the pale striated cells typically is smooth, lacking either microvilli or indications of pinocytotic activity. The pale cytoplasm contains a relatively large number of elongate mitcochondria, most of which are positioned within the infolded basal membrane and have their long axis oriented along the apical-basal axis of the cell (Fig. 65). Only a very few, short and slightly swollen strands of GER are found within the cytoplasm of these cells (except between adjacent basal infoldings). Clusters of free RNP particles are abundant, especially in the apical two-thirds of the cytoplasm (Fig. 65). Golgi complexes have not been observed in these cells.

Vesiculated dark cells comprise nearly 30 per cent of the cells of the striated duct (Figs. 62, 64, 65). These cells are characterized by a highly irregular outline, a small amount of extremely dense cytoplasm, and a relatively large (in proportion to the cytoplasm) heterochromatic nucleus. The main body of each vesiculated dark cell is positioned near the lumen but communicates with the outer surface of the duct by means of an elaborate and often highly interdigitated cytoplasmic extension. The "basal" and lateral plasma membranes either are complexly interdigitated or are flat and adherent to adjacent cells. The apical membrane is irregular and apparently involved in pinocytosis (Fig. 62). In Fig. 62, a narrow projection of apical cytoplasm extends into the lumen and is surrounded by the flocculent material contained therein. The adjacent apical cytoplasm is characterized by vesicles of various sizes; these clearly are membrane bound and most contain flocculent material indistinguishable from that found within the lumen (Fig. 62). Although GER apparently is either lacking or uncommon in the vesiculated dark cells, clusters of free RNP particles are found throughout the cytoplasm, with possible excepton of the apical-most portion. A few ovoid mitochondria, each with a low number of cristae in comparison to those in the pale striated or secretory cells, are located throughout the cytoplasm with exception of the apical region. These cells also are characterized by an abundance of nonoriented bundles of fibrils. A small Golgi complex of flattened lamellae is positioned between the nucleus and apical membrane (Fig. 62).

The third type of cell found within the striated duct can be described as basal. These relatively simple cells are positioned at the periphery of the duct (Figs.
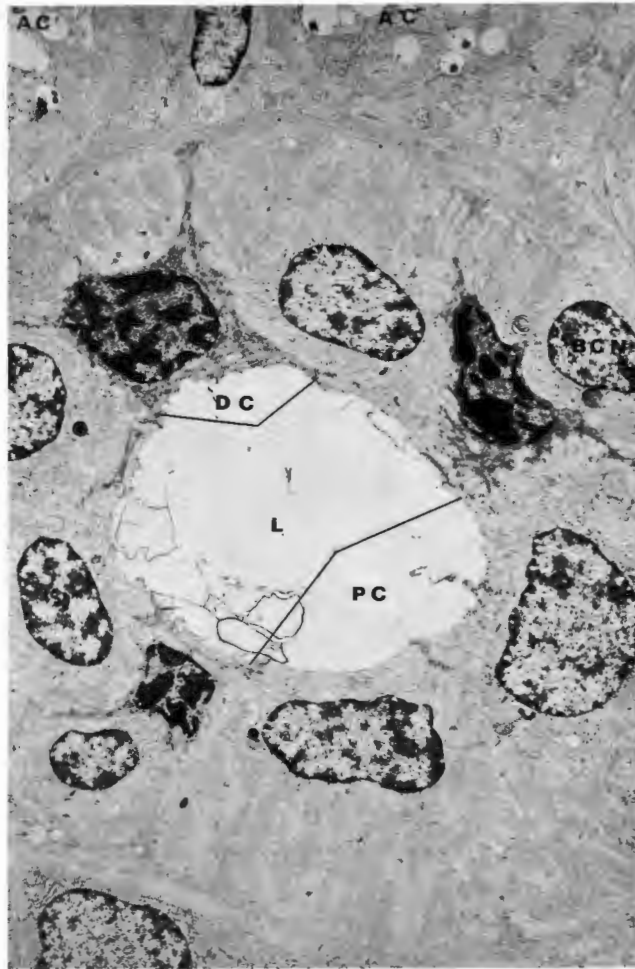
FIG. 64.—A TEM survey comparison of pale striated duct cells (PC) with dark cells (DC). Abbreviation not explained in Fig. 60 is: L, lumen. 3400×.

64, 65) and characterized by large, ovoid, euchromatic nuclei and an extremely small amount of pale cytoplasm (Fig. 65). The basal membrane is smooth and, therefore, unlike that of adjacent striated cells (Fig. 65). The remainder of the cell surface is either smooth or slightly folded and adherent with membranes of adjacent cells. A few small, ovoid mitochondria, fibrils, and a low number of free RNP particles are all that characterize the limited cytoplasm.

Submandibular.—The submandibular salivary gland is of the mixed tubuloacinar type; the tightly packed secretory alveoli are large and branched. When seen through a light microscope, a group of seromucoid cells appears to cap, or form a demilune, over a somewhat tubular segment of serous cells. The two types of submandibular secretory cells can be easily distinguished at the ultrastructural level (Figs. 66, 67).
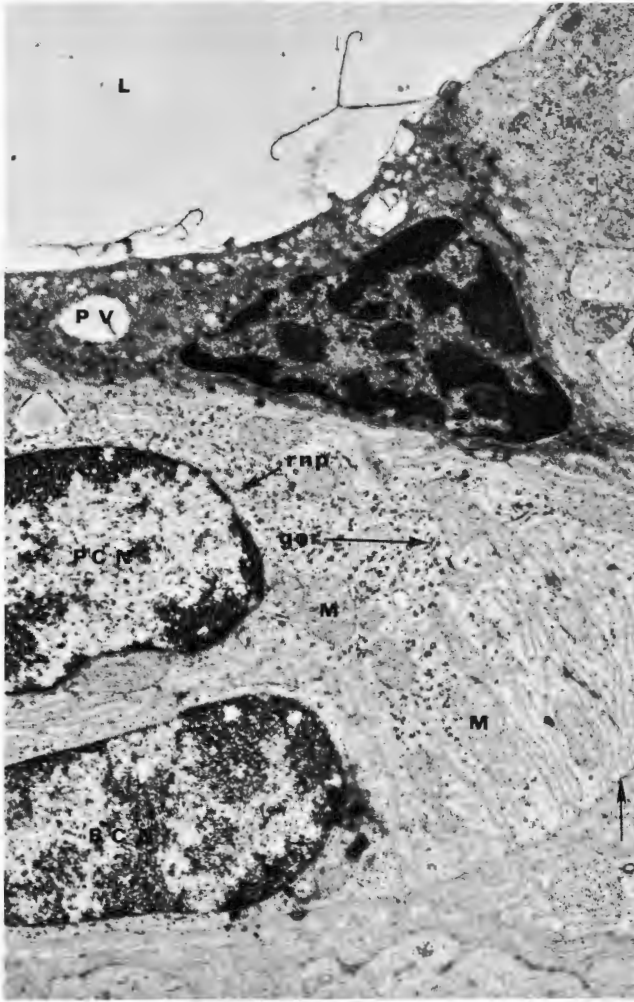
FIG. 65.—TEM view of cytoplasmic details in pale striated cells; note the infolded basal plasma membrane (arrow), clusters of free RNP particles (rnp), and short strands of granular endoplasmic reticulum (GER). See Figs. 60, 61, and 62 for other abbreviations. 9860×.

The relatively small serous cells are narrow and columnar and sometimes appear to be partly wedged between demilunar cells (Figs. 66, 67). The basal plasmalemma of the serous cell is only slightly infolded. The lateral cell surfaces are relatively smooth and very slightly separated from those of adjacent cells; the apical one-third of the lateral membrane usually is tightly adherent and characterized by extensive desmosomal complexes (Figs. 66, 67). The apical membrane also is mostly smooth and unspecialized, although short microvilli can be found, usually in groups. The large ovoid nucleus frequently is positioned in the basal third of the cell and is somewhat heterochromatic (Fig. 66). The entire cytoplasm of the serous cell contains short to moderately long and greatly
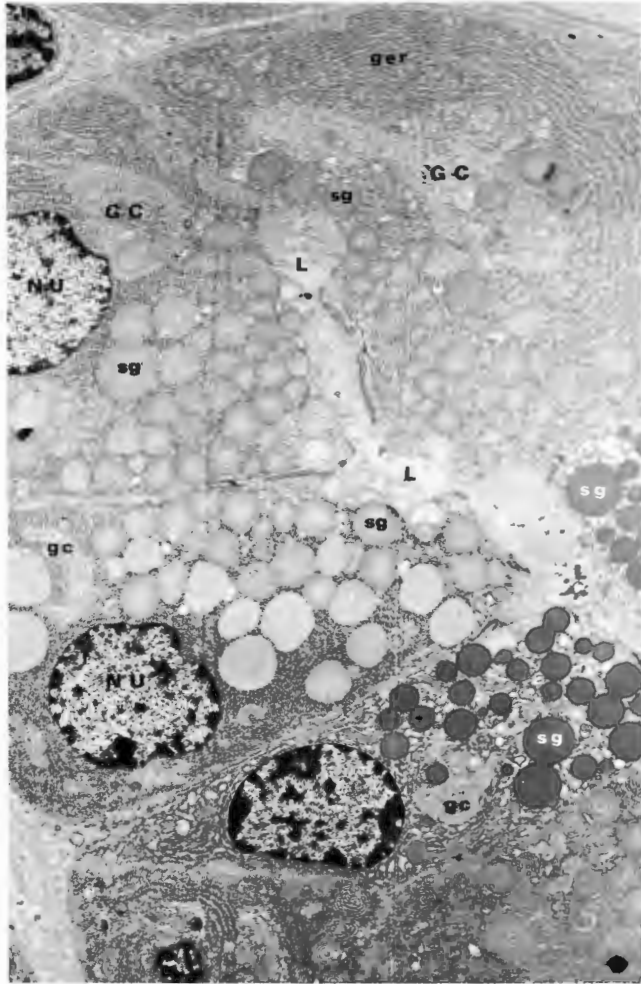
FIG. 66.—Survey TEM view of seromucoid and serous cells in the submandibular gland of *Artibeus phaeotis*. Note the extensive, stacked GER and Golgi complexes (GC) in the seromucoid cells at the top of the micrograph. See previous figures for other abbreviations. 3230×.

swollen granular endoplasmic reticula. Their cisternae contain a moderately electron dense, uniform material. A small number of free RNP particles are found in the restricted cytoplasm between swollen strands of GER. A relatively low number of mitochondria also are found within the restricted cytoplasm. These organelles appear to be arranged and oriented randomly except that they are lacking from the most apical portion of the cytoplasm where secretory granules are being extruded. A moderate-sized but nevertheless prominent Golgi complex(es) usually is found juxtanuclear (Fig. 66). It is characterized by extensive, flat lamellae and is associated with pale, nascent secretory granules.

The mature serous secretory granules are round, usually abundant, uniformly electron dense, and restricted to the apical one-third of the cell (Figs. 66, 67).
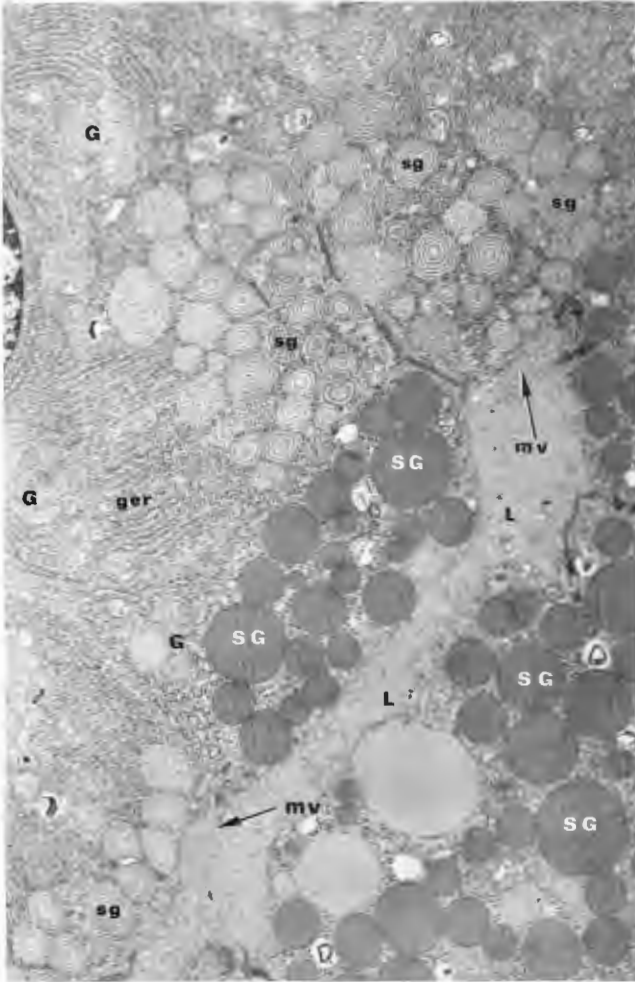
FIG. 67.—A TEM comparison of serous (SG) and seromucoid (sg) secretory granules. Note the apical microvilli (mv) on the seromucoid cells. See previous figures for other abbreviations. 4420×.

In 1-micrometer epoxy sections these granules are intensely stained with toluidine blue and in 7-micrometer paraffin sections(formalin-fixed) they are strongly PAS positive.

The demilunar cells are especially striking at the ultrastructural level. These cells are numerous, large sized, and typically have a wedge-shaped outline (Fig. 66). Their ultrastructural morphology suggests that they are seromucoid.

The plasma membrane of these cells is relatively simple. The basal plasmalemma is nearly smooth although at intervals it shows a complex, looped infolding. The lateral membranes, where there are seromucoid cells, is smooth or slightly folded and is tightly adherent along the apical two-thirds. This latter portion is characterized by extensive, long desmosomal junctions (Figs. 66, 67). With ex-

ception of sites at which extrusion of secretory product is underway, the apical membrane is densely covered by long microvilli (Fig. 67).

The extraordinarily long, stacked, flat GER is a dramatic cytoplasmic feature of the submandibular seromucoid cells (Figs. 66, 67). In overview, the GER appears to cradle the nucleus and is most concentrated in the basal two-thirds of the cell although some strands can be traced nearly to the apical membrane. Free RNP particles also are abundant and are found throughout the cytoplasm (Figs. 67, 68). A moderate number of elongate mitochondria are found in the basal two-thirds of the cell; for the most part these do not appear either positioned or oriented although they generally are lacking from cytoplasm containing concentrations of secretory product. In some instances mitochondria seem to be concentrated in the vicinity of Golgi complexes but this can not be determined with certainty.

The Golgi complexes, because of their extreme size, are prominent cytoplasmic feature (Fig. 66). Golgi components and several initial steps in synthesis of secretory granules are shown in Fig. 68. The border of the complex consists of flat lamellar membranes. The apparent steps of granule formation within the Golgi complex, as illustrated in Fig. 68, are as follows: 1) There is development of a tubular, membrane-bound unit that becomes swollen with accumulation of small, electron-dense particles, pale flocculent material, and distinct (membrane-bound) clear vesicles. 2) The small vesicles increase in number and the tubule loses its swollen appearance. 3) Spherical, membrane-bound saccules containing several small vesicles and some flocculent material become isolated in the cytoplasm. 4) The small vesicles disintegrate, producing a larger granule with a distinct, thick outer boundary that is either the result of the original limiting membrane being joined by the membranes that bound the vesicles or is due to an accumulation of electron-dense materials at the outer margin of the interior of the granule. The granules at this stage contain irregularly shaped clumps of moderately electron-dense material and a paler, uniform background material. These granules frequently coalesce with one another.

The secretory granules resulting from these steps at the Golgi complex occasionally are found throughout the cytoplasm but most often are restricted to the apical one-half of the cell. In general they can be classified into three distinct morphological types: unorganized strands, concentric rings, and tubular networks. The first type (Figs. 69, 70) probably represents an intermediate (condensing) stage between the Golgi complex and the mature product. The other two possibly are stable, mature forms. Serial sectioning demonstrates that the two presumed mature forms of granules are structurally distinct, rather than different in appearance due to sectioning angles (Fig. 70). The simpler form (concentric rings), actually is comprised of concentric spherical shells of electron-dense material. The other type is comprised of convoluted tubules. Occasionally, secretory granules of mixed morphological type or granules containing areas of electron-dense material also are found. That all of these forms represent mature granules and possibly reflect slight chemical variability, is suggested by the fact that they all are extruded from the cell regardless of their morphology. The secretory
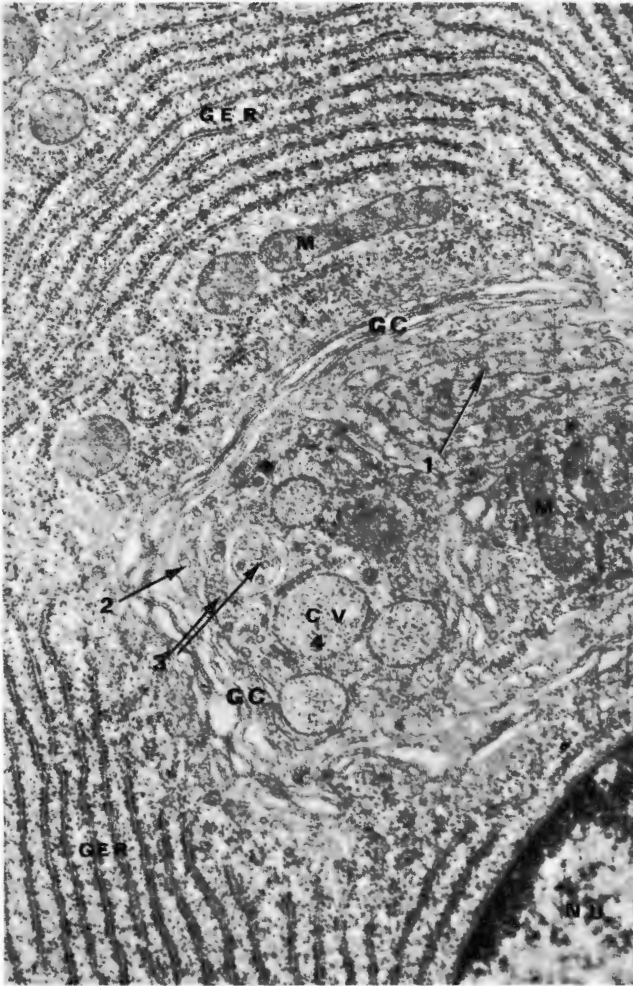
Fig. 68.—TEM detail of seromucoid cell Golgi complex, showing numerically the probable packaging sequence (numbers correspond to those in text) and condensing vacuoles (CV). 12,716×.

granules are negative to both toluidine blue (1-micrometer epoxy sections) and PAS (7-micrometer formalin-fixed paraffin sections).

The method of apical extrusion does not appear to be unusual. The membrane of the secretory granule becomes fused with the apical plasmalemma; microvilli are lost or at least lacking from the site. The contents of the granule are extruded into the lumen and apparently are broken down immediately as the only material found within the lumen appears as a pale, flocculent background.

Discussion and comparisons.—The ultrastructure of the parotid and submandibular salivary glands of *Artibeus phaeotis* can not yet be compared directly to that for any other chiropteran. Judging from obvious interspecific differences
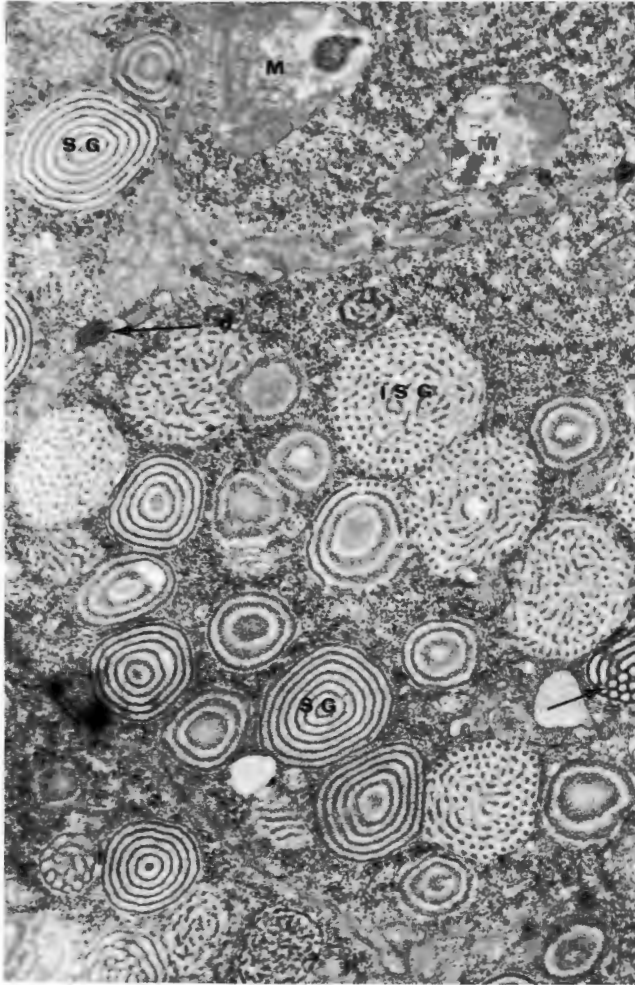
FIG. 69.—A TEM comparison of mature (SG) and immature seromucoid secretory granules (ISG). Note the tubelike morphology of some granules (arrow). 24,480×.

in general histology of salivary glands, such comparisons, when possible, should prove to be unusually interesting and valuable to both oral biology and evolutionary studies.

The parotid secretory cells of *Artibeus phaeotis* qualify morphologically (but not tinctorially) as seromucoid based on the definition given by Shackleford and Wilborn (1968). The GER is flat and the Golgi complexes prominent. Serous secretory cells, by way of contrast, frequently exhibit swollen GER with flocculent material visible within cisternae (Parks, 1961; Kayanja and Scholz, 1974; Tandler and MacCallum, 1972) and, thus, resemble pancreatic acinar cells (Jamieson and Palade, 1967*a*, 1967*b*, 1971). The secretory granules are considerably more electron lucent in *A. phaeotis* than are those found in parotid cells of other mammals for which data are available. For example, in albinistic house
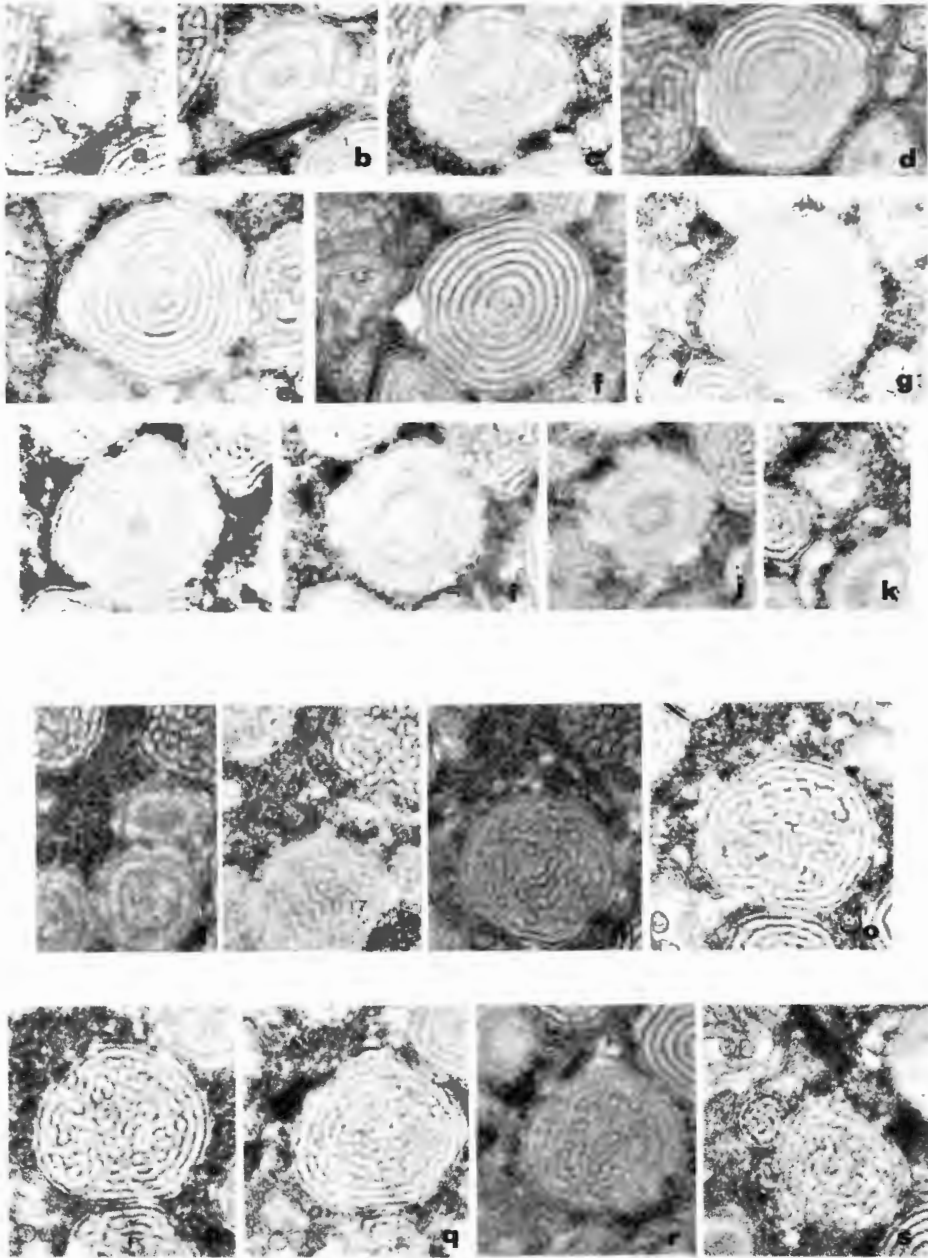
Fɪɢ. 70.—TEM serial sections through the concentric shell (a-k) and "tubular" (i-s) secretory granules in the submandibular seromucoid cells. 35,000×.

mice (*Mus musculus*) the secretory product is denser although often bizonal (Parks, 1961) and in ungulates it typically is uniformly electron dense (Kayanja and Scholz, 1974). Aside from the relatively small, irregular masses of electron-dense material, the secretory granules in *A. phaeotis* morphologically resemble

mucous granules. It is surprising, therefore, that the parotid secretory cells in this phyllostomatid are reactive to neither PAS nor toluidine blue.

The extensive infolding of the basal plasma membrane and basal two-thirds of the lateral plasma membrane suggests a specialization for intake of raw materials. The arrangement of mitochondria adjacent to the apices of membrane folds probably is more reflective of the role of mitochondria in supplying ATP for active transport (DeRobertis *et al.*, 1970) than it is a reflection of lack of space elsewhere in the cytoplasm. The relationship between adjacent parotid secretory cells in *A. phaeotis* differs somewhat from the usual pattern. In *A. phaeotis*, the intercellular canaliculi are narrow in diameter and of uncertain length, and in no case do adjacent cells have a loose interdigitation. In the squirrel monkey (*Saimiri sciureus*) and in several species of ungulates and rodents, adjacent secretory cells generally are loosely interdigitated and have large intercellular canaliculli (Cowley and Shackleford, 1970a; Kayanja and Scholz, 1974; Shackleford and Schneyer, 1964).

The duct system of the parotid of *A. phaeotis* is not unusual at the ultra-structural level although it differs in detail from that of other species for which data have been published. The intercalated portion apparently is secretory, judging from the presence of PAS positive granules of variable electron density within the cytoplasm of the major cell. The general cytoplasmic features of these cells, particularly the presence of large numbers of fibrils, are consistent in a variety of species in both the parotid and submandibular salivary glands (for example, see Shackleford and Wilborn, 1968, 1970a, 1970b; Wilborn and Shackleford, 1969). The ultrastructural characteristics of the intercalated duct cells in *A. phaeotis* do not suggest adult functions aside from a possible secretory role, even though the possibility exists that the intercalated ducts are involved in certain physiological functions (Rutberg, 1961).

The striated portion of the ductal system is nonsecretory in *A. phaeotis*. The absence of small, electron-dense granules in the apical cytoplasm and the smooth apical membrane in the pale "striated" cells make them different from homologous cells in rodents and certain primates (Parks, 1961; Cowley and Shackleford, 1970a). The complex, loose infoldings of the basal plasmalemma and obvious association of oriented mitochondria found in *A. phaeotis* is typical of striated cells. The striking ultrastructural similarity between these cells and those of the renal distal tubule has led to frequent physiological and ultrastructural comparisons (Rhodin, 1958a, 1958b; Rutberg, 1961; Tandler, 1963). Although these striated cells vary considerably from species to species, active resorption likely is one consistent role (for example, see Rutberg, 1961).

The presence of dark cells (characterized by dense cytoplasm) among typical striated cells is common in mammals. Histologists generally either have overlooked, or at least have not reported, this type of cell even though it can be recognized in typical histological preparations because of its small size and small heterochromatic nucleus located adjacent to the ductal lumen. The function(s) and origin of these cells are unknown although in *A. phaeotis* the available micrographs strongly suggest pinocytotic activity along the luminal surface. We

found no evidence indicating that the dark cells are in any way necrotic although others (for example, Kayanja and Scholz, 1974) have reported possible mito-chondrial destruction in similar cells.

The ultrastructure of the submandibular of *A. phaeotis* is unique among studied species of mammals. The arrangement of serous cells capped with an extensive seromucoid demilune differs from the structural features of primates and rodents (Cowley and Shackleford, 1970b; Shackleford and Schneyer, 1964). In man, for example, the submandibular is basically a serous gland although there also are isolated mixed alveoli in which mucous cells are capped by a demilune of serous cells (Sicher and Bhaskar, 1972). The arrangement in *A. phaeotis*, which is typical in the submandibular of chiropterans, structurally resembles that found in the European hedgehog, *Erinaceus europaeus* (Tandler and MacCallum, 1972).

Useful ultrastructural comparisons presently possible can be made between *Artibeus phaeotis* and *Erinaceus europaeus*. In *A. phaeotis*, the submandibular serous secretory cells can be described as typical, whereas the seromucoid demi-lunar cells are highly unusual. In the European hedgehog, on the other hand, the demilunar mucous cells are typical and the serous secretory cells are highly un-usual (Tandler and MacCallum, 1972). In the latter species the immature secre-tory product of the serous cells morphologically resembles, to a remarkable extent, the mature secretory product of the seromucous cells in *A. phaeotis*. In both instances the granules have the appearance of concentric rings of alternating pale and dense material. As Tandler and MacCallum (1972) pointed out, similar complex secretory products have been found in a wide variety of cells in both vertebrate and invertebrate species.

From an evolutionary point of view, it can be argued that apparently the sero-mucoid cells in the submandibular of *A. phaeotis* have evolved from a more primitive demilunar mucous cell. Consequently, the seromucoid secretory product in *Artibeus phaeotis* is not produced by a cell that is homologous to the serous cell of the submandibular of *Erinaceus europaeus*, even though the secretory products are morphologically similar. Aside from secretory granules, the two types of cells are different in most ultrastructural aspects including those characteristics that reflect the process of synthesis of secretory product. In *A. phaeotis*, the extensive GER is flat and stacked, whereas in the European hedgehog it is short and greatly swollen and the cisternae contain flocculent materials during the active phase of synthesis (Tandler and MacCallum, 1972). The Golgi complexes in *A. phaeotis* consist of flat lamellae, swollen cisternae containing small vesicles, and adjacent condensing vacuoles, whereas that of the hedgehog secretory cell primarily con-sists of lamellae that give rise to small saccules that in turn become condensing vacuoles (Tandler and MacCallum, 1972). Furthermore, the secretory granules in *A. phaeotis* are negative to both PAS and toluidine blue, whereas those in the European hedgehog are PAS positive. Overall, it can be said that the striking ultrastructural similarity between the two types of secretory product is not the result of a similiar process in synthesis and possibly not a reflection of similarity in basic chemical composition.

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ECHOLOCATION AND COMMUNICATION

EDWIN GOULD

Interpreting the sounds of members of the Phyllostomatidae offers a special challenge to the descriptive and experimental zoologist. No family of bats in the New World has radiated with such diversity in kind (137 recent species, Jones and Carter, 1976:7), food habits (fruit, nectar, pollen, blood, insects, and vertebrate prey), and habitat (deserts, grasslands, forests, and woodland clearings from the lowlands to the highlands) as have the Phyllostomatidae. Is the richness of their ecological adaptations matched by equally diverse options of communication and echolocation systems? Extensive descriptive studies essential to investigating diversity should reveal clues to the variety of phyllostomatid sound systems.

As many as 11 species may simultaneously occupy the same roosting site (availability of roosting sites is thought to be one of the factors that limit the presence of bat species in a region, Tamsitt, 1967). Herein may lie the clues to selection for the distinctive communication signals that typify phyllostomatids. Diversity in terms of vocalizations will be described.

Microchiropteran bats, including all of the phyllostomatids studied, orient acoustically by responding to the echoes of their own ultrasonics. Bats typically emit pulses at increasing repetition rate as they approach an object, take off, or land. Search phase, approach phase, and terminal phase have been designated as the three phases of altered pulse emission during goal-oriented flight. The sounds are high frequency, frequency modulated, and of short duration. From the echoes of their emitted pulses a bat can determine direction, distance, and velocity and some aspects of size, shape, and nature of objects (Novick, 1971). Despite the diversity of phyllostomatid food habits, the families Phyllostomatidae and Vespertilionidae (a family with most species having similar food habits) display similar pulse-emission patterns.

Phyllostomatid bats have been used for a number of experiments in the study of echolocation. This work will be reviewed briefly. The intensity of sonar calls of phyllostomatids has received considerable attention and also will be discussed. Another feature of interest in the phyllostomatids is the nose leaf and its possible function. The major aim of this review is to discuss ultrasonic vocalizations emitted by phyllostomatid bats. Most of the published literature relates to calls that function as echolocation signals. I will present some new descriptive and functional information on the calls of young and adult bats; some of these calls in young bats are precursors of echolocation sounds in adults. Other calls in young and adult bats probably function as communication signals. The function of some other vocalizations is not clear; perhaps depending on circumstance, these calls serve as communication as well as echolocation signals. At the very least, these new data will indicate a greater diversity of ultrasonic vocalizations than has hitherto been described.

Why consider vocalizations used for communication in the same discussion as vocalizations used for echolocation? Konstantinov (1973) worked with *Myotis oxygnathus* and with *Rhinolophus ferrumequinum*; he demonstrated that onto-genetic continuity between sounds of the same class emitted by young and old bats are communication and echolocation signals respectively. Woolf (1974) confirmed Konstantinov's work by demonstrating a continuum of communication vocalizations emitted by infant *Eptesicus* with sonar vocalizations emitted by the adult; Woolf has referred to this continuum as a sonar family. Gould (1971) reasoned that in the course of evolution, sonar calls were modifications of already existing communication signals.

The social behavior and associated vocal communication of most bats are still so poorly studied that we can only speculate on the extent to which some ultrasonic signals are used for echolocation or communication. In a preliminary examination of communication, Gould *et al.* (1973) described species-specific ultrasonic communication calls in five species of phyllostomatids. I will attempt to examine here some of the variability not reported on by Gould *et al.*

TERMINOLOGY

The following terminology, the first six terms of which are from Struhsaker (1967), will be used in this paper. Synonyms used in other publications are included.

Unit.—The unit is the basic element of a sound uninterrupted by periods of silence or abrupt changes in frequency. The unit is represented as a continuous tracing along the temporal (horizontal) axis of the sonogram. "Note" is a synonym.

Phrase.—The phrase is a group of units separated from other similar groups by a time interval greater than any time interval separating the units within a phrase.

Bout.—A bout is a grouping of one or more phrases separated from other similar groupings by a time interval greater than that separating any of the phrases within a bout.

Nontonal unit.—A nontonal unit is composed of sound that is more or less continuously developed over a wide range of frequencies; synonyms are "noise" (Andrew, 1964) and "harsh noises" (Rowell and Hinde, 1962).

Tonal unit.—A tonal unit is composed of sound characterized by one or more relatively narrow frequency bands and has been referred to as "clear calls" by Rowell and Hinde (1962) and "sound" by Andrew (1964). Units with a multi-harmonic structure are included in this category.

Compound unit.—A compound unit is composed of both nontonal and tonal sounds that appear as a sequentially continuous tracing on a sonogram.

Mixed unit.—Units composed of both tonal and nontonal sounds that occur superimposed (simultaneously) on one another are called mixed units. The tonal and nontonal aspects are more or less separated by differences in frequency.

Isolation call [*i*-call (Gould, 1971)].—The *i*-call is a tonal unit with nearly constant frequency with a duration of about 20 to 60 milliseconds (msec.).

Synonyms are Stimmfuhlungslaute (Kulzer, 1962), attractive pulse calls (Konstantinov, 1973), and Verlassenheitslaut (Schmidt, 1972).

FM pulse.—Woolf (1974) described FM pulses as tonal calls that are "monotonically decreasing, frequency modulated vocalizations which sweep through roughly one octave." The sweep is not linear and has a duration of about 1 to 7 milliseconds. It appears that some infant bats may emit FM pulses that function mainly for communication. Thus, terms that refer exclusively to physical characteristics of the calls will prevent any premature and prejudicial designation as to function. The FM pulse frequently has been referred to as an echolocation signal or sonar call by Griffin (1958) and throughout the extensive literature on bat echolocation; Konstantinov (1973) used the term "location signals." Occasionally, monotonic frequency modulated vocalizations increase in frequency; these are designated as an ascending FM pulses.

FM glide (FMG).—The FM glide is a single unit, frequency modulated pulse that sweeps about one octave and for which frequency is held more or less constant at the beginning (FMGB) or at the end (FMGE). Mixed pulse (Suthers, 1965) is a synonym, but this term is avoided because of its inconsistency with Struhsaker's reference to an unrelated term, "mixed unit" (see above).

Double note (Gould *et al.*, 1973; Woolf, 1974).—DN is identified by the close temporal association between two notes, a long and a short call regardless of their order. Repetition rate of DNS (plural of DN), even in bouts, is usually less than that of FM pulses. The DN varies widely, particularly in regard to the number of notes; a long-short call may be followed by two FM pulses, and, sometimes, one of the units of the DN is repeated once or twice (thus the designation "and higher multiples"). Rarely do the notes number more than four in a phrase. Verlassenheitslauten (Schmidt, 1972) is a synonym.

Warble.—A short, single tonal unit in which frequency rises and falls two or more times.

Reunion.—Infants separated from their mothers for 15 minutes or longer were placed 20 or more centimeters away from their mothers. From the time of placement to the time that the infant attached to the mother's nipple is a reunion.

Contact.—The moment any portion of the mother or infant's body touched the other is the moment of contact.

METHODS

Bats were collected from the following localities: *Leptonycteris sanborni*, Sonora, México; *Macrotus californicus*, southern Arizona; *Carollia perspicillata*, Trinidad; *Phyllostomus hastatus*, Trinidad; *Desmodus rotundus*, Costa Rica; and *Artibeus*, México. Sample size and ages of bats used for recordings are summarized in Table 1.

Leptonycteris, *Macrotus*, *Desmodus*, and *Artibeus* were kept in darkened cages that measured 23 by 23 by 37 centimeters. Two *Artibeus* in healthy condition (judged by their vigor and the condition of their pelage), but abandoned by their mothers, were received from Roy Horst, but they failed to survive more than two weeks. *Macrotus* were maintained on glop, mealworms, and crickets. *Lepto-*

TABLE 1.—*Sample size and ages of bats used for recordings. Age in number of days is followed by sample size in parentheses if greater than one. R identifies recordings of reunions; Ad, adults.*

Desmodus	Leptonycteris	Phyllostomus	Macrotus	Carollia		Artibeus
1 (2)	1 (2) R	1 (2) R	1 (2) R	1 (2)	13 (2)	20-30 (2)*
4	2	2	2 R	2	16 R	
5 R	4 R	3 R	7	3	17	
6	5 R	4	11 R	4	19	
7	7	7 R	9	5	20 R	
9	8 R	18	Ad (2)	7 R	21	
16 R	9	45 R		9	24	
17	15 R	Ad (2)		10	25	
20	Ad (2)			Ad (4)	40	
41						
65						
180						
Ad (2)						

*Age in days is approximate.

nycteris, *Carollia*, and *Phyllostomus* were maintained on diets identical, or similar, to those described by Rasweiler (1973). *Desmodus* were fed fresh and frozen beef blood. Two hand-raised infants (from 2 and 7 days old) were fed Esbilac (Taylor et al., 1974).

The *Phyllostomus* infants used for sound recordings lived more than 10 months and reached adult size. Despite long periods in a 77 by 56 by 52-centimeter cage, they could fly well and high (7 meters) in a 18.3-meter geodesic dome. *Leptonycteris* and *Macrotus* were released in the wild after the observations were complete. The *Leptonycteris* flew vigorously, and the *Macrotus* (infants 15 to 21 days of age and their mothers) were released in apparently healthy condition at the place of their capture, a concrete chamber beneath a bridge.

Most of the recordings of *Carollia* were obtained from D. Kleiman's colony at the National Zoological Park in Washington, D.C. Two reunions of 7 and 16-day-old *Carollia* were observed and recorded in the environmental chamber. The entire colony was removed from the chamber. An infant was removed from its mother's nipple. In an isolated room, sounds of mother and infant were recorded separately under various circumstances. Then the infant was placed, facing a microphone, on a slender, horizontal branch near the center of the dimly lighted chamber. The microphone was placed 7.5 cm from the infant and behind the branch. With an assistant I watched the reunion through the chamber window. The mother was released in the chamber. Her attempts to approach the infant from the rear were thwarted by baffles placed behind the microphone. Thus, whenever the mother attempted to reunite with her infant, she flew toward the microphone. The moment the mother landed next to the infant was obvious because her claws scratching the branch were clearly audible on playback. Scratching was also recorded as the mother took off with the infant attached to her nipple.

Observations of reunions of other species were conducted with the use of cages equal in size to those in which the bats were maintained (see above). An infant bat was removed from its mother, often by detaching it from a nipple. The mother was placed in another cage; then the sounds of the isolated infant were recorded. The door of the mother's cage was opened; the infant was placed as far from the mother as possible and the door was shut. A microphone was fastened inside the cage and oriented so as to optimize detection of calls from both mother and infant. My commentary on mother-infant behavior was tape-recorded on one channel of a Precision Instrument tape recorder at 76.2 centimeters per second; the bats' sounds were recorded on the other channel (see Gould, 1971, for details). Timing of the reunion began when the infant was introduced into the cage and it continued until body contact between mother and infant occurred. I used a dim red light to observe reunions.

Sounds emitted by precocial newborn bats often closely resembled calls emitted by adults. To facilitate my ability to discriminate the calls of mother and infant during reunions, I first recorded the sounds of isolated mothers and infants. Later, when I analyzed recordings, I listened to the slowed recordings of isolated individuals and then listened to the recordings of reunions.

EXPERIMENTAL STUDIES OF ECHOLOCATION

Investigators have demonstrated the skillful ability of bats to avoid obstacles in a rather standardized experimental design utilizing evenly spaced vertical wires. The bats' skills are about equal regardless of taxonomic position (Grinnell, 1970). Obstacle avoidance ability is impaired when ears are plugged or the bat's voice is altered by cutting the motor branch of the superior laryngeal nerves.

The ability of leaf-nosed bats to avoid a plane of vertical wires by means of echolocation has been demonstrated several times. Grummon and Novick (1963) demonstrated that *Macrotus* could avoid wires down to 0.27 millimeter in diameter and could even avoid wires 0.19 millimeter in diameter at a rate better than that expected by chance alone. Their unprecedented large sample indicated considerable variability of individual performance. *Macrotus*, *Carollia*, and *Artibeus* are equally adept at avoidance (see also Griffin and Novick, 1955). *Glossophaga* performed better than did *Macrotus*, *Carollia*, and *Artibeus* by scoring 89 per cent misses when avoiding wires 0.175 millimeter in diameter.

Howell (1974) has evaluated dental and skeletal morphology and food habits in combination with obstacle avoidance behavior in selected bats (*Glossophaga soricina*, *Anoura geoffroyi*, *Leptonycteris sanborni*, *Choeronycteris mexicana*) that feed on nectar, pollen, and insects. The ability of *Glossophaga soricina* and *Anoura geoffroyi* (wild-caught specimens of which Howell reported to contain 46 and 90 per cent insects, respectively) to avoid wires 0.28 millimeter in diameter was superior to that of *Leptonycteris sanborni* and *Choeronycteris mexicana* (which Howell found rarely to eat insects).

Vampyrum spectrum is capable of using echolocation to make rather difficult discriminations between targets of different shape or size (Bradbury, 1970). This species could detect and select one of two lucite targets at distances be-

failed to link the function of the nose leaf in *Macrotus* with echolocation. Likewise, echolocation in *Carollia* is not effected by amputation of the nose leaf (Griffin and Novick, 1955). Thus, the function of the nose leaf in the Phyllostomatidae remains obscure.

WHISPERING BATS

Leaf-nosed bats have a curious behavior that makes their sounds difficult to study; they characteristically emit low intensity FM pulses. Griffin (1958) first characterized FM pulses of certain phyllostomatid bats as "whispered" pulses. Among the species of whispering bats, he recognized *Glossophaga soricina*, *Artibeus jamaicensis*, *Uroderma bilobatum*, *Desmodus rotundus*, and *Carollia perspicillata*. Griffin estimated the intensity of these whispered pulses at about 3 to 5 dynes/cm^2 or about 100 to 1000 fold less intense than *Myotis* FM pulses. When the mouths of three *Carollia* were tightly sealed, the pulses were either quite normal or slightly reduced in intensity (Griffin, 1958:248); when their nostrils were covered, two *Carollia* emitted pulses. Sealing the nostrils or the mouth of *Carollia* had little effect on vocal emission. "*Carollia* (and presumably others of the Phyllostomatidae) thus differ from the typical [species of] Vespertilionidae in being able to emit sound through either the mouth or the nostrils as well as in the frequent scanning movements of their external ears" (Griffin, 1958). Their very short pulse durations set the phyllostomatids apart from the horseshoe bats, which emit long duration sounds through the nose. Probably the methods of phyllostomatid echolocation are more like those of the Vespertilionidae.

A number of investigators, including Griffin, have noted that not all phyllostomatid pulses are "whispered." *Desmodus rotundus* on some occasions emits fairly intense 2 or 3-msec. pulses having a constant frequency between 20 and 30 kHz (Griffin, 1958). Bradbury (1970) in Trinidad recorded pulses from *Vampyrum spectrum* that differed from pulses recorded during discrimination tests in the laboratory in the United States. The unique pulses were longer and louder than the discrimination pulses and, based on a fundamental of 20 kHz, included a complete harmonic series up to the seventh harmonic. In one such record, the bat shifted in one jump from the long harmonic pulses to the short discrimination ones. The shift in one jump and the interval of about 20 msec. between units (Bradbury, 1970, fig. 6) are similar to DNS described below.

Sealing the nostrils of *Macrotus* limits vocal output to abnormally long duration pulses, possibly cries of emotion (Grummon and Novick, 1963). Sealing the mouth did not seem to affect the duration of recorded pulses; however, pulses tended to be at higher amplitude than normal. In both cases, the mean frequency was unchanged from that of the normal bat. But bats with nostrils blocked were unable to orient in an obstacle course. In *Macrotus*, nasal emission appears necessary for acoustic orientation. Grummon and Novick's (1963) observations of *Macrotus* suggest that high intensity calls are emitted via the nostrils. These examples of high intensity sound emission provide little information about function.

However, Howell (1974) has presented evidence that some phyllostomatids control amplitude during obstacle avoidance.

During analysis of ultrasonic vocalization of six phyllostomatid species I have noted frequent cases of bats emitting calls of much higher intensity than whispered FM pulses. Some of these high intensity calls were FM pulses. Others obviously were not and will be described below. High intensity calls were recorded from *Leptonycteris, Carollia, Phyllostomus, Desmodus,* and *Macrotus* (Fig. 2). In some cases, these calls were detected only in the infants; in others, the calls were obtained from adults as well (see details that follow). Decibel differences between the two calls were measured in three to five bouts: *Carollia,* 15-22 decibels (db); *Artibeus,* 8-12; *Leptonycteris,* 8-12; *Phyllostomus,* 12-14.

ANNOTATED LIST OF ULTRASONIC VOCALIZATIONS EMITTED BY ADULT AND INFANT PHYLLOSTOMATID BATS

Although Howell (1974) and Novick (1963) have speculated on the potential interspecific variability in FM pulses of the Phyllostomatidae, only sparse data support their suggestions. For example, Novick (1963) stated that "*Desmodus* pulses (FM) are, indeed, not describably different from most of the Phyllostomatidae such as *Artibeus* or *Macrotus.*" Novick (1963) urged caution in the interpretation of earlier data from Griffin and Novick (1955) on *Phyllostomus, Lonchorhina,* and *Macrophyllum.* Griffin's and Novick's (1955) evaluation should probably be considerably revised in view of technically more successful recordings showing a frequency modulated, harmonic pattern found generally among the Phyllostomatidae (Novick, 1963).

Howell (1974) noted that all genera studied could emit calls at an intensity of approximately 2.5 dynes/cm^2. As the wire diameters decreased in an obstacle avoidance experiment, *Glossophaga, Anoura,* and *Choeronycteris* increased their pulse amplitude to 5, 4, and 4 dynes/cm^2, respectively. Specimens of *Leptonycteris* did not increase the amplitude of their cries beyond 2.5 dynes/cm^2. Howell did observe, however, that *Leptonycteris* emitted pulses of longer duration than did the three other phyllostomatids studied. This verified Novick's (1963) observation; Novick also noted that the frequency pattern was similar to that of *Glossophaga* and *Lonchophylla.* In some of the sonographs, the ability of phyllostomatids to emit long or short FM pulses is apparent (Figs. 4F, 4G).

Diversity of recording situation has repeatedly been mentioned as a key factor in determining the characteristics of FM pulses. The review of species below (Fig. 3) as well as Fig. 1 seem to indicate that all phyllostomatids emit brief, low intensity, multiharmonic FM pulses. There is little indication of a correlation between the ability to emit higher frequencies and size of the bat. The highest frequencies detected in leaf-nosed bats are from *Glossophaga*; but *Vampyrum spectrum,* the largest member of the family, can emit sounds above 100 kHz, which is somewhat higher than sounds emitted by other species (Fig. 3). Similarly, in birds there is no consistent relationship between frequency in the song and size of the bird. Large birds such as the osprey and Laysan albatross sing at high frequency whereas the morning dove and several small owls have deep voices (Greenewalt, 1968).
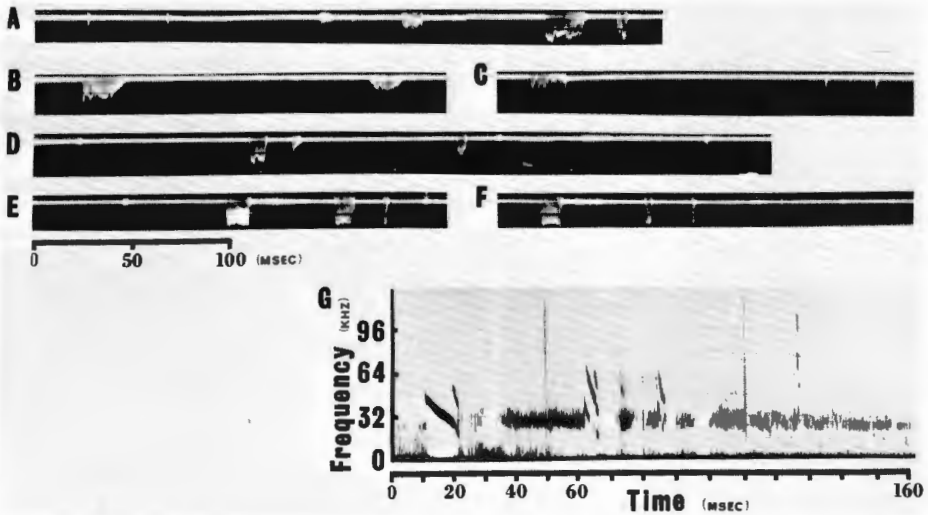
FIG. 2.—**A-F.** Oscillographic records of DNS and FM pulses emitted in the same bout of vocalizations. Long duration, high intensity units are DNS; short duration, low intensity units are FM pulses. Upper lines of dots represent a time base of 60 dots per second. Record speed was 30 ips (inches per second); reproduce speed, 1 ⅞ ips. **A.** *Artibeus*, about 14+ days of age. **B** and **C.** *Leptonycteris*, 7 days old; pulses in C occurred about 400 msec. after those in B. **D.** *Phyllostomus*, 7 days old. **E** and **F.** *Carollia*, 7 days old. **G.** Sonograph of the five units shown in F; these include a DN of three units, one long and two short followed by two FM pulses that are indistinguishable from FM pulses of a flying adult. Note the intensity difference between longer units (DNS) and shorter units (FM pulses). Listening to slowed recordings of *Carollia*, I heard several hundreds of bouts containing DNS and FM pulses.

Species differences in intensity, duration, and frequency probably have to be worked out in the context of obstacle avoidance experiments. Bradbury's (1970) description of the sounds made by *Vampyrum spectrum* is the only detailed study of the variation in FM pulses emitted during different phases of echolocation. The lack of data in this area is because studies of that sort are tedious.

The following descriptions of vocalizations include data obtained from recordings of six species of bats during several experimental situations in which bats were: reunited (mother and infant), hand-held, isolated and exploring a strange box, walking on the floor, and flying in a geodesic dome. Nearly all of the information on FM pulses is taken from Novick (1963) and Pye (1967); my recordings of FM pulses generally corroborated their findings.

Macrotus californicus

FM pulses (Fig. 1P).—Duration, 1.7 to 3.9 msec.; frequency fundamental beginning at 35 to 40 kHz and ending at 26 to 30 kHz; second harmonic beginning at 78 kHz and ending at 34 kHz. When the fundamental frequency dropped below 34 kHz (34-29), a third harmonic appeared and swept from 102 to 81 kHz. Calls resemble those of *Artibeus* and *Desmodus* (Novick, 1963).

FREQUENCIES OF FM PULSES
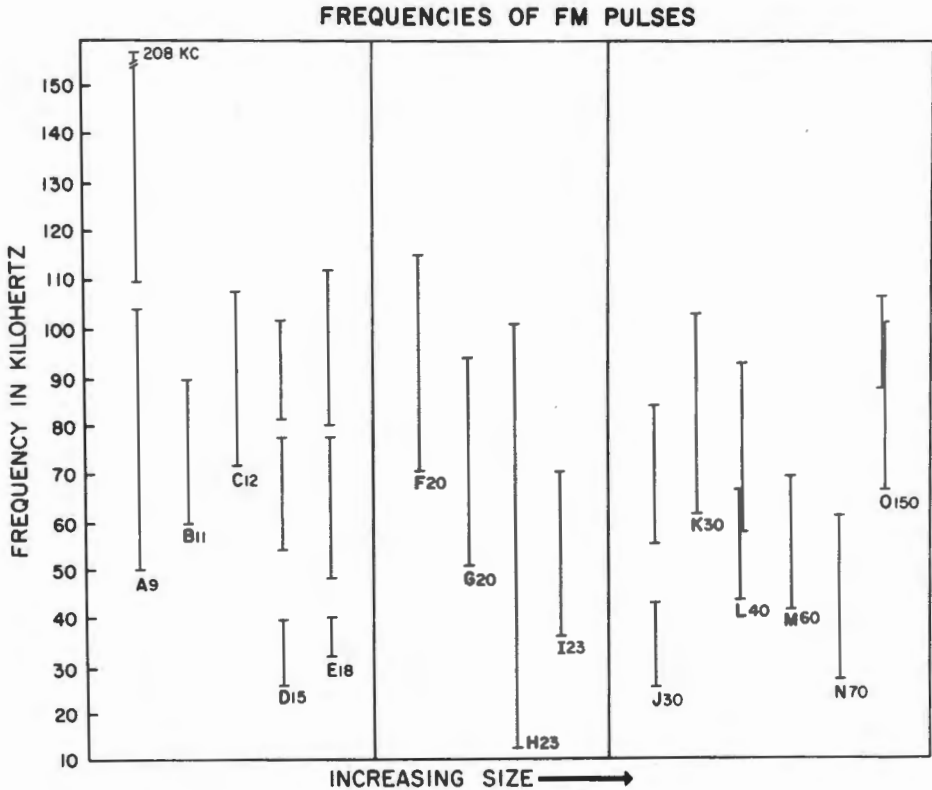
FIG. 3.—Frequencies of FM pulses of 16 different genera of phyllostomatid bats. Data were obtained from Novick (1963), Pye (1967), and this study. The figure is somewhat over-simplified because there is no indication as to which harmonic or harmonics contain the greatest energy. Vertical lines indicate the range of frequencies occurring in FM pulses. Broken lines indicate the harmonic structure; the lower line may be the fundamental, and the lines above represent the second and third harmonics. For example, in E the fundamental is about 40 to 30 kHz, the second harmonic about 80 to 40 kHz, and the third harmonic about 112 to 80 kHz. The numbers adjacent to the letters are the approximate weights in grams of the adult bats, and the species represented are: A, *Glossophaga longirostris, Glossophaga soricina,* and *Anoura geoffroyi;* B, *Artibeus cinereus;* C, *Vampyrops helleri;* D, *Macrotus californicus;* E, *Carollia perspicillata;* F, *Centurio senex;* G, *Sturnira lilium* and *S. tildae;* H, *Leptonycteris nivalis;* I, *Phylloderma stenops;* J, *Desmodus rotundus;* K, *Chiroderma villosum;* L, *Artibeus jamaicensis* (Pye, 1967, listed the second harmonic as 65 to 42 kHz and the third harmonic as 92 to 55 kHz; Novick, 1963 reported the primary component to be 49 to 56 kHz falling to 32 and the second harmonic at 104 to 64 kHz); M, *Artibeus lituratus;* N, *Phyllostomus hastatus* and *Phyllostomus discolor,* O, *Vampyrum spectrum.* The data have been arranged into three size groups in order to point out the lack of correlation between weight of the adult and frequency of emitted pulses.

DN (Figs. 1Q, 4T).—Duration of phrase, 61.5 msec. (43-91.5, *N* = 10); frequency beginning at 13 to 32 kHz, with a middle of 7 to 11 kHz, and an ending, 11 to 32 kHz. DNS were emitted by two isolated infants (one and 11 days old) and adults; three adults emitted DNS during reunion with their offspring. Care-
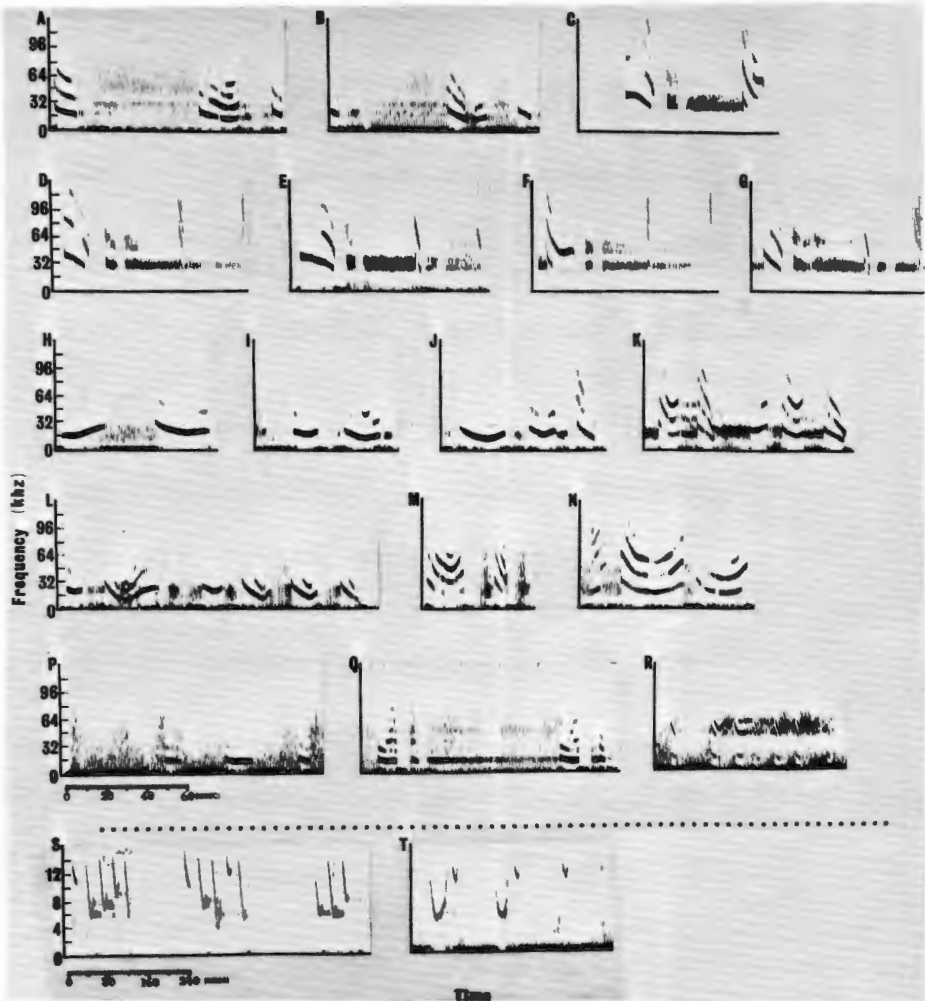
FIG. 4.—DNS of five genera of bats. **A** and **B**. DNS of the same specimen of *Artibeus*, an infant of about 14 + days of age. **C, D, E, F, G**. Sonograms of *Carollia* DNS. C, D, F, and G are from the same 7-day-old infant described under "profiles" in text; E, 16 day-old infant described under "profiles" in text. Note similarity between D and E. Call in D was emitted while the mother was roosting quietly. Call in E was emitted near the moment of bodily contact of mother and infant. C, D, F, and G show calls that were emitted while mother was roosting quietly. **H, I, J, K, L, M, N**. Sonograms of *Desmodus* DNS arranged to show order of increasing complexity: H, seven-day-old; I and J, 5-day-old infant; K, one-day-old; L, seven-day-old; M, 20-day-old; N, 20-day-old. **P, Q, R**. Sonograms of an isolated specimen of *Phyllostomus*: P and Q, one-day-old; R, aroused 45-day-old, isolated bat. The latter sounded like a DN in a mixed unit; compare with Fig. 7A (65-day-old *Desmodus*). **S**. Sonogram of an aroused four-day-old *Desmodus* that had been hand-raised from day one. Recorded on a Uher tape recorder at 7 ½ ips and slowed to 1 ⅞ ips. **T**. Sonograms of adult *Macrotus* responding to its calling one-day-old infant. At the time of this recording, the infant was removed from the range of the microphone. Record and reproduce was the same as in S.
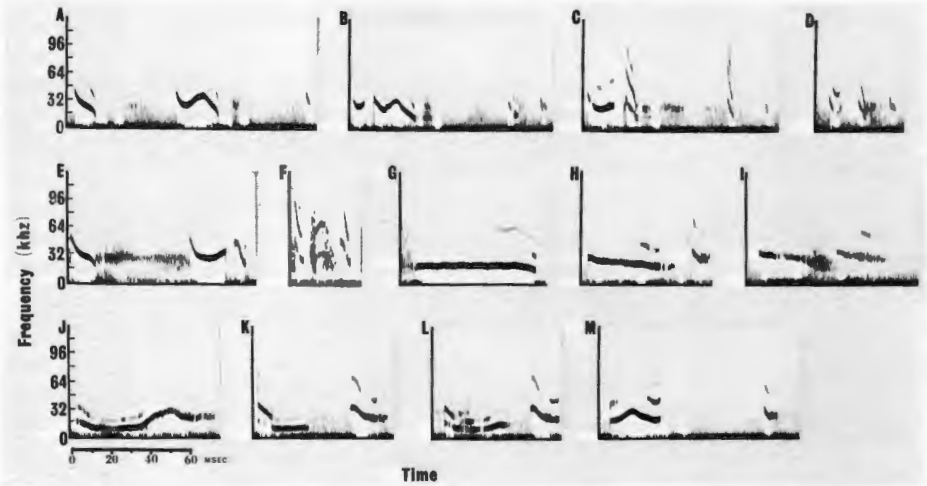
FIG. 5.—Selected sonograms showing short duration units that result from omissions in long units; Woolf (1974) has referred to this continuum as a "sonar family." **A, B, C, D.** Calls of the same isolated one-day-old *Carollia*. Compare the second unit (from the left) in A with the second unit in B with the first and second units in C and with the first and second units of D. This series shows breaking up of a longer unit into components. The terminal portion of the second unit in A resembles the fundamental of the FM pulse. C is a typical DN with three units: a long, a short, and after a longer interval a second short note. **E and F.** DNS emitted by an isolated 13-day-old *Carollia*. Compare sonograms in A and E. These are recordings from different bats. F appears to be a variant of the last three units of E. Dark hashing between first and second units of E is caused by background noise; background noise produced similar effects on other sonograms. **G.** *i*-call emitted by one-day-old *Leptonycteris*. **H.** DN emitted by same bat as in G; note the FM features of the second unit. **I.** DN emitted by eight-day-old *Leptonycteris*. **J, K, L, M.** Calls of an adult *Macrotus* just after its vocalizing from the recording area. Compare the frequency contours of the units in K, L, and M with those of the single unit in J.

ful study of this call may reveal that its units derive from a division of a single unit (Fig. 5J-L). Sound frequency of DNS dropped at about the same rate as the sweep of FM pulses; it then rose to slightly more or slightly less than the frequency at which it started. Bouts usually contained 2 to 6 units. Infant and adult *Desmodus* emit a similar call (Fig. 4S).

Warble (Fig. 5J).—Duration 62.9 msec. (57.5-70.0); frequency 16, 6, 32, and 24 kHz (measured at four extreme points). Although this call is long and modulated, it does not fall in the higher frequency range typical of the warble of *Desmodus* and *Leptonycteris*. This call seems to have two continuous but distinctive components; it begins with an intermediate frequency, drops to about 6 kHz, and rises to about 32. It was recorded from adults during reunion with infants in the same circumstances described above for DNS. Sometimes only the low frequency portion, other times only the high frequency portion was emitted. Other variants are a two and three-part call as shown in Fig. 5 K-M; these seem to result from partial deletions of the complete call.

Carollia perspicillata

FM pulses (Figs. 1A-C).—Duration, 0.5-1.0 msec. (Pye, 1967; my recordings); frequency beginning at 80 kHz (Pye, 1973); 112 kHz (this study) and ending at 55 kHz (Pye, 1973); 80 kHz (this study). Recordings of FM pulses were obtained from two mother *Carollia* as they flew toward their infants (and the microphone). FM pulses were also emitted by a seven and a 16-day-old infant of *Carollia* when their mothers were flying in the room or near them (see details below). Some FM pulses of young bats (a 17-day-old for example) had their primary energy concentrated between about 24 and 40 kHz. Other young bats emitted calls that closely resembled those of adults (Fig. 1). The fundamental sweeps from about 48 to 24 kHz, the second harmonic from about 80-48 kHz, and the third harmonic from about 112 to 80 kHz. Usually the greatest energy is in the second and third harmonics.

DN (Fig. 4C-G, 5 A-D).—Duration of phrase, 65.5 msec (13.5-90, $N=14$); frequency beginning at 16 to 24 kHz and ending at 40 to 66 kHz. DNS were detected from isolated *Carollia*, one to 24 days old (Fig. 4C-G). Calls from a one-day and two 13-day-old bats were very similar; most had three units. The three units have a quality like that of a bird song when slowed 16 times; their sonograms are as complex as the sonograms of a Connecticut warbler's song (see sonograph in Greenewalt, 1968, fig. 34). The variability of the call may be seen in Fig. 5A-D. The sequence of four calls in Fig. 5 indicates the way in which a single unit breaks up into units that resemble DNS and FM pulses.

FMGB and FMGE (Fig. 4C, F).—On three occasions, a 16-day-old *Carollia* emitted DNS composed of FMGE when its mother flew close to it. On one of these occasions, this 16-day-old *Carollia* was emitting FMGE; the approaching mother emitted one FMGE a fraction of a millisecond after the FMGE of the infant. The adult's call sounded quite different from the infant's. Sometimes DNS were composed of FMGB or FMGE. Frequently, FMGE was emitted just before or just after DNS; FMGE then graded into FM pulses. It was also emitted in pairs by a seven-day-old bat that was recorded during a reunion. FMGE is usually of much higher intensity than FM pulses.

Buzz.—*Carollia* rarely emitted this call. However, good recordings were obtained from one 19-day-old bat that became very aroused during handling. The buzz occurred as a mixed and as a compound unit in association with FM pulses and FMGE.

Leptonycteris sanborni

FM pulses (Fig. 1D).—Duration, 2.0 to 7.9 msec.; frequency beginning at about 58 and 100 kHz (third and fourth harmonics) and ending, at 25 and 50 kHz (third and fourth harmonics); fundamental, 12 kHz. Sound emission appears to be nasal (Novick, 1963). The dominant frequency sweep begins at 58 kHz and drops to 25 kHz. Series of harmonics with one or two harmonics predominate. FM pulses have a longer duration than in *Glossophaga* and *Lonchophylla*. Both Novick (1963) and Howell (1974) were impressed with the variable duration of

pulses emitted by *Leptonycteris nivalis* and *L. sanborni* (2 to 8 msec, Howell, 1974).

DN.—Duration of phrase, 64 msec. (53-79, $N=10$; see Fig. 9); frequency beginning at 8 to 30 kHz and ending at 24 to 66 kHz ($N=9$). Isolation calls break up into DNS as in *Eptesicus* (Woolf, 1974). Thus, frequency contours of DNS are similar to those of *i*-calls. Note that the time from the beginning of the first to the end of the second pulse in the DN shown in Fig. 5G and 5H is roughly the duration of an *i*-call. This is typical of DNS emitted by *Leptonycteris*. On occasion the *i*-call breaks up into three notes and contains a short, slightly more modulated first note.

Isolation call (Fig. 5G).—Duration, 64.6 msec. (55.5-77.5, $N=10$) emitted by one and four-day-old infants; frequency, 14 to 25 kHz. Compared to FM pulses, *i*-calls have relatively constant frequency. Isolation calls were recorded from infants one to four days old that were hand-held and from infants that had recently been placed in a cage with the mother after 30 to 60 minutes of isolation.

FMGB and FMGE.—This call was described briefly by Novick (1963) as part of the adult repertoire; the constant frequency portion lasted 1 to 2 msec. An FMGE is shown in Fig. 1E.

Warble (Fig. 6B, D, F).—Duration, 70.6 msec. (52-112.5, $N=5$); frequency, 70 to 48, 17 to 40, 48 to 50, 19 to 32, 48 to 64, and 28 to 40 kHz. Frequency was measured at six extreme points on five sonograms of adult calls. Four sonograms of calls from an 8-day-old bat measured 35 to 40, 16, and 32 to 64 kHz at three extreme points. This call was detected during close contact of mother and infant (one four days old and another eight) after a separation of 20 to 60 minutes. In some instances, a rather stereotyped call sounded like an unsuccessful attempt by infants (one, eight, and 15 days old) to emit a warble (Fig. 6D, F); two units are separated by a change in frequency rather than by a silent period as typified by a DN.

Desmodus rotundus

FM pulses (Fig. 1F-M).—Duration, 1.1-2.3 msec.; frequency beginning at 38 to 42 kHz and ending at 24 to 29 kHz. Vampires appear to emit their orientation sounds nasally. Second harmonic at high amplitude: 76 to 83 kHz (Novick, 1963; Pye, 1967). "The beginning may typically have two component frequencies, 40 and 80 kHz, the middle three, 30, 60, and 90 kc and the end three, 27, 54, and '81 kc" (Novick, 1963). FM pulses of *Desmodus* are not describably different from those of other phyllostomatids, such as *Macrotus* or *Artibeus* (Novick, 1963).

DN (Fig. 4H-N, S).—Duration of phrase, 83 msec. (45.5-146.5, $N=10$); frequency fundamental usually ranged from 16 to 32 kHz, beginning at 10 to 16 kHz and ending at 32 to 34 kHz ($N=10$). Harmonics are apparent in most of the sonograms. *Desmodus* DNS seem to possess more variation within individuals than I could detect in DNS of other species. DNS were emitted when *Desmodus* infants were hand-held, during reunion with the mother, and when isolated. The quality of many DNS was to my ear indistinguishable from that of *Artibeus* when
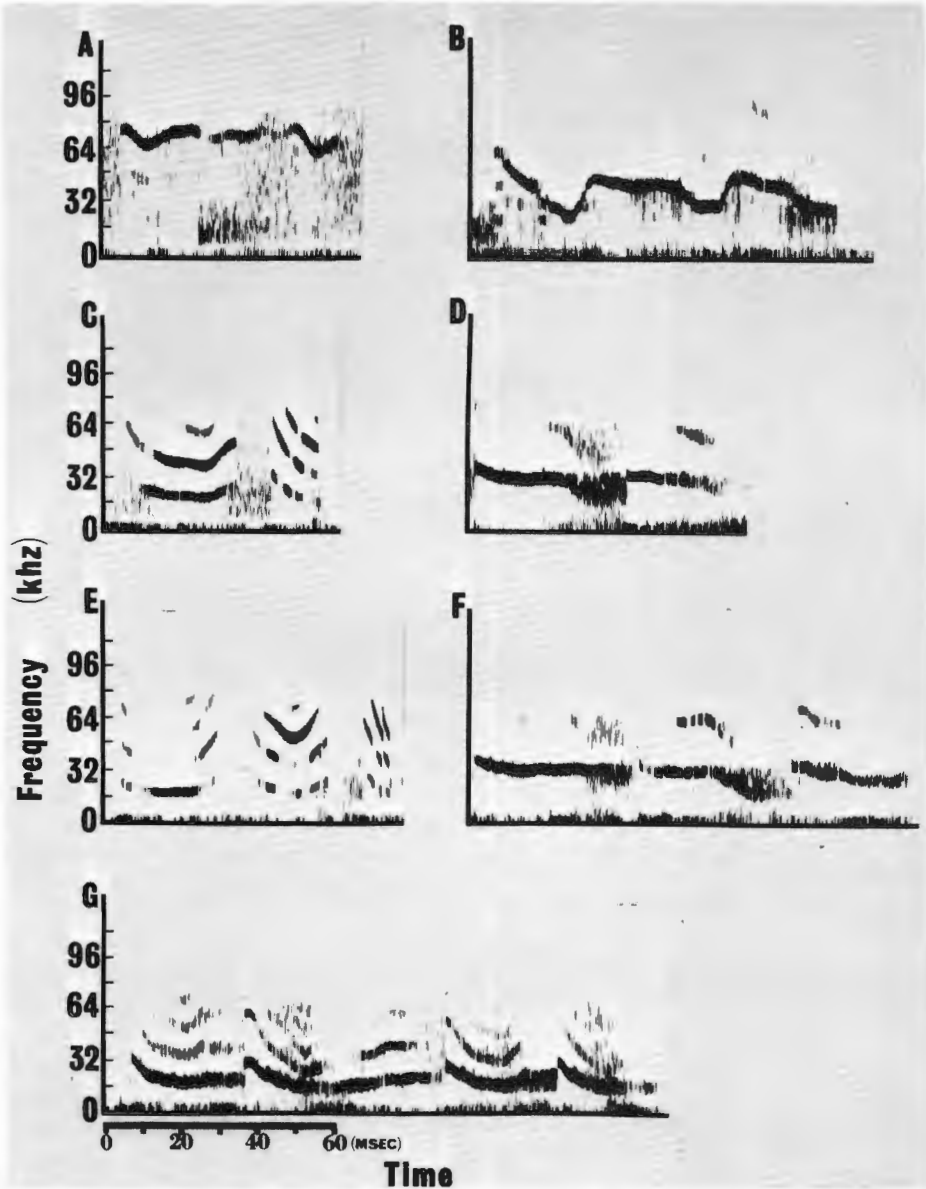
FIG. 6.—Warbles of *Desmodus* and *Leptonycteris*. **A.** Warble emitted by mother of five-day-old *Desmodus* at the moment of bodily contact during a reunion. **B.** Warble emitted by mother of five-day-old *Leptonycteris* at the moment of bodily contact during a reunion. **C.** Isolated 5-day-old *Desmodus* exploring flat substrate; compare with E. **D.** *Leptonycteris*, 15 days old approaching its mother during a reunion. This call and the one in F, both from different animals, resembled the warble emitted by their mothers (for example B). It seemed as though the infants were attempting to imitate their mothers. **E.** Isolated 41-day-old *Desmodus* exploring flat substrate; this bat had been hand raised from day seven. **F.** *Leptonycteris*, an eight-day-old infant, near contact with its mother. **G.** Isolated five-day-old *Desmodus* while being held in hand.
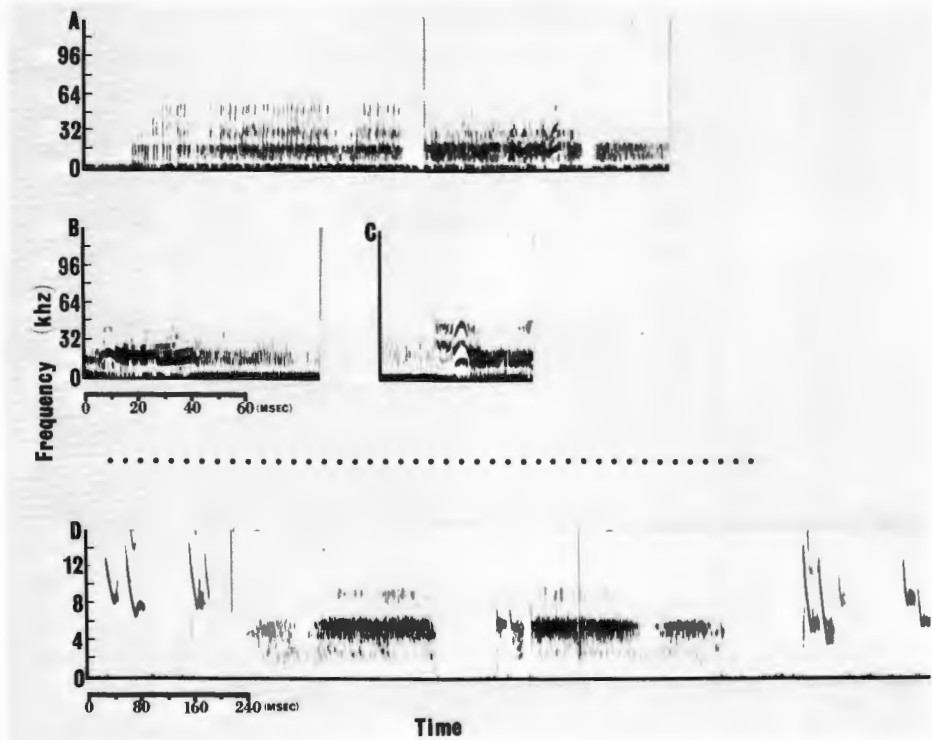
FIG. 7.—Mixed and compound units: **A.** Mixed unit emitted by a hand-held, 65-day-old *Desmodus*. A buzz is superimposed on an FM pulse and an ascending FM pulse. **B** and **C.** Calls of one-day-old *Desmodus*. Mixed units of buzz superimposed on slightly more structured pulses. **D.** Compound unit of DNS and buzz emitted by a 41-day-old *Desmodus* hand raised from day seven. Three sonograms are arranged so as to preserve the correct timing. Recording was with Uher tape recorder at 7 ½ ips and slowed to 1 ⅞ ips.

the sounds were heard 16 times slower than recorded speed. Sounds of two *Artibeus*, about two to three weeks old, were compared with those of a nine and a 10-day-old *Desmodus*. DNS were emitted frequently by the one to seven-day-old, but they were heard less and less as the infant matured. Schmidt (1972) found frequency, duration, and interval differences in a female and male six and nine months old, respectively. Schmidt (1972) found that initial calls are often introduced by single units with the first part missing; I also found this to be true.

Buzz (Fig. 7A-C).—Duration, 300 to 800 msec. (Schmidt, 1972); frequency, wide range of frequencies up to 56 kHz. This call was detected from young and adult *Desmodus* during high levels of excitation. See next section for more details.

Warble (Fig. 6A, C, E, G).—Duration, 56 msec. (50-200 msec, Schmidt, 1972); frequency, 58 to 78 kHz. Only one sample of a warble from an adult female *Desmodus* was obtained. It was emitted as I gently and quietly placed a five-day-old infant next to its mother. The infant warble may be a different class of call from the warble obtained from an adult. It was obtained only from one five-day-

old and one 41-day-old *Desmodus* while the bat was hand-held and later when placed on a table (Fig. 6C, E). The notes of the 41-day-old's warble seemed similar in quality to its DN. The adult's warble may be the same call as the "Kontaktlaut" of the mother described by Schmidt (1972): Duration, 50 to 200 msec.; Frequency, 6 to 12 kHz. The frequency range of our electronic equipment differed; Schmidt's equipment was designed for detection of low frequencies, whereas mine was designed for detection of high frequencies.

Peep.—I did not detect this call, but Schmidt (1972) described peeps as calls of very low intensity made by infants in body contact with their mothers. Following such calls, the infant was licked and suckled by the mother. These short duration (about 15 msec.) peeplike calls could not be analyzed because of their low intensity (Schmidt, 1972).

Phyllostomus hastatus

FM pulses (Fig. 1N).—Duration, 0.5 to 4.0 msec.; frequency beginning at 42 to 50 kHz and ending at 25 to 30 kHz. Both *P. hastatus* and *P. discolor* emit similar FM pulses.

DN (Fig. 4P, Q).—Duration of phrase, see Fig. 9; frequency fundamental at about 12 kc. Many units of one-day-old infants' DNS are of constant frequency. Units of a four-day-old infant swept from about 18 to 14 kHz.

Species Differences in DNS

When I listened to DNS slowed 16 times, I could repeatedly recognize qualitative differences in the DNS of *Macrotus*, *Leptonycteris*, *Phyllostomus*, and *Carollia*. Compare DNS of *Carollia* (Fig. 1C-G) and *Phyllostomus* (Fig. 1P, Q) and note differences in frequency and frequency contour. In each case frequency and frequency change were most distinctive to my ear. Only the DNS of *Artibeus* ($N = 5$ DNS) and *Desmodus* seemed so similar as to be at times indistinguishable. A comparison of intervals and durations of units within DNS revealed some species differences. For example, compare DN intervals of *Carollia* with those of *Desmodus* (Fig. 8). In general, DN intervals of the five species studied ranged from about 20 to 60 msec. Duration of DN phrases and duration of units within phrases differed among some species (Fig. 9). The age of the bats from which the records were obtained varied. It would be difficult at this stage of the study to select ages that were comparable in anatomical development because those species for which recordings were made are born in different degrees of precocity (Gould, 1975).

Recordings of DNS were obtained from a variety of circumstances including hand-held, reunions, and exploring. I attempted to recognize DN variants that occurred during specific behavioral circumstances. No such relationship existed. Some variants that occurred in a hand-held bat also occurred during reunions. Even a comparison of DNS from bats of differing ages indicated no apparent contrast (Fig. 4D, E). However, I did not attempt a statistical analysis in regard to DN features emitted by bats of different ages or by bats during different circumstances. Brown (1973) has shown the existence of signatures in infant *Antrozous*.

SOUND INTERVALS
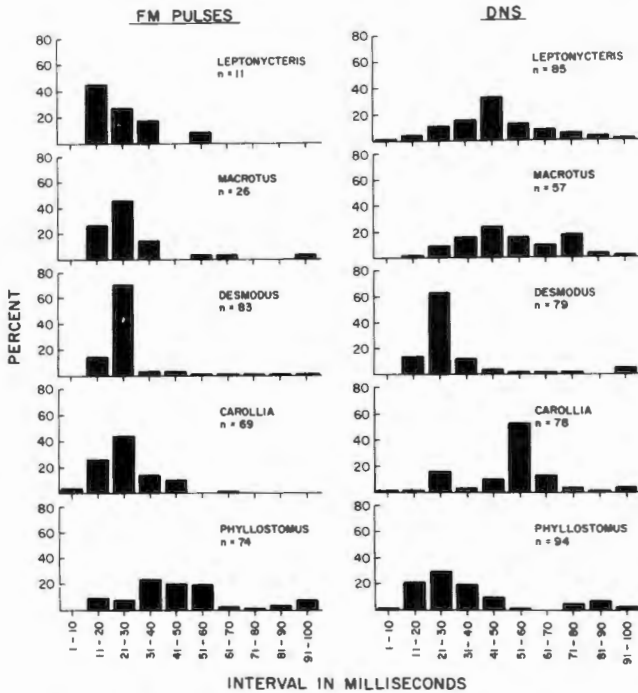
FIG. 8.—Sound intervals of pulses emitted by five genera of bats. Intervals were obtained by measuring from the beginning of one pulse to that of the next. All FM pulse intervals were obtained from calls emitted by young bats within a second or two of DN emission. The intervals of all units within DNS were measured. Ages of bats sampled included the following: *Leptonycteris*, 1, 2, 4, 7, 9, and 15 days old; *Macrotus*, 1, 7, and 11 days old and adult; *Desmodus*, 1, 5, 6, 7, 17, 20, and 41 days old and adult; *Carollia*, 2, 7, 9, 13, 16, 17, and 19 days old; *Phyllostomus*, 1, 4, and 7 days old.

ULTRASONIC VOCALIZATIONS EMITTED DURING REUNIONS OF MOTHER AND INFANT BATS

Most studies of bat vocalizations have concentrated on FM pulses. Usually calls have been recorded while the bats were flying (Novick, 1963) and sometimes while flying toward obstacles or two objects that the animals were trained to discriminate (Bradbury, 1970). My observations extend past studies by sampling calls of bats at different ages and during mother and infant reunions. I have observed and recorded ultrasonics during reunions of five phyllostomatid genera (Table 2).

Being able to discriminate the infant's FM pulses from those of the mother was essential. Several conditions permitted me to identify the source of the sounds.

1. On one channel of the sound tapes, I dictated a running commentary of the mother's and infant's position. At times *Carollia* flew 1.5 to 2 meters away from the microphone and her sounds were not recorded on the tape. Relatively high intensity FM pulses were clearly detectable on the tape recording; these pulses
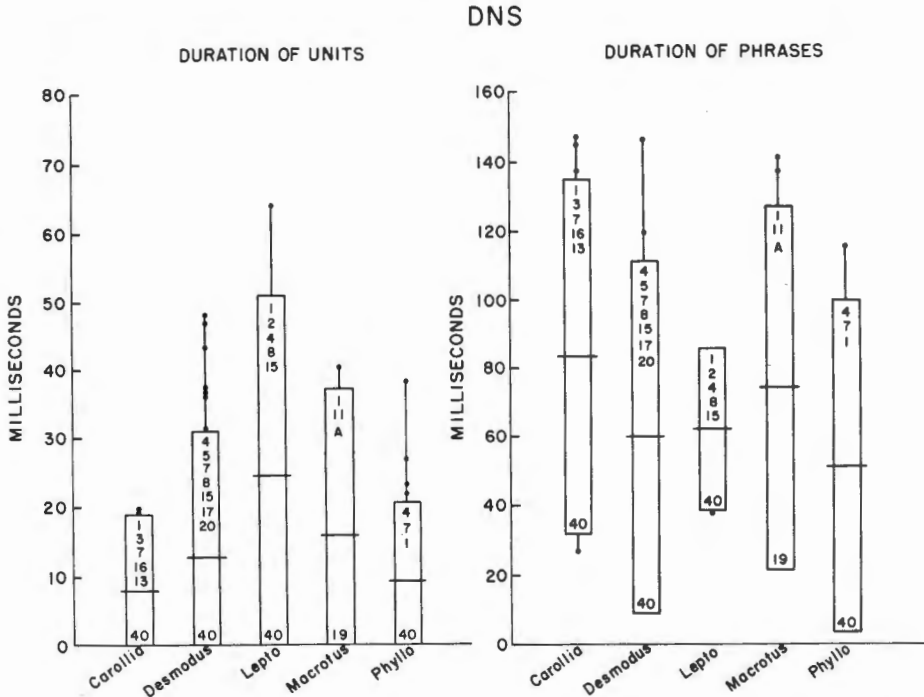
FIG. 9.—Duration in msec. of phrases and units within phrases of five genera of bats: vertical lines represent the extremes; rectangles, two standard errors; horizontal lines, mean; numbers in rectangles, age of bats sampled; number at bottom of each rectangle, sample size; stars, extreme data points; Lepto, *Leptonycteris*; Phyllo, *Phyllostomus*.

were certainly the sounds of the infant (positioned 7.5 centimeters from the microphone).

2. As the mother *Carollia* approached the infant and the microphone, both bats emitted a rapid battery of FM pulses. When slowed 128 times, the calls of the mother and infant could be distinguished and counted. During each approach, the infant's calls began first; the mother's calls steadily increased in intensity as she approached the microphone.

3. As the mother flew away from the microphone the intensity of her sounds waned. Only when she approached again were her sounds recorded. The paucity of the mother's calls on the tape is consistent with the whispered character of *Carollia's* FM pulses.

4. Except during the mother's approach, FM pulses never overlapped with DN phrases. Criteria similar to the above were used for determining the source of sounds during reunions with other species.

Profiles of Mother and Infant Carollia Reunion

In a breeding colony of *Carollia* that included 30 infants, Kleiman (personal communication) observed no instances of fostered infants. The specificity with which mother bats nurse only their own infant is apparent in several species

TABLE 2.—*Seven types of vocalizations emitted by individuals of five genera of phyllostomatid bats during different circumstances. Numbers represent age of individual bats in days; s, infant separated from mother or mother silent during a reunion; a, mother's approach during reunion; e, mother emitting FM pulses during reunion; c, mother making contact during reunion.*

Carollia	Leptonycteris	Phyllostomus	Desmodus	Macrotus	
i-call		1s, 1s, 4s			
DN	1s, 7saec, 16saec, 13e, 17s	1s, 7ces, 8s	1cs, 7as	5sa, 1as, 1a 17s, 9a	1s 1s 11s
FM pulse	7es, 16ae, 9s	4s	1 4s	1s	1s 1s 11s
FMGB	13s, 7c	Novick (1963)			
FMGE	16a	4s*, 4a			
Warble		4d†, 8d††		41s*, 5c	
Buzz	19d			5c, 180**, 270**, 1s, 180s, 41s	

An asterisk identifies a hand-raised infant; double asterisks, data from Schmidt (1972), age in days is approximate; dagger, vocalizations probably from mother only; and double dagger, vocalizations probably from mother and infant (see Fig. 6D). Novick (1963) recorded FMGB from adult *Leptonycteris*.

(Gould, 1970, 1971). This specificity in *Carollia* is consistent with the behavior described below.

The vocal exchange between mothers and infants in the following two descriptions typifies reunions that I observed of other species in somewhat different circumstances.

Seven-day-old *Carollia*

Minus 0.—Infant was placed on horizontal branch and remained there until reunion with mother.

0-23 sec.—Tape recorder on. Mother released in chamber. Mother flies the width of the room several times. Infant emits FM pulses (low intensity unless otherwise noted) and numerous DNS.

24-50 sec.—Mother hangs up on ceiling. Infant stops emitting FM pulses; infant continues emitting DNS.

51 sec.-2min., 9 sec.—Mother continues flights across room and intermittently hangs up. Infant emits DNS and FM pulses when mother flies.

2 min., 10 sec.-3 min., 40 sec.—Mother flies back and forth across the width of the room and hangs up three times. Infant emits DNS when mother hangs up. While mother flies but does not approach infant, infant emits DNS and FM pulses. In one sample of 33.7 sec. of infant vocalizations in which FM pulses graded into and out of DNS, infant emitted 20 DNS and 302 FM pulses. During mother's three hang ups lasting a total of 50 seconds infant emits 11 DNS and no FM pulses (Fig. 10).

3 min., 41 sec-3 min., 43 sec.—Mother flies toward infant and approaches within 12 centimeters of infant. Infant increases rate of DN and rate of FM pulses (Fig. 10).

3 min., 44 sec.-18 min. Mother approaches infant 12 times; infant increases rate of DNS and FM pulses during each approach. Mother hangs up 16 times. Mother flies back and forth 7 times.

18 min., 5 sec.—Mother approaches infant. Infant emits FM pulses, 0 to 19.5 + pulses per second (in eleven 0.95-sec. consecutive samples) and DN 0.4-2.3 calls per second (in the same 11 samples). During the same 11 samples, FMGB and FMGE sounds are emitted, probably by the infant (Fig. 4C, F). Mother hangs up next to infant and guides infant to
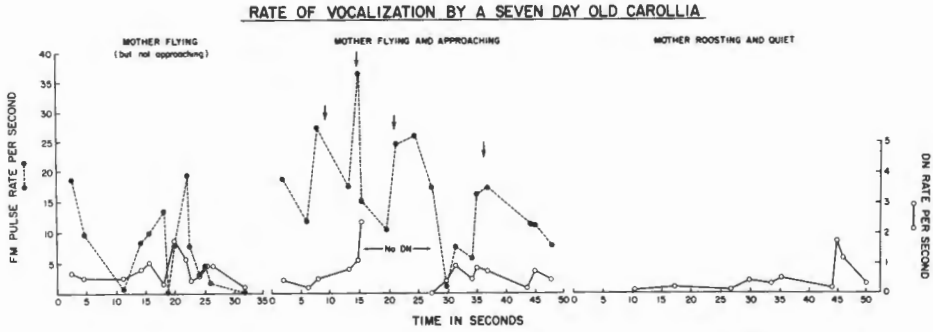
FIG. 10.—Rate of vocalizations by a seven-day-old *Carollia* during a reunion. The three sets of data were obtained as the infant remained motionless on a branch and the mother flew toward the infant or roosted quietly at a distance from the infant. Four arrows indicate the times that the mother flew toward the infant. The mother's FM pulses were not detected on the tape recording when the mother was flying about the room or when the mother was quiet. When the mother approached the infant, her FM pulses were detectable. The rate of her calls was not determined. Rates of DN and FM pulse emission while mother was flying and approaching (left and middle set of data) were obtained by slowing the recordings 128 times; the number of infant FM pulses was counted during the intervals between DNS. From these two tallies, the number of FM pulses per DN interval and the DN interval were used to compute the two rates. Intervals were measured from the beginning of one DN to the beginning of the next. Note that the vertical scale on the right refers to DNS; the vertical scale on the left refers to FM pulses.

nipple. Infant attaches to nipple. Just before mother flies from branch with infant attached, mother emits six FM pulses.

The tape recorder was on for 6 minutes, 15 seconds during which time infant emitted 162 DNS. The ratio of DNS to FM pulses varied from 1:3 to 1:4. Note that the tape recorder was only on about 35 per cent of the time. I plotted rate of FM pulse emission against time between DN phrases. The rate of FM pulse emission decreased as the time between DNS increased. The relationship is most apparent from the data obtained during the mother's approach to the infant. The plot of data obtained when the mother was flying but not approaching the infant is scattered.

Sixteen-day-old *Carollia*

Minus 0.—Infant was placed on horizontal branch and remained there until reunion.

0-1 min., 35 sec.—Tape recorder on. Mother released in chamber. Mother flies back and forth across room and then hangs up. Mother hangs up seven times. Infant emits a few FM pulses while mother flies. Infant is silent when mother hangs up.

1 min., 40 sec.-1 min., 45 sec.—Mother approaches infant within 12 centimeters for the first time. Infant emits burst of FM pulses with increased repetition rate during mother's approach.

1 min., 50 sec.-25 min.—Mother hangs up 22 times. Mother approaches infant within 12 to 20 centimeters 16 times. Infant emits burst of FM pulses each time mother approaches. During eight approaches, infant also emitted a total of 16 DNS that included FMGB (14) and FMGE (2). In three approaches, infant FM pulses could be distinguished clearly from those of the mother. During those three approaches, infant FM pulse rate emission increased in a similar pattern: in 940 msec. following the infant's first call, it emitted 8, 9.1 and 8.5

TABLE 3.—*DN emission decreases as the bat matures. R identifies data obtained from recordings of reunions; the remainder of the data was obtained from recordings of isolated infants.*

Species*	Age	Number of DNS	Time sampled in sec.	Rate/sec.
Leptonycteris	1R	89	246	0.37
	15R	24	450	0.04
Phyllostomus	2	38	120	0.3
	7	0	60	0
Desmodus	1	107	12.4	8.6
	5	60	16.8	0.3

*Each set of data derives from a different bat.

pulses/second in the three approaches respectively; in the next 940 msec., 8, 16, and 7.5 pulses/second, and in the last 940 msec., 1.6, 0.6 and 2.1 pulses/second. All three outbursts (composed of a total of 26, 23 and 17 FM pulses) were preceded and followed by long periods of silence from the infant. The mother's calls also were evident on the recording.

25 min., 10 sec.—Mother lands near infant. Six DNS with FMGB units are emitted, probably by the infant. Mother guides infant to her nipple. Just before taking off, mother emitted FM pulses of higher intensity than any of those recorded from the infant.

The tape recorder was on for 8 minutes, or 31.8 per cent of the time; it was turned off primarily when the mother was hanging. The infant emitted 34 DNS. The DNS were so infrequently emitted that I usually could not determine interval between calls. Four DN intervals measured 1.3 to 1.6 sec., and four measured 4 to 11.25 sec.

Table 2 shows the incidence of various calls during reunions and other experimental situations. In general, older bats emit fewer DNS (Table 3). For the 16-day-old *Carollia* and 15-day-old *Leptonycteris*, DN emissions were associated with approach and contact; younger bats emitted DNS more often and under more varied circumstances than did older ones. The rather abrupt decrease in DN emissions from *Carollia* at about 18 days of age is coincident with the time at which young begin to fly (Fig. 11). At 18 to 20 days of age, these bats should be able to take a more active part in their attempts to reunite with their mothers.

Macrotus

I have observed reunions of mother and infant in eight genera of bats. None of the mothers displayed as much determination to make contact with the infant as did those of *Macrotus californicus*. In 7 trials with three different mothers and their one-day, two-day and 11-day-old infants, the behavior was the same. As the calling infant was brought within hearing range (at least 3 meters) of the mother, the mother lunged from the back of her cage onto the door where she clung and "frantically" emitted DNS. When the infant was beyond hearing range of the mother, the mother was quiet. DNS are probably the mother's responses to the infant's calls. Two adult *Macrotus* responded to the calls of their infants by emitting DNS; the infants were held 0.75 meters from the mother and the microphone

RATE OF DN EMISSION BY CAROLLIA

fly, turn, gain altitude
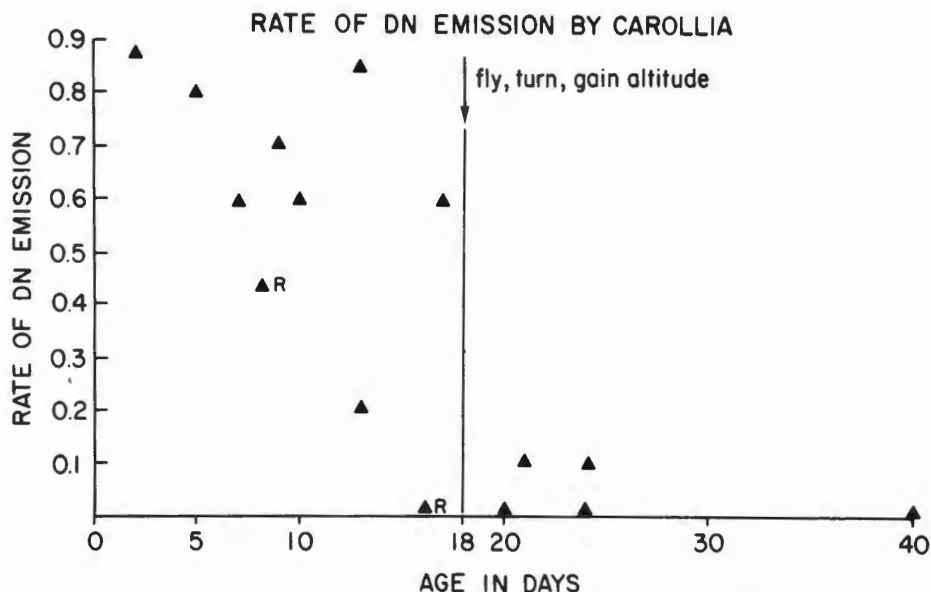
RATE OF DN EMISSION

FIG. 11.—Rate of DN emission of 15 individual *Carollia* at ages from two to 40 days. Recording samples ranged from 51 to 480 seconds (mean, 99; mode, 116). An *R* next to the symbol means that data were obtained during a reunion of the mother and infant. All other data points were obtained from isolated bats that experienced similar handling and exploration in a box. According to Bleier *et al.* (this volume), *Carollia* can maintain and gain altitude and turn and avoid obstacles at 18 days of age. Emission rate is expressed as pulses per second.

was placed a few centimeters from the mother. A sample of 74 phrases (usually two units per phrase) in six bouts had rates varying from 2.9 to 15.0 phrases per second (mean, 8.8). As soon as the infant was placed in the cage, the mother guided it to her teat even while the infant was still in my hand. The mother's and infant's DNS were so similar and so often emitted by both mother and infant that data analysis during close contact was next to impossible. Greater separation in a large enclosure is essential for further study of this species.

A reunion in a large enclosure (366 by 732 by 183 centimeters; Bee Tent, Chicopee Mfg. Co., Cornelia, Ga. 30513) revealed unexpected maternal behavior from an 11-day postpartum mother. *Macrotus californicus* generally gives birth to a single infant. Two infants, one and 11 days old, were placed about 15 centimeters apart on a fence post. The mother of the older infant was released in the enclosure and photographed with a 16-millimeter motion picture camera that was synchronized with repetitive flashing strobe lights (about 2.1 meters from the post). The film showed clearly, and substantiated our direct observation, that the mother approached the younger infant first and guided it to her nipple, she then crawled to her own infant and guided it to her other nipple and flew off with both infants securely attached. Before the mother landed, the younger infant called incessantly while the older infant called occasionally.

Leptonycteris

As two infant (one and eight days of age) *Leptonycteris sanborni* approached their mothers, they increased emission rates of DNS just prior to contact. In both reunions, the mother remained motionless and often quiet in the corner of the cage most distant from the door (during the first week or so after birth, *Leptonycteris* infants can walk; they then lose this ability and never regain it, Dietz, 1973). During the 13.8 seconds before contact, the 8-day-old infant emitted six DNS having the following intervals: 560, 180, 4009, 4009, 130, and 130 msec. respectively (range of repetition rate, 0.3 to 7.7 per second). The last three DNS were emitted just before, or when, the infant made contact with its mother. Both infants flapped their wings as they hung from the roof of the cage opposite their mothers. Each bout of wing flapping was accompanied by DN emissions. The force of the flapping raised the infants to a nearly horizontal position. Two to three-week-old young also flapped their wings; however, wing flapping in this case was accompanied by FM pulse emissions.

Warbles were detected on recordings of reunions of four and eight-day-old infants with their mothers. I could not determine whether the mother or infant emitted the call.

At least three naturalistic observations of *Leptonycteris sanborni* suggest the importance of acoustic communication.

1. In Colossal cave, near Tucson, Arizona, large concentrations of these bats gathered in small groups of 50 to 75, circled and then departed in a "string" composed of many small groups (four to six individuals each, Hayward and Cockrum, 1971). Other species leave their cave roost in a single massed evening flight. In the dark of a cave, group flights may be organized by acoustic signals such as wing flapping, FM pulses or DNS, or the like.

2. Hayward and Cockrum (1971) suggested that twittering (probably the audible component of DNS) seems to serve as a bond in keeping members of a *Leptonycteris* colony together; females hovered over, and landed on, sacks containing loudly twittering adults.

3. During reunion, the mother would wrap her forearms about a juvenile in front of her, draw it to her breast, then release her hold on the ceiling and fly away. This apparent search for, and identification of, a particular young bat was noted many times. Other young might attempt to attach but they were given no notice other than a fending off motion of the forearm. Of course, olfaction may play an important roll in the reunion.

Desmodus

Reunions of mother and infant *Desmodus rotundus* were similar to those of *Leptonycteris sanborni* in that the mothers remained motionless in the rear of the cage and only occasionally vocalized. Infants called often, frequently emitted DNS, and took the initiative by approaching their mothers. At or near contact, infants increased their DN repetition rate. Schmidt (1972) described reunions typified by more active mothers. His descriptions, including the vocal exchange between mother and infant, resemble my observations of *Macrotus californicus*.

This resemblance in our data could be derived from population variation or to undetermined disturbances in my colony; the infants in my study did reach adult size.

Schmidt (1972) noted the relationship between DN emission and the relative distances of a young of *Desmodus rotundus* from an adult. The isolated young (about 6 months old) emitted bouts of 2 to 5 calls; the young that could hear other bats emitted bouts of 40 calls. These observations, which concur with my own, indicate that increasing levels of excitement evoke longer and more frequent bouts. For example, each evening I drove home with two isolated infant bats that I was hand raising. (I began hand raising them when one was one day and the other seven days old). Throughout the ride, the infants emitted frequent DNS: the DN emission rate increased when I drove over bumps. One hand-raised infant ceased emission when it was about 30 days old. DNS were emitted by adult *Desmodus* (in the absence of young) when courtship was probably occurring.

A warble and a low intensity buzz were also detected from the mother or infant at or near contact. A one-day-old *Desmodus* emitted the buzz when close to its mother. A five-day-old infant that I had hand raised from its day of birth was placed in a container and allowed to become quiet. I slowly, and very quietly, introduced various strange objects, which I held a few centimeters from the bat. The animal immediately emitted brief DNS followed by a buzz. Schmidt (1972) found that when young animals recognized their mothers they emitted a long rattling (Schnarrilaut) call. This call is regularly emitted when a young animal is reunited with its mother after a long separation (Schmidt, 1972). Schmidt reported that a young female emitted the buzz when its mother was 15 meters away. I also detected this call from young animals during reunion with their mothers. The sonogram of this lower intensity buzz is indistinguishable from louder buzzes emitted during states of higher arousal, but a larger sample of better recordings might reveal discrete differences between loud buzzes emitted in high states of arousal and low intensity buzzes emitted during mother-infant reunions.

Schmidt (1972) also described a contact call (Kontaktlaut) (not heard in this study) that the mother emitted as she sniffed and licked her offspring.

Phyllostomus hastatus

During reunions, infants of *Phyllostomus hastatus* did not seem to emit DNS as often as other species. The paucity of DNS may reflect the predominance of visual cues in reunions of *Phyllostomus*. A three-day-old infant emitted only three bouts of DNS in three minutes; one bout occurred at the moment of contact with its mother. The mother climbed to the door of the cage as soon as I opened it and placed the infant inside. DNS were detected from one, two, three, four, and seven-day-old infants. During reunions of seven and 45-day-old infants with their mothers, infants emitted batteries of FM pulses that sometimes overlapped with FM pulses of the mother. I detected no calls from the mothers other than FM pulses. A colony of *Phyllostomus* emits various vocalizations audible to man; none was detected during the reunions.

Discussion

Studies of obstacle avoidance (Griffin, 1958; Grummon and Novick, 1963; Howell, 1974) show no clear trend distinguishing phyllostomatids from other groups of microchiropterans. Rather, differing echolocation acuities within the phyllostomatids have accompanied the evolution of diverse food habits (Howell, 1974). Physiological studies dealing with signal processing in phyllostomatids indicate no features unique to the family (Simmons, 1973; Grinnell, 1973). Likewise, laryngeal function (based on nerve section studies) is similar to vespertilionids (Novick and Griffin, 1961). Curiously enough, the function of the prominent nose leaf, which distinguishes this family from other groups of New World bats, remains a mystery.

Whispered FM pulses with multiharmonic structure are the most outstanding features characterizing the vocalizations of phyllostomatids. *Plecotus*, nycterids, and megadermatids also emit low intensity sonar calls (Griffin 1958; Novick 1963). In addition, all of these bats fly near large surfaces; they either feed on or perch near animals (*Desmodus*), fruits and flowers (*Carollia* and *Leptonycteris*), trees and shrubs (numerous leaf-nosed bats), walls or tree trunks (Nycteridae and Megadermatidae).

An examination of vocalizations emitted by young phyllostomatids reveals the pervasiveness of relatively high-intensity ultrasonics during communication between mother and infant. No less than four other investigators (Griffin, 1958; Grummon and Novick, 1963; Howell, 1974; Bradbury, 1970) have noted high-intensity vocalizations emitted by adult bats. Perhaps the most notable is Howell's finding that intensity control during approach to obstacles is a prominent feature of three species.

Phyllostomatid bats emit at least two fundamental types of ultrasonic vocalizations: FM pulses and DNS. Previously, I suggested that graded repetitive calls of bats and various Insectivora lie on a continuum that accompanies changing levels of excitation (Gould, 1971). Many sonograms of DNS particularly those of calls emitted by *Desmodus* and *Macrotus* resemble "twitters." A twitter refers to a short call that descends and ascends steeply; the sonogram resembles a chevron (Andrew, 1964). The level of excitation and associated behaviors that accompany emission of chiropteran DNS and soricid twitters (Gould, 1969, 1971) is somewhat comparable.

Several observations suggest the position of DNS in the continuum of graded signals.

1. When newborn infant *Desmodus*, *Phyllostomus*, *Carollia*, or *Macrotus* are isolated and at rest or gently stimulated by touching, they emit DNS. Simulated flight, which probably represents a higher level of excitation than rest, usually evokes the emission of FM pulses. In flight simulation, one gently holds the bat by the nape of the neck and moves it up and down.

2. One week old *Carollia*, *Leptonycteris*, and *Desmodus* emitted DN and FM pulses when their mothers called during a reunion. When the mother was quiet, the infant emitted only DNS.

3. Bouts of FM pulses often occur in bouts with DNS. When FM pulse repetition rates rise during high levels of arousal, DNS are no longer emitted. These observa-

tions imply that DNS can reflect a lower excitation level than do FM pulses. However, both FM pulses and DNS can occur concurrently. Two such vocalizations being emitted during the same level of excitation suggest two functional attributes: the simultaneous emission of two separate "messages" and the presence of two separate call-generating mechanisms.

One-day-old phyllostomatid bats of at least four genera can emit FM pulses. To suggest that a one to seven-day-old bat is using FM pulses for echolocation begs the question. What are the infant phyllostomatids detecting and why? The questions are particularly difficult to answer because leaf-nosed bats are relatively immobile during the first few days and weeks after birth (Dietz, 1973). If the infant could discriminate its own approaching mother from other mothers, how could it respond? A more tenable hypothesis is that both FM pulses and DNS serve as communication signals during reunions of mothers and infant. Of course, the problems of reunion are multiplied many fold in a large colony. Indeed, Davis *et al.* (1962) may have been correct when they noted that in a large colony of bats mothers nurse any infant. Such observations, however, do not obviate the possibility that the very same species may practice different nursing habits in smaller colonies. Certainly Kleiman's observations of fidelity in a captive *Carollia* colony along with other evidence in the literature (reviewed by Gould, 1970; also see Beer, 1970, review of bird literature) supports the idea that some mother bats nurse only their own offspring (see contrary evidence above for *Macrotus*).

Based on data from recordings of vocalizations and behavior during reunions of mother and infant, the following is a tentative model of how the reunion is accomplished.

1. Mothers leave the roost. Infants emit DNS at low repetition rates.

2. Mothers return to the roost and emit FM pulses as they fly. Infants emit DNS, which alert mothers to their presence. Mothers are attracted to the DN source. Infants emit DNS and FM pulses in response to adult FM pulses.

3. Mothers approach infants (see Bleier *et al.*, this volume). Infants increase the rate of FM pulse and DN emission. FM pulses provide pinpoint location of infants at close range.

4. Each mother determines acoustically or by olfaction, or both, the identity of her infant before or after landing. DNS provide information for individual recognition. A mother guides the infant to her nipple. Brown's (1973) descriptions of *Antrozous* reunions are not at variance with this model. Brown observed mothers approaching "wrong" infants, but eventually a mother did retrieve her own infant.

Echolocation and communication may function simultaneously. We cannot always assume that because a bat is flying, its vocalizations are being used for echolocation. In fact, Suthers (1965) described the emission of a probable communication signal from *Noctilio* that occurs during flight: "these relatively low frequency sounds have been termed 'honks' since they are apparently a means of warning an oncoming bat of an imminent collision." A honk might provide acoustic orientation information for the echolocating bat as well as warning information for an approaching bat. If behavioral information shows the bat avoiding obstacles or catching insects, surely the likelihood is great that the calls are functioning

primarily for echolocation. But when an infant bat emits FM pulses only when its mother is flying close by, we may infer that in this case FM pulses are probably being used primarily for communication; simultaneously, however, the infant might be obtaining information on the mother's location. I observed reunions in subdued red light. The visual ability of phyllostomatid bats was established by Suthers (1970); the mother and infant's ability to locate one another may be facilitated by visual clues.

Measurements of FM pulses and DNS emitted by *Desmodus* are consistent with Woolf's (1974) finding in *Eptesicus* that a pulse interval of about 20 to 30 msec. is a common feature of bat sounds. The existence of this pattern in both FM pulses and in DNS further substantiates the notion that communication and echolocation signals may be ontogenetically related. Intervals of all units within DNS were measured. The incidence with which intervals of a specific length occur among DN units may depend on the number of units. For example, DNS emitted by *Carollia* were often composed of two units of unequal duration, having intervals of about 20 to 30 msec.; one or two units of equal duration may precede or follow the two units of unequal duration. The interval from one of the equal duration units to one of the unequal duration units is about 50 to 60 msec., and this might explain the spread of data in Fig. 8. In *Carollia* and *Leptonycteris*, longer units break up into two subunits (Fig. 5), one of which is the FM pulse; the cleavage resembles Woolf's description of the *i*-call of *Eptesicus*, which divides into a DN. Woolf's (1974) designation of "sonar family" seems appropriate for the development of *Carollia* and *Leptonycteris* DNS and FM pulses. The variable vocalization units of an adult *Macrotus* suggest that divisions of this species' vocal repertoire (Fig. 5J-M) resemble divisions in *Carollia* and *Leptonycteris*.

These observations add support to the idea that sonar calls are derived from communication signals (Gould, 1970, 1971). This hypothesis was first verified by Konstantinov (1973) and then supported by Woolf (1974). Their conclusions depended on the deduction that calls from helpless, immobile infants are communicative. As a bat matures, the calls increase in frequency and decrease in duration.

Descriptions of phyllostomatid vocalizations are still too meager for speculations on phylogenetic relationships. *Glossophaga*, *Lonchophylla*, and *Leptonycteris* emit FM pulses with similar frequency patterns (Novick, 1963); *Desmodus*, *Macrotus*, and *Artibeus* are likewise grouped as having a similar FM pulse frequency pattern (Novick, 1963). DNS of *Macrotus* and *Desmodus* are similar; calls of both genera are low in frequency and possess a roughly similar chevron-shaped sonogram. In that they show no amplitude change when bats approach obstacles, *Leptonycteris* FM pulses differ from those of *Anoura*, *Glossophaga*, and *Choeronycteris* (Howell, 1974).

The greatest differences in species-specific vocalizations are seen by comparing DNS. DNS emitted by different species of bats differ most when frequency and frequency contour are compared (see sonograms in Fig. 1Q, 4A-T, 5A-M). Some differences are seen in intervals between units. Duration of phrases and duration of units within phrases showed the least differences among species (Fig. 9); the

20 to 30 msec. interval shows up in a few species of phyllostomatid bats. A similar interval occurs in *Eptesicus* (Woolf, 1974). These findings suggest that DNS may be as basic to chiropteran communication as FM pulses are to chiropteran echolocation. The probable role of DNS in communication is consistent with Marler's (1957) statement concerning bird signals: "signals that are in some way involved in reproductive isolation are likely to be highly divergent between closely allied sympatric species." The expression "reproductive isolation" is interpreted loosely. If roost sites limit bat populations (Tamsitt, 1967), and numerous species roost in the same site (Goodwin and Greenhall, 1961), then species specific vocalizations would facilitate communication among conspecifics. Thus, high intensity DN signals that have specific distinctiveness would operate over long distances (compared to whispered FM pulses). Whispered FM pulses might be characterized as signals with "moderate specific distinctiveness" (found in close-range signals, Marler, 1957).

Most of my recordings of DNS are from young animals. The decrease in emission of DNS by older bats suggests an association of DNS with early dependence. *Carollia* fly well at 18 days of age; at about that age, isolated *Carollia* rarely emit DNS. On the other hand, nursing mother *Macrotus* emit DNS during reunions, and adult *Desmodus* emit DNS in small captive colonies. The ubiquity of DNS in young bats, their diminution in juveniles, and the infrequency of DNS in adult bats suggest that the DN becomes associated with specific behavioral situations as the bats mature. In some cases, the frequency contours of DNS resemble complex bird songs. Physical characteristics of bat ultrasonics differ among species. In studies of social behavior of adult emballonurids, Bradbury (1972) described vocal exchanges as chirps, pure notes, and raspy buzzes grouped into themes. Andrew (1964) and Gould (1969) have noted the recurrence of infant primate and shrew vocalizations in adult displays. The implication is that species specific ultrasonic calls having the complexity (and musical beauty when slowed 16 times) of bird songs typify the vocal repertoire of infant and adult phyllostomatid bats. Many mammalian social organizations have their basic foundations in the bond between mother and infant and extensions of the family unit. This principle may hold for bat social organization. Studies of maternal-infant communication should eventually elucidate the process by which chiropteran social groups are formed and maintained.

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THERMOREGULATION

John J. McManus

There is a substantial literature on mammalian thermoregulation, and several comprehensive reviews are available for different orders of mammals (Whittow, 1971). Excellent surveys of existing literature on temperature regulation in bats were prepared by Stones and Wiebers (1965), McNab (1969), and Lyman (1970) and these should be consulted for general coverage of the Chiroptera. Also, because many species of bats enter torpor, the order is frequently discussed in context with the evolution and adaptive significance of heterothermy (Hudson, 1973; Whittow, 1973). Most earlier papers on bat metabolism and thermoregulation dealt with temperate zone microchiropterans (Hock, 1951; Reeder and Cowles, 1951) or tropical megachiropterans (Burbank and Young, 1934; Bartholomew *et al.*, 1964). A rough pattern emerged from these studies, which contrasted the relatively precise homeothermy achieved by the large, frugivorous megachiropterans with the pronounced thermolability and capacity for torpor shown by the smaller, insectivorous species that inhabit areas with more rigorous thermal environments. Within the past decade, many additional species of tropical microchiropterans have been examined. Most of these have proved to be intermediate in their temperature regulation and, collectively, they illustrate the continuum of thermoregulatory strategies that exists within the order Chiroptera. These recent works include data on temperature relation in more than two dozen members of the Phyllostomatidae, and the scope of this chapter will be restricted principally to a summary of this information. Some attempt will be made to place what is known of thermoregulation in phyllostomatids in evolutionary perspective and to suggest possible directions for future studies on New World leaf-nosed bats.

STATUS OF THERMOREGULATION BY PHYLLOSTOMATIDS

Problems of Measurement

Even the most casual survey of the literature indicates that within the Chiroptera there is an extraordinarily wide variation in the quality of temperature control. This variability makes generalizations regarding thermoregulatory strategy difficult and forces a careful analysis of the sources that contribute to wide differences in results, even at the species level. Lyman (1970) has enumerated some of the more important factors that should be considered in assessing temperature regulation in bats: 1) phylogenetic antiquity of the order; 2) high species diversity; 3) broad geographic distribution; 4) wide differences in habitat preference, feeding habits, and daily and seasonal levels of activity; 5) preponderance of smaller size classes; 6) high surface area to volume ratios; 7) capacity for energetically costly sustained flight; and 8) peculiarities of behavior and habitat requirements in the wild that often make it difficult to simulate ecologically realistic

conditions for testing the thermoregulatory capacity of captive animals. Thus, it is not surprising that various investigators have employed quite different methods and criteria for assessing temperature control in bats. All of the above constraints apply to the literature of the Phyllostomatidae and these should be noted when the following comparisons are made. A tabular summary of recent work on phyllostomatid thermoregulation is given (Table 1).

Effect of Body Weight on Basal Heat Production

In general, maintenance of a differential between body temperature and reduced ambient temperatures requires the generation of metabolic heat at levels just equal to the rate at which heat is lost from the body. Because heat production occurs within the volume of the body and heat loss is primarily a surface phenomenon, the ratio between surface area and body volume is important in establishing the level at which heat production and heat loss are balanced. Smaller animals, in which the surface area is high in relation to body mass, will have proportionally higher rates of heat loss and heat production than would be found in larger species. The predictive relationship between weight-specific metabolic rate (heat production per unit weight per unit time) and body weight takes the general form $M = kW^b$, where M is weight specific heat production, W is body weight, and k and b are constants. When heat production for many species of mammals at thermoneutrality is calculated as milliliters of oxygen per gram per hour (ml. O_2 g/hr), the constants k and b take the values 3.8 and -0.27, such that $M = 3.8W^{-0.27}$ (Brody, 1945; Kleiber, 1961).

McNab (1969) compared the basal metabolic rates of 23 species of New World leaf-nosed bats to the rates predicted for mammals within the weight range of nine to 97 grams (Fig. 1). As in other bats, the basal metabolic rates of phyllostomatids are inversely related to body size, and, for most species, the measured rates of heat production tend to be higher than those predicted by body weight. This is expected in view of the high surface area to volume relations caused by the presence of wings, large ears, and associated membranes.

The level at which body temperature is maintained is dependent on the ratio of heat production to heat loss and appears to be weight dependent (McNab, 1969, 1970). Smaller species of bats tend to have lower body temperatures than do larger species and this generalization seems to hold true for those phyllostomatids for which body temperatures have been recorded (Fig. 2). It is obvious, however, that smaller species of leaf-nosed bats show considerable variation in resting body temperatures and in many instances it is not clear whether this is the result of species differences or a reflection of such confounding variables as differences in physiological state, nutritional status, activity level, or methods of body temperature measurement (Lyman, 1970; Studier and Wilson, 1970). Nevertheless, because heat loss depends directly on the differential between internal and external temperature, even slight reductions in the set-point temperature by smaller phyllostomatids are advantageous in that they decrease the levels at which heat must be produced for maintenance of homeothermy.

Effect of Diet on Basal Heat Production

Phyllostomatids can be placed in categories based on their feeding habits—fruit and nectar feeders, larger carnivorous feeders, insect feeders, and blood feeders (McNab, 1969, 1970). Excepting the sanguivores and perhaps some of the most specialized nectar feeders, it is likely that insects are taken to varying degrees by all leaf-nosed bats, but the preceeding categories will be used as approximate indices of the bulk of the diet.

Frugivorous.—The leaf-nosed bats as a group are principally fruit eaters and this dietary commodity apparently has exerted a strong influence on temperature regulation in the family. McNab (1969) argued persuasively the notion that seasonal availability of fruit and nectar in Neotropical areas has allowed frugivorous phyllostomatids the luxury of elevated metabolic rates (Fig. 1) and has made nonessential the diurnal and seasonal torpor characteristic of temperate-zone insect feeders, the food supply of which is subject to severe daily and seasonal fluctuation. Arata and Jones (1967) posed a similar hypothesis and extended the reasoning to include tropical insect feeders. Despite a high degree of variation, resting body temperatures of frugivorous leaf-nosed bats (Fig. 2) tend to be held at relatively high levels, approximately 5 to 10°C higher than those of insectivorous species of comparable size (McNab, 1969: fig. 31; Lyman, 1970: table 1). It seems reasonable that this could be achieved only if energy sources were readily available to support the high levels of heat generation needed for such homeothermy.

Carnivorous.—The meat-eating phyllostomatids (*Tonatia bidens, Phyllostomus discolor, P. hastatus, P. elongatus, Chrotopterus auritus*) appear to approximate or slightly exceed the basal metabolic rates predicted by weight. They also are among the largest of the phyllostomatids. Practically nothing is known about the diet of carnivorous bats in the wild, but I presume that vertebrates comprise its bulk. Considering the relative stability of vertebrate populations in tropical areas, compared to the more pronounced fluctuations in abundance and availability of populations in temperate zones, one can speculate that larger carnivorous phyllostomatids have adjusted their energy expeditures in response to food reserves that remain relatively fixed in supply throughout the year. Availablity of food and large body size contribute to their fairly precise control of body temperature. However, the carnivorous species of leaf-nosed bats apparently depend on food supplies that, while temporarily available, may be spatially distributed in a way that cannot support second-level consumers. McNab (1971) observed that carnivorous species are the first to disappear from bat faunas on tropical islands with depauperate vertebrate communities.

Insectivorous.—Although Arata and Jones (1967) postulated that tropical insect feeders may resemble fruit and nectar feeders in thermal ecology, McNab's (1969) study suggested that they are quite different. Tropical insect feeders more closely resemble temperate zone taxa in their proclivity to relax thermoregulatory control when at rest and in their tendency to have lower basal metabolic rates. This apparently results from the fact that insectivorous species tend generally to be smaller and gain considerable metabolic savings by reducing body temperature-
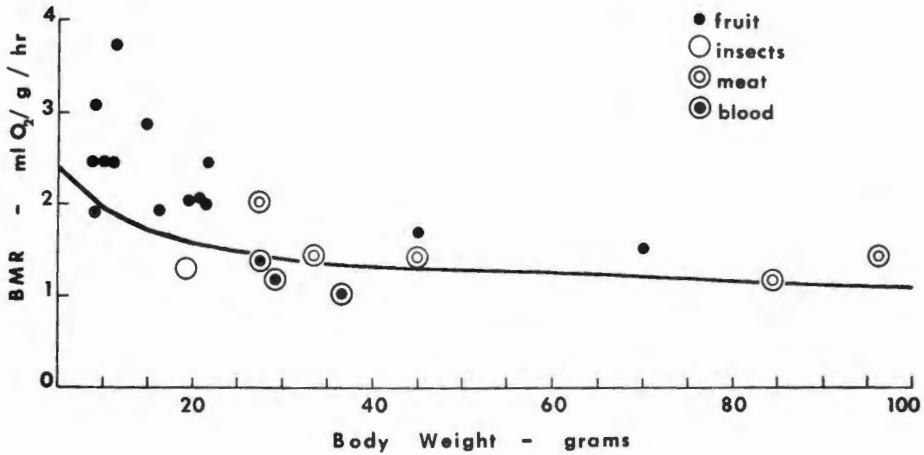
FIG. 1.—Basal metabolic rates of phyllostomatid bats. The regression line indicates the level of metabolism expected for a given weight based on the general relationship for many species of mammals: $BMR = 3.8W^{-0.27}$ (Kleiber, 1961). Data are based on McNab's (1969) study.

ambient temperature differentials. In addition, for many tropical areas, the presumption of a constant level of availability of insect foods is unfounded; tropical insect populations may respond seasonally to rainfall in a fashion similar to the response of temperate zone insects to seasonal temperature changes (Janzen and Schoener, 1968). Thus, tropical insect feeders do not utilize a dietary item in constant supply and cannot afford the luxury of the elevated metabolic rates seen in frugivorous species. Of the phyllostomatids studied, metabolic data are available for only one insectivorous species, *Tonatia sylvicola* (Fig. 1). It appears to conform to the pattern seen in other tropical insect feeders.

Sanguivorous.—Because of their unique feeding habits, vampire bats have attracted the attention of several investigators, and details of the thermoregulation and bioenergetics of one species, *Desmodus rotundus*, are as well known as for any bat. Early observations (Wimsatt, 1962) indicated that despite its moderate size (30 grams), *Desmodus rotundus* was surprisingly ineffective at controlling body temperature. At rest, body temperatures of vampire bats fell close to ambient temperatures (even at environmental temperatures as high as 33°C, Lyman and Wimsatt, 1966), and responses of individuals to reduced ambient temperatures varied markedly. McNab (1969, 1973) provided data for *Diaemus youngii* and *Diphylla ecaudata*, as well as for *Desmodus rotundus*, and both basal metabolic rates and body temperatures tended to be low in these species (Figs. 1, 2).

The effect of diet on the thermal economy of desmodontines was considered extensively by McNab (1969, 1973) and the following is a summary of his findings. The use of mammalian or avian blood by a vampire bat requires transporting all or part of the blood meal in flight. The size of the meal that can be ingested, therefore, is limited by the ability of the bat to carry it back to the roost (Crespo *et al.*, 1970). Furthermore, whole blood has a relatively low caloric density
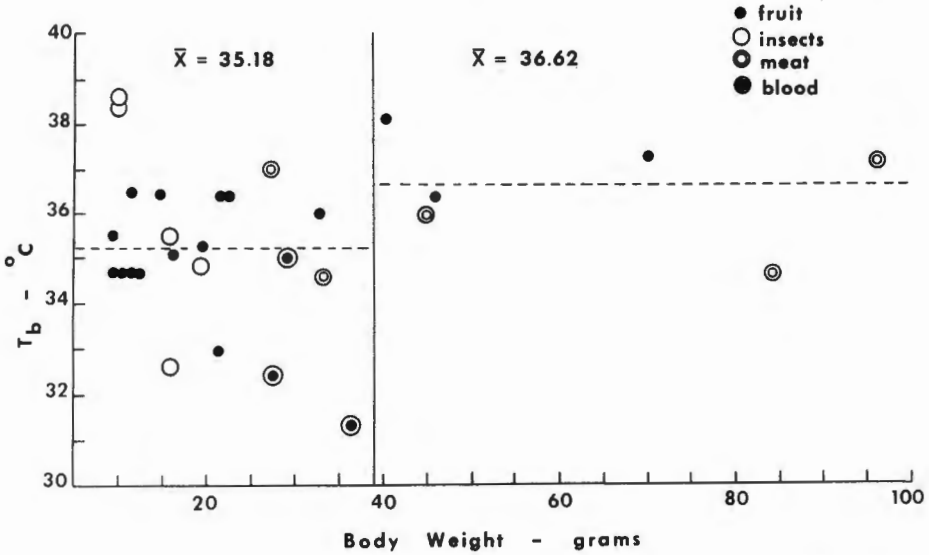
FIG. 2.—Resting body temperatures of phyllostomatid bats. Temperatures measured at ambient temperatures greater than 25°C. Based on data in Table 1.

and, although some concentration of the meal may occur prior to flight (by urination while feeding—McFarland and Wimsatt, 1969), vampires appear to be limited by the amount of energy they can acquire and process per foraging flight. Such limitations on energy intake would presumably be most severe for females near the end of pregnancy when load-lifting capacity is lowered and absolute energy needs are greatest. The conclusion drawn, then, is that the type of food employed by vampire bats forces them to conserve energy at times other than flight by relaxing control of body temperature while at rest and by sustaining relatively lowered rates of basal metabolism.

Resistance to Hyperthermia

With the exception of a few species, high temperature tolerance has not been studied systematically in leaf-nosed bats. The temperate zone species *Macrotus californicus* responded to increasing ambient temperatures (T_a) by initiating a series of slow wing-flapping movements when body temperature (T_b) reached 32.6°C (Reeder and Cowles, 1951). At T_b 34.7°C, wing movements increased in frequency and at T_b 38.7°C constant fanning occurred; after 26 minutes, T_b was held at 39.0°C in a T_a of 40.6°C. Wimsatt (1962) reported *Desmodus rotundus* to have surprisingly little tolerance of even moderately high air temperatures and suggested that the critical tolerance level was within the T_a range of 27 to 30°C. In controlled experiments, Lyman and Wimsatt (1966) found this same species unable to tolerate T_a's of 33 to 34°C for more than two hours. No wing fanning or salivation responses were noted.

Unpublished observations (McManus and Nellis) on *Artibeus jamaicensis* indicated that individuals of this species can tolerate T_a 40°C for up to five

TABLE 1.—*Thermoregulation data for various phyllostomatid bats. M_b is basal metabolic rate expressed as ml. $O_2/g/hr$. C is thermal conductance given as ml. $O_2/g/hr/°$ C. All temperatures are in degrees centigrade.*

Species	Weight in grams (N)	Resting			Tb after 2-5 hr. at approx.**			Lethal Temperatures				Diet	Remarks	Reference
								Upper		Lower				
		Tb	Mb	C	Ta 20°	Ta 15°	Ta 10°	Tb	Ta	Tb	Ta			
Phyllostomatinae														
Micronycteris megalotis	4-16*	38.6	—	—	29.5	29	17.5	—	—	5.3	3.0	insects, fruit	—	12
Micronycteris hirsuta	4-16*	36-41	—	—	25-34	19.5-30.5	14.5-30	—	—	—	—	insects, fruit	—	12
Macrotus waterhousii	12-20*	33.5-37.5	—	—	33.5	33	32	—	—	—	—	insects	shivers below Tb 24.3°; wing fanning above Tb 40°	10
Macrotus californicus	12-20*	32.6	—	—	—	—	—	40	41.6	18	5	insects		1,2,4
Tonatia bidens	27.4(many)	37.0	2.01	0.20	32.5-35.5	35-37.5	36.5-37	—	—	—	—	meat	—	10
Tonatia sylvicola	9-30*	34.8	1.3	—	32	37	37	—	—	—	—	insects	—	10
Phyllostomus discolor	33.5(11)	34.6	1.43	0.21	29-35	29.5-35	36	—	—	9	—	meat, fruit	clustering increases thermolability at Ta 20°	8,10
Phyllostomus hastatus	84.2(many)	34.7	1.19	0.15	34-37	31-36	32-37	42-46	41-43	—	—	meat, fruit	—	8,10
Phyllostomus elongatus	40-50*	36.0	1.43	—	—	—	—	—	—	—	—	meat, fruit	—	10
Chrotopterus auritus	96.1(10)	37.2	1.47	0.14	35-38	35-38.5	37-38.5	—	—	—	—	meat	—	10
Glossophaginae														
Glossophaga soricina	9.6(many)	35.5	3.06	0.45	31-37	25.5-38	11.5-36	—	—	6.8	6	nectar	food deprivation for one night induces torpor	8,10,11,12
Leptonycteris sanborni	22.0(30)	33+	2.0	0.26	33	34.5	37	41.9	42	—	10	fruit, insects	shivers below Ta 15°; no saliva spreading at high Ta	7
Anoura caudifer	11.5(many)	36.5	3.71	0.36	36.5	34.5	34-35	40.2	34	—	—	fruit, nectar	—	10

Species	Weight (n)											Food	Notes	Ref.
Carolliinae														
Carollia perspicillata	14.9(many)	36.4	2.89	0.35	22-37	17-38	12-37	39-40	37-39	—	—	fruit	lactating ♀ maintained Tb at Ta's 7.1-26.3°	6,10
Rhinophylla pumilio	9.5(9)	34.7	1.96	0.37	34-36	19.5-34.5	34	38.8	37.5	—	—	fruit	—	10
Stenoderminae														
Sturnira lilium	21.9(many)	36.4	2.43	0.25	35-37	34.5-38	34-38	—	—	—	—	fruit	survives Tb 41°	8,10
Uroderma bilobatum	16.2(6)	35.1	1.95	0.30	34	—	—	—	—	—	—	fruit		10
Vampyrops lineatus	21.9(11)	36.4	2.05	0.22	34.5-36	—	36	—	—	—	—	fruit	survives Tb 41°	8,10
Vampyressa nymphaea	10.5(5)	34.5	2.46	0.33	36	33	—	—	—	—	—	fruit		10
Vampyrodes caraccioloi	33(1)	34-38	—	—	26-35	26-33.5	13-31	—	—	—	7.8	fruit	maintains Tb 5.8-10.5° above Ta's from 7.8-33.1°	12
Artibeus cinereus	10.5(5)	34.5	2.46	0.33	35	—	31	—	—	—	—	fruit		10
Artibeus concolor	19.7(9)	35.3	2.02	0.27	33.5-34.5	34.5	—	—	—	—	—	fruit		10
Artibeus jamaicensis	45.2(4)	36.4	1.70	0.17	35-36.5	34.5-38	18-38	42-43.5	41.5-42	18	10	fruit	maintains Tb 6.6-8.3° above Ta's from 8.0-33.2°	8,10,12,13
Artibeus lituratus	70.1(many)	37.3	1.54	0.14	37-38	37-39	37	43.8-44.8	40-43	—	—	fruit	survives Tb 8.2; Tb 2-3° above Ta 20° after several hrs.	9,10,12
Artibeus hirsutus	44-53(1)	35	2.36	0.12	32	32.5	32	—	38	—	—	fruit	vigorous panting at Ta 38°; shivers below Ta 7.5°	7
Ametrida centurio	10.5(1)	34.5	2.46	0.33	34	30	20	—	—	—	—	fruit		10
Phyllonycterinae														
Brachyphylla cavernarum	40.1(32)	—			—	—	32.5-35	—	—	—	—	fruit	Tb > 21° after 24 hrs. at Ta 10°	13
Desmodontinae														
Desmodus rotundus	29.4(many)	35.0	1.18	0.19	33-37	33-36	32-36	—	33	—	3-5	blood	cannot rewarm from Tb 20°; no salivation or wing fanning at high Ta	3,5,10,14
Diaemus youngii	36.6(2)	31.3	1.02	0.17	32.5	—	—	—	—	—	—	blood	—	10,14
Diphylla ecaudata	27.8(13)	32.4	1.39	0.19	30-33.5	31-32.5	31-32.5	—	—	—	—	blood	—	10,14

*Where weights were not given they were taken from Walker et al. (1968).

**Tb rounded to the nearest 0.5°C; most were read from graphs.

References: 1, Reeder and Cowles (1951); 2, Bradshaw (1961); 3, Wimsatt (1962); 4, Leitner and Ray (1964); 5, Lyman and Wimsatt (1966); 6, Arata and Jones (1967); 7, Carpenter and Graham (1967); 8, Morrison and McNab (1967); 9, LaVal (1969); 10, McNab (1969); 11, Rasweiler (1970); 12, Studier and Wilson (1970); 13, McManus and Nellis (1972); 14, McNab (1973).

hours, but die within two hours at T_a 45°. Lethal body temperature is near 43°C. Carpenter and Graham (1967) found that *A. hirsutus* begins panting vigorously at T_a 38°C and suggested that these bats probably cannot survive higher ambient temperatures. The same authors reported that *Leptonycteris sanborni* maintained a body temperature between 39.2 and 41.5°C after a four-hour exposure to 41.5°. Although *Leptonycteris* was quite efficient at resisting hyperthermia, no conspicuous thermoregulatory behaviors such as wing fanning or salivation occurred. The lethal body temperatures listed in Table 1 usually were recorded after accidental deaths during oxygen uptake tests. Collectively, they resemble those of other mammals, although lethal T_b values for *Carollia perspicillata* and *Rhinophylla pumilio* are suspect because death probably resulted from causes other than hyperthermia. Levels of ambient temperature tolerated by phyllostomatids tend to be high, but not exceptional. This probably reflects the moderating nature of most roost sites and the nocturnal habits of the animals.

Resistance to Hypothermia

As a rule, leaf-nosed bats show little tendency to experience large reductions in body temperature when exposed to low ambient temperatures for short periods (Table 1). As exposure time increases, however, body temperatures vary erratically, particularly at ambient temperatures outside the normal range of temperature encountered in the wild. Additionally, the length of time between capture and testing appears to confuse the issue (McNab, 1969; Studier and Wilson, 1970) and nutritional status undoubtedly influences the magnitude of T_b-T_a differentials sustained. In several species, exposure to low ambient temperatures causes a drop in body temperature, but to some relatively constant level above the ambient temperature. Studier and Wilson (1970) computed regression formulas to describe the relation between T_b and T_a for two species at various ambient temperatures. Between T_a 33.2 and 8.0°C, *Artibeus jamaicensis* gave the response $T_b = 8.8 + 0.9333\ T_a$ whereas between T_a 33.1 and 7.8°C, *Vampyrodes caraccioloi* showed $T_b = 12.0 + 0.813\ T_a$. McManus and Nellis (1972) found *A. jamaicensis* able to maintain T_b above 35° after six hours at 10°C and one individual was able to keep T_b above 18° for at least 14 hours at 10°.

Brachyphylla cavernarum held T_b above 25° after 24 hours at 10°. There are no known species of phyllostomatids that naturally enter deep torpor—even those species, such as *Macrotus californicus* or *Leptonycteris sanborni*, which are native to, or regularly enter, temperate areas. Carpenter and Graham (1967) observed that *Leptonycteris sanborni* and *Artibeus hirsutus* were able to regulate body temperature within levels of precision equivalent to those of other small mammals of comparable size, and McNab's (1969) study extended this pattern to many other species.

An interesting observation made by McNab (1969) on *Phyllostomus discolor*, *Tonatia bidens*, and *Chrotopterus auritus* was that these species may show a temporary relaxation of temperature control at moderately reduced ambient temperatures (approximately similar to those of their roost sites), yet are capable

of more effective thermoregulation at lower temperatures. The implication is that temporary hypothermia may be "intentionally" tolerated and serves to decrease the differential between ambient and core temperature. Such a strategy would reduce energy requirements during periods of inactivity and may explain in part the rather pronounced diurnal variation in resting body temperatures noted by Morrison and McNab (1967). Nevertheless, the overriding tendency among the majority of leaf-nosed bats examined is to maintain body temperature at a roughly constant level when exposed to moderately low ambient temperatures. When forced to withstand temperatures well below those normally encountered, responses vary markedly, with larger species tending to conserve body heat more effectively than smaller kinds (Table 1). Compared to temperate zone microchiropterans that regularly enter deep torpor, the lower lethal minima for phyllostomatids appear to be higher by 10°C or more.

Social Thermoregulation

With one exception, the energetic significance of clustering as a means of behavioral thermoregulation has been neglected in New World leaf-nosed bats. In torpid microchiropterans from temperate areas, clustering is regarded as a means of reducing variations in body temperature by decreasing the exposed surface area of any individual in a cluster. In contrast to the result of such behavior in strict homeotherms (Tertil, 1972, and references therein), clustering in hibernating bats is not intended to conserve heat, but rather to keep body temperature low and to avoid temporary increases in ambient temperature (Twente, 1955). Such behavior promotes the most prudent use of stored fats during hibernation by keeping metabolic rate low (Hock, 1951; McManus and Esher, 1971). Apparently a similar strategy is employed by at least one species of phyllostomatid, *Phyllostomus discolor*. McNab (1969) found that clustering at 20°C resulted in a drop in both mean body temperature and mean resting metabolic rate of bats in a cluster as compared to that of single individuals. Whether such behavior is widespread among leaf-nosed bats is unknown. Additionally, the object of social thermoregulation in species with more precise thermoregulatory control than *P. discolor* (see preceeding section) may in fact be heat conservation rather than maintenance of reduced body temperatures. Finally, for species of bats that regularly form clusters while roosting, the testing of an individual in a metabolism experiment is an abnormal situation and may contribute greatly to variation in physiological performance. I suspect that this area would yield interesting results with further study.

Torpor

Deep torpor and seasonal hibernation are found only in the families Vespertilionidae, Rhinolophidae, and to a lesser extent in the Molossidae. Viewing this as one extreme condition and precise endothermy as the other, phyllostomatids appear to occupy a broad portion of the spectrum. Hudson (1973) regarded the ability of Neotropical bats to tolerate low body temperatures as "an ancestral phenotype (as well as genotype) which could easily be modified to give the 'deep'

or 'true' hibernator. Under tropical conditions, such a thermoregulatory per-
formance represents a solution for which there is no problem." A similar thesis
was advanced by Studier and Wilson (1970) who suggested the possibility that
the thermolability of tropical bats may be nonadaptive. Although this may be
true for frugivorous and perhaps carnivorous bats, the facultative capacity to
experience and tolerate slight reductions in body temperature during periods
of inactivity is clearly advantageous for small insect feeders and sanguivores.

CONCLUSIONS

The family Phyllostomatidae presents a varied mosaic of thermoregulatory
strategies, but the problems of measurement, coupled with natural variation in
levels of temperature control among species, make broad generalizations difficult.
Perhaps the easiest way to summarize this review is to indicate those parameters
that appear to have influenced the development of thermoregulation in leaf-nosed
bats.

Body size appears to affect resting rates of metabolism and resistance to hypo-
thermia in much the same way as it does in other mammals. Qualitatively, smaller
species have higher basal metabolic rates and poorer temperature control at
reduced temperatures than do larger species. Quantitatively, the peculiar surface
area to volume ratios unique to bats cause the levels of metabolism to be higher in
general than those of other mammals of comparable weight. This disparity is
most obvious in small and intermediate-sized phyllostomatids.

Diet and trophic position seem to be of particular import in determining thermo-
regulatory performance. First-level consumers feeding on spatially and temporally
available foods such as fruits and nectar achieve higher basal rates of metabolism
than do most second-level consumers. Carnivorous species have fairly precise
thermoregulation, but this is associated with their generally larger body size.
Insect feeders and blood feeders, for which food supplies are temporally or lo-
gistically limited, or both, seem to have developed either a more relaxed pattern of
temperature control or have reduced the set-point at which metabolism proceeds.
One glaring insufficiency in our knowledge of thermoregulation in leaf-nosed
bats (and most other bats) is the paucity of data on food intake under natural
conditions or in the laboratory. Associated with this is the scarcity of field temper-
atures for bat roost sites upon which any type of bioenergetic analysis must de-
pend.

Social aggregation is suspiciously well developed in several species of leaf-nosed
bats and, along with such obvious factors as availability of roost sites and synchro-
nization of reproductive activities, the thermoregulatory significance of such
behavior merits investigation. The climatic history of New World leaf-nosed bats
during their evolution seems to have allowed considerable latitude in the degree
of temperature control. Thermal stresses comparable to those encountered in
temperate regions have not been present in sufficient strength to force the develop-
ment of precise homeothermy, nor have they caused the adoption of "deep torpor"
capabilities typical of bats at higher latitudes. One broad generalization that
can be made with respect to the family Phyllostomatidae is that they are extremely
diversified in details of their temperature control.

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[Editors' note: John J. McManus died on 22 August 1975 without having an opportunity to read galley proofs or correct any errors inadvertently incorporated, or overlooked, in his contribution to this volume.]

FEEDING HABITS

Alfred L. Gardner

> There is something fascinating about science. One gets such wholesale
> returns of conjecture out of such a trifling investment of fact.
>
> Mark Twain

With few exceptions, knowledge of bat food habits, like that of many other
aspects of chiropteran biology, is superficial or wanting. Nevertheless, the study
of bats sometimes has been stimulated because of the interest generated by their
unusual or economically important food habits: the sanguivorous diets of vam-
pires, flower-feeding habits of glossophagines, and the carnivory of some phyl-
lostomatines.

General knowledge of food habits was used in some of the early classifications
of bats. Gray (1821:299) divided his class Cheiroptera into two orders, the Fruc-
tivorae and the Insectivorae. Along the same lines, Koch (1862-1863:298)
erected the two suborders Carpophagen and Entomophagen, and Gill (1872,
1886) separated the Chiroptera into the suborders Animalivora and Frugivora
(again representing major differences in food habits). In these examples, the In-
sectivorae, Entomophagen, or Animalivora included all of the known forms of the
Phyllostomatidae. The Fructivorae, Carpophagen, or Frugivora are equivalent to
the Old World fruit bats, the Megachiroptera.

Other names applied to members of the Phyllostomatidae reflect known or
alleged feeding habits. The generic names *Vampyrum*, *Vampyrops*, *Vampyrodes*,
and *Vampyressa* refer to the alleged blood-feeding habits of vampires. *Diaemus*
means blood-stained, an appropriate name for a true vampire. *Glossophaga* lit-
erally means to eat with the tongue. *Lichonycteris* means a bat that licks, also
in reference to using the tongue when feeding. *Musonycteris* implies an associa-
tion with banana plants. The name *Anoura werckleae* was employed to reflect the
feeding relationship of this bat with the plant *Wercklea lutea*. The trivial name
mordax refers to biting (*Lonchophylla mordax* and *Sturnira mordax*).

Common names often refer to presumed food habits as well. Some of these are
the "Cuban Fruit-eating Bat" (*Brachyphylla nana*), the "Hairy Fruit-eating Bat"
(*Artibeus hirsutus*), and the "Cuban Flower Bat" (*Phyllonycteris poeyi*). A few
names suggest diets when, in fact, the foods consumed are not known (for in-
stance, the "Red Fig-eating Bat," *Stenoderma rufum*; the "Brown Flower Bat,"
Erophylla bombifrons).

My principle objective in surveying the food habits of the Phyllostomatidae
was to bring together most of the available published information on the diets
of these bats in a form that not only will provide an accessible information source,
but also will encourage future investigations on this aspect of bat biology. I have
reviewed most of the accessible literature with disappointing results. With few
exceptions, very little has been recorded on the diets of these animals, and much

of this is superficial and noninformative. The information presented in the species accounts deals almost exclusively with the diets of free-living bats as reported in the literature. A few personal observations on food habits as well as some literature references on foods consumed in captivity have been included when considered pertinent, although the chapter, Care in Captivity, by Greenhall adequately covers the latter subject. Inferences on diets as suggested by dental and alimentary tract anatomy are equally restricted because the chapters, Oral Biology, by Phillips *et al.*, and Gastro-intestinal Morphology, by Forman and Rouk, provide ample information on these aspects as well. The diet for each species follows the scientific name in the food habits accounts below.

Table 1 is a list of those plant genera and species for which parts have been reported as foods consumed by phyllostomatid bats.

PROBLEMS IN DETERMINING FOOD HABITS

If we could observe and record the variety and quantity of foods as they are gathered and consumed by bats, the determination of diets would be a relatively simple matter. Because this usually is not possible, the examination of feces or digestive tract contents would appear to be the next best method. However, the comminuted remains of insects and small vertebrates are usually difficult to identify; a problem intensified by the habit of many bats to discard the harder, and often the only diagnostic, parts of their prey. For example, the abdomens of lepidopterans and other large insects are often the only parts consumed, the other parts being discarded. The taxonomy of many of the insects consumed by bats is little known and reference collections of insects from areas where the bats were collected are usually not available. Therefore, the determination of the insect order or family may be the only identification possible from fecal or stomach contents. Masticated remains of fruits found in stomachs are almost impossible to identify if associated seeds are not present. Seeds found in stomach contents and feces also are difficult to identify, particularly without the aid of a comprehensive reference collection of seeds. Nevertheless, fruits are often emphasized when diets are reported because when seeds are available, they are usually easier to identify than insects. This is especially true when the fruits come from locally conspicuous and well-known plants.

Some items such as seeds, fruit, or bits of sand or gravel found in the stomachs of omnivorous and carnivorous bats can be misleading because they may have been consumed by an animal before it was ingested by the bat itself. Stomach content analyses also can be deceptive if the bats are maintained alive together in small cages or cloth bags subsequent to their capture. Fighting and cannibalism among bats held under these conditions is common, and finding blood or the remains of bats in the stomachs of these bats should not be considered as indicative of normal diets unless, of course, the bats are vampires or species with known carnivorous habits.

Detailed analyses of stomach contents can be very informative. The excellent study by Alvarez and Gonzalez Q. (1970) demonstrated that analyses of the digestive tracts of pollinivorous species not only indicate what flowers are being

TABLE 1.—*List of plants for which products are known to be included in the diets of phyllostomatid bats.*

Acacia	Leguminosae, Mimosoideae
Achras sapota	Sapotaceae
Acnistus	Solanaceae
Acrocomia aculeata	Palmae
Agave schottii	Amaryllidaceae
Albizzia	Leguminosae, Mimosoideae
Alexa grandiflora	Leguminosae, Papilionoideae
Alnus	Betulaceae
Anacardium excelsum	Anacardiaceae
Anacardium occidentale	Anacardiaceae
Anamomis umbellulifera	Myrtaceae
Andira inermis	Leguminosae, Papilionoideae
Annona muricata	Annonaceae
Annona pisonis	Annonaceae
Annona squamosa	Annonaceae
Anoda	Malvaceae
Anthurium	Araceae
Arbutus	Ericaceae
Aristolochia	Aristolochiaceae
Artocarpus integrifolia	Moraceae
Bactris	Palmae
Bauhinia pauletia	Leguminosae, Caesalpinioideae
Beilschmiedia	Lauraceae
Berberis	Berberidaceae
Bombax	Bombacaceae
Bougainvillea spectabilis	Nyctaginaceae
Brosimum alicastrum	Moraceae
Bursera	Burseraceae
Byrsonima spicata	Malpighiaceae
Caesalpinia	Leguminosae, Caesalpinioideae
Calliandra	Leguminosae, Mimosoideae
Calocarpum mammosum	Sapotaceae
Calophyllum brasiliense	Guttiferae
Calycolpus warszewiczianus	Myrtaceae
Carica papaya	Caricaceae
Carludovica palmata	Cyclanthaceae
Carnegiea gigantea	Cactaceae
Casimiroa edulis	Rutaceae
Cecropia bureaniana	Moraceae
Cecropia obtusifolia	Moraceae
Cecropia peltata	Moraceae
Ceiba pentandra	Bombacaceae
Centropogon	Campanulaceae
Cereus hexagonus	Cactaceae
Cerocarpus (= Eugenia) disticus	Myrtaceae
Chlorophora tinctoria	Moraceae
Chrysalidocarpus (Areca) lutescens	Palmae
Chrysobalanus icaco	Polygonaceae
Chrysophyllum cainito	Sapotaceae
Citharexylum	Verbenaceae
Coccoloba uvifera	Polygonaceae

TABLE 1.—*Continued.*

Coccothrinax	Palmae
Coffea	Rubiaceae
Conzattia	Leguminosae, Caesalpinioideae
Cordia bicolor	Boraginaceae
Cordia collococca	Boraginaceae
Cordia dodecandra	Boraginaceae
Crataeva benthami	Capparaceae
Crescentia amazonica	Bignoniaceae
Crescentia cujete	Bignoniaceae
Croton	Euphorbiaceae
Cynometra retusa	Leguminosae, Caesalpinioideae
Datura	Solanaceae
Dendropanax arboreus	Araliaceae
Diospyros digyna	Ebenaceae
Diospyros ebenaster	Ebenaceae
Diospyros kaki	Ebenaceae
Diospyros mabola	Ebenaceae
Dipteryx odorata	Leguminosae, Papilionoideae
Durio zibethinus	Bombacaceae
Echinocactus	Cactaceae
Elizabetha paraense	Leguminosae, Caesalpinioideae
Eperua falcata	Leguminosae, Caesalpinioideae
Epiphyllum hookeri	Cactaceae
Eriobotrya japonica	Malaceae
Eucalyptus	Myrtaceae
Eugenia jambos	Myrtaceae
Eugenia malaccensis	Myrtaceae
Eugenia nesiotica	Myrtaceae
Eugenia uniflora	Myrtaceae
Ficus benjamina	Moraceae
Ficus cotinifolia	Moraceae
Ficus glabrata	Moraceae
Ficus insipida	Moraceae
Ficus obtusifolia	Moraceae
Ficus padifolia	Moraceae
Ficus radula	Moraceae
Ficus religiosa	Moraceae
Ficus retusa	Moraceae
Flacourtia indica	Flacourtiaceae
Genipa	Rubiaceae
Gentiana	Gentianaceae
Geranium	Geraniaceae
Heisteria	Olacaceae
Hibiscus	Malvaceae
Hohenbergia	Bromeliaceae
Hylocereus lemairei	Cactaceae
Hymenaea courbaril	Leguminosae, Caesalpinioideae
Inga	Leguminosae, Mimosoideae
Ipomoea arborea	Convolvulaceae
Iriartea exorrhiza	Palmae
Jambosa vulgaris (= *Eugenia jambos*)	Myrtaceae
Kigelia aethiopica	Bignoniaceae

TABLE 1.—*Continued.*

Lantana	Verbenaceae
Lecythis zabucajo	Lecythidaceae
Lemaireocereus	Cactaceae
Licania	Chrysobalanaceae
Livistona chinensis	Palmae
Lonchocarpus	Leguminosae, Papilionoideae
Lucuma (= *Pouteria*) *caimito*	Sapotaceae
Madhuca latifolia	Sapotaceae
Malpighia glabra	Malpighiaceae
Malvaviscus acerifolius	Malvaceae
Mammea americana	Guttiferae
Mangifera indica	Anacardiaceae
Manilkara bidentata	Sapotaceae
Manilkara zapota	Sapotaceae
Marcgravia	Marcgraviaceae
Melicocca bijuga	Sapindaceae
Mimosa	Leguminosae, Mimosoideae
Mimusops elengi	Sapotaceae
Morus (= *Chlorophora*) *tinctoria*	Moraceae
Mucuna andreana	Leguminosae, Papilionoideae
Muntingia calabura	Elaeocarpaceae
Musa paradisiaca	Musaceae
Myrcia joboticaba	Myrtaceae
Myrtillocactus	Cactaceae
Ochroma lagopus	Bombacaceae
Oenothera	Onagraceae
Parkia gigantocarpa	Leguminosae, Mimosoideae
Parkia pendula	Leguminosae, Mimosoideae
Parmentiera alata	Bignoniaceae
Passiflora quadrangularis	Passifloraceae
Persea americana	Lauraceae
Pilocarpus pinnatifolius	Rutaceae
Pimenta racemosa	Myrtaceae
Pinus	Pinaceae
Piper amalago	Piperaceae
Piper auritum	Piperaceae
Piper hispidum	Piperaceae
Piper sanctum	Piperaceae
Piper tuberculatum	Piperaceae
Pitcairnia	Bromeleaceae
Platyopuntia	Cactaceae
Poulsenia armata	Moraceae
Pouteria multiflora	Sapotaceae
Pseudobombax	Bombacaceae
Pseudolmedia oxyphyllaria	Moraceae
Psidium guajava	Myrtaceae
Psidium mediterraneum	Myrtaceae
Purpurella grossa	Melastomataceae
Putranjivora roxburghii	Euphorbiaceae
Quararibea funebris	Bombacaceae
Quercus	Fagaceae
Rheedia edulis	Guttiferae

TABLE 1.—*Continued.*

Roupala	Proteaceae
Roystonea oleracea	Palmae
Rubachia (= *Marlierea*) *glomerata*	Myrtaceae
Salix	Saliaceae
Salvia	Labiatae
Sapindus saponaria	Sapindaceae
Sideroxylon quadrioculare	Sapotaceae
Solanum paniculatum	Solanaceae
Spondias cytherea	Anacardiaceae
Spondias lutea	Anacardiaceae
Spondias mombin	Anacardiaceae
Spondias purpurea	Anacardiaceae
Stemmadenia	Apocynaceae
Symbolanthus latifolius	Gentianaceae
Syzigium (= *Eugenia*) *jambos*	Myrtaceae
Terminalia catappa	Combretaceae
Theobroma cacao	Sterculiaceae
Turpinia pinnata	Staphylaceae
Vismia latifolia	Hypericaceae
Vitis vinifera	Vitaceae
Vochysia	Vochysiaceae
Wercklea lutea	Malvaceae
Zea	Graminae
Zingiber	Zingiberaceae

visited but can provide evidence on the movements of populations, seasonal changes in diets, and competition for the same foods by sympatric species. The recovery and identification of pollen grains from the fur of bats may indicate the flowers visited as well (Heithaus *et al.*, 1975; Howell and Burch, 1974). Analyses of blood meals in the stomachs of vampires have indicated if mammals, birds, or both were the prey (Villa-R. *et al.*, 1969).

When names of the food items of bats are reported (Greenhall, 1956; Goodwin and Greenhall, 1961; Wilson, 1971; Vázquez-Yáñez *et al.*, 1975), they most often are based on identifications of dropped or discarded parts of plants, insects, or vertebrates found associated with bat roosts. Here the problem is to associate the remains with the bats that left them. Correctly associating food remains is difficult if the roost sites where the remains were recovered are used by one or more species during the day and by yet other species at night.

Observing, photographing, or collecting bats as they feed on flowers or fruit are ways to associate species with the foods they eat. Another way is to identify items the bats are carrying when captured in mist nets. Among the Phyllostomatidae, the commonest food items found in nets are fruits; however, Valdez and LaVal (1971) recovered an *Anolis lemurinus* after it had been carried into a net by a *Trachops cirrhosus*.

Food Habits

The Phyllostomatidae display a wide variety of food preferences, and relatively few species are restricted to a specific dietary regime. Only piscivory, among the types of chiropteran food habits, has not been found in the New World leaf-nosed bats.

The majority of the Phyllostomatinae are omnivores; however, some have strong tendencies toward carnivory. The only true insectivore in the subfamily (and family) may be *Macrophyllum macrophyllum*. *Vampyrum spectrum* and *Chrotopterus auritus*, both principally carnivorous, prey upon a variety of small vertebrates, including bats. Fruits and flowers are important components in the diets of many phyllostomatines, and some species, such as *Phyllostomus hastatus*, serve an important function in flower pollination (chiropterogamy) and plant dispersal (chiropterochory). Most phyllostomatines have the ability for hovering flight and, as suggested by their relatively large ears and eyes, probably are able to detect and capture prey on the ground or from foliage, tree trunks, and other surfaces.

The diets of the Glossophaginae include pollen, nectar, and, occasionally, parts of the corolla of flowers. As specialized flower feeders, these bats also play an important role in chiropterogamy. The majority is known to consume a variety of fruits, and some are suspected to pursue actively insects in addition to eating those captured at flowers. Wind borne pollen (*Alnus* and *Pinus*, see Alvarez and Gonzalez Q., 1970) has been found in the stomachs of *Glossophaga*, *Leptonycteris*, *Choeronycteris*, and *Anoura*. These pollen grains probably were ingested from flowers and watering places where they settled (on pools of water, in bromeliads, and in cavities or depressions in trees).

The Carolliinae and Stenoderminae perhaps are best considered as frugivorous and some species indeed may be obligate frugivores (for example, *Pygoderma*, *Ametrida*, and *Centurio*). Many, however, also consume flower parts, pollen, nectar, and insects, particularly the Carolliinae, which are known to consume quantities of insects (Fleming *et al.*, 1972). Stenodermines undoubtedly consume insects in the course of eating fruit because many fruits contain insect larvae. Frugivorous bats, as pointed out by Ayala and D'Alessandro (1973) and Forman (1973), probably must consume large amounts of fruit because adequate proteins, fats, and minerals are not abundant in this food. Several bats have been caught in fruit-baited traps placed on the ground and their capture supports the observations of Jimbo and Schwassmann (1967) that bats will feed on ripe fruit that has fallen to the ground. *Artibeus* has been reported to capture insects (Tuttle, 1968) and eat nestling birds (Ruschi, 1953j); other stenodermines may prove to be insectivorous or carnivorous.

The Phyllonycterinae are an assemblage of fruit, pollen, nectar, and insect-eating species restricted in distribution to the Antilles. The limited information available on their food habits indicates a preference for pollen and insects, although soft fruits are eaten as well.

The Desmodontinae are obligate sanguivores and, within the Phyllostomatidae, have the most specialized dietary requirements. Insects and bits of flesh have

been found in the stomachs of *Desmodus rotundus* (Arata *et al.*, 1967; Greenhall, 1972). These items, however, were most likely ingested during bite site preparation or when feeding on the host. The ectoparasite reported by Arata *et al.* (1967) in a *Desmodus* stomach probably was consumed during grooming activities. *Diaemus* and, to a lesser extent, *Diphylla* show a preference for bird blood. *Desmodus* preys on birds as well, but apparently prefers mammalian blood. Population densities of vampires probably have increased owing to the readily available food source supplied by domestic livestock. Before the availability of livestock and the widespread use of mosquito netting, vampires (particularly *Desmodus*) may have depended on human populations as a major food source. Cashinahua Indians living at Balta, Departamento de Loreto, Perú, an area with very few *Desmodus* and no domestic livestock, like mosquito netting as much for keeping away vampires as for protecting against insects. These people have been using mosquito netting for relatively few years and clearly remember having been bitten by bats in the past.

SUBFAMILY PHYLLOSTOMATINAE

Genus MICRONYCTERIS Gray

Micronycteris megalotis

A variety of insects and fruits.

Gaumer (1917), observing that *M. megalotis* flew slowly and near the ground in Yucatán, México, surmised that they ate insects caught close to the ground. Ruschi (1953*d*) mentioned insects and the fruits of *Musa paradisiaca, Psidium guajava, Jambosa vulgaris, Cecropia* sp., *Eriobotrya japonica*, and *Solanum paniculatum* as part of the diet of Brazilian *M. megalotis*. Guavas (*Psidium guajava*) were also reported as a food item of this species in San Luis Potosí, México, by Dalquest (1953), who believed that they probably feed on many kinds of fruit. He found them feeding on small guavas, which they plucked and carried off to a nearby tree to eat, often dropping and losing much fruit in the process. Goodwin and Greenhall (1961) classified *M. megalotis* as a fruit-eating bat apparently fond of small ripe guavas, yet noted both insects and yellow fruit pulp in the stomachs of some specimens from Trinidad. The stomachs of specimens taken during the daytime in Veracruz, México, were empty; however, the stomachs of two collected at night were filled with the remains of insects (Hall and Dalquest, 1963). Howell and Burch (1974) reported that a Costa Rican specimen had consumed an "unknown green fruit." The categorization of *M. megalotis* as a nectar-eating species by Valdivieso and Tamsitt (1962) appears to be unsupported.

Micronycteris schmidtorum

Insects and probably fruit.

Howell and Burch (1974) reported two Costa Rican specimens of *M. schmidtorum* that had consumed Lepidoptera.

Micronycteris minuta

Insects and fruit.

Goodwin and Greenhall (1961) believed *M. minuta* to consume fruit or insects or both. Fleming *et al.* (1972) examined 12 individuals from Costa Rica and Panamá and found 76 per cent insect and 24 per cent plant material, by volume, in the stomachs of four.

Micronycteris hirsuta

A variety of insects and fruits.

Goodwin and Greenhall (1961) considered this species to be fruit eating but said it may also consume some insects. Fleming *et al.* (1972), reporting on the stomach contents of three Panamanian specimens, found only the remains of insects. Wilson (1971) reported on the food remains he gathered at intervals between January and July from under roosting sites located on Orchid Island in the Panama Canal Zone. The major insect food items found represent the families Blattidae, Tettigoniidae, Scarabaeidae, Cerambycidae, Curculionidae, Cicadidae, Saturniidae, Sphingidae, Aeschnidae, and Formicidae. The insects recovered are winged forms capable of flight; however, they spend much of their time moving about on vegetation at night, suggesting that *M. hirsuta* may be gleaning them from vegetation as well as taking them in flight. The majority of the insect material, primarily whole wings, pieces of legs, and other hard parts, consisted of cockroaches (Blattidae), katydids (Tettigoniidae), and June beetles (Scarabaeidae). The remains of fruits recovered from the roosts represent *Carludovica palmata*, *Piper* sp., *Beilschmiedia* sp., *Anacardium excelsum*, *Vismia latifolia*, *Passiflora* sp., *Calycolpus warszewiczianus*, and *Eugenia nesiotica*. Wilson concluded that *M. hirsuta* is primarily insectivorous and that the small quantity of fruit eaten is consumed mainly in the dry season (February to March) when fruits are abundant. Howell and Burch (1974) reported the remains of Lepidoptera in a Costa Rican specimen.

Micronycteris brachyotis

Insects and fruit.

Goodwin and Greenhall (1961) reported finding fruit pulp, plant fibers, and insects in the stomachs of *M. brachyotis* from Trinidad. They also reported a "white milky substance" in the stomach of a juvenile. This individual probably was still nursing. Villa-R. (1967) noted that this bat feeds on pulpy fruits and insects as do other members of the genus. Howell and Burch (1974) mentioned insect remains (Hymenoptera and Coleoptera) recovered from a Costa Rican *M. brachyotis*.

Micronycteris nicefori

Fruit and insects.

A diet of fruit and possibly some insects was proposed by Goodwin and Greenhall (1961).

Micronycteris sylvestris

Fruit and insects.

A diet of fruit and possibly some insects was suggested by Goodwin and Greenhall (1961).

Summary.—Apparently there is no information available on the food habits of *Micronycteris pusilla*, *M. behni*, and *M. daviesi*.

According to Duke (1967) species of the genus *Micronycteris* are primarily insectivorous, although in Panamá they may be secondarily frugivorous. Walker *et al.* (1964) stated that the molar pattern is indicative of an insectivorous diet. The reports by Wilson (1971), Hall and Dalquest (1963), Fleming *et al.* (1972), and Howell and Burch (1974) support the contention that insects are the primary food source of these omnivorous bats. A variety of fruits are consumed by *Micronycteris*; however, their importance in the diet probably varies seasonally, as Wilson (1971) found in Panamanian *M. hirsuta.*

Genus MACROTUS Gray

Macrotus waterhousii

Large insects and fruit.

Osburn (1865:74) reported finding the wings and legs of large Orthoptera under a roost in a cave in Jamaica and mentioned that bats, presumed to be *M. waterhousii*, would drop the remains of the fruits of *Morus tinctoria*, *Brosimum alicastrum*, and *Eugenia jambos* from their night roosts. He also described (p. 75) a female killing a nursling bat (not hers, but one that was placed on her) and consuming its blood. This incident may have prompted Dobson (1878) to include small bats along with insects and fruit as food items of *M. waterhousii*. Dobson said the stomach of one specimen contained a yellowish mass with harder parts of insects, including the remains of orthopterans.

Macrotus californicus

A large variety of larger night-flying insects, some nonflying insects such as lepidopterous larvae, some fruits, and possibly green vegetative matter.

The remains of beetles of the species *Ligyrus gibbosus*, *Chlaenius sericeus*, and *Polyphylla decemilineata*, plus parts of "various species of flies," were reported by Grinnell (1918:256) as scattered over the floor of a cave inhabited by *M. californicus* in southern California. She also cited an incident (p. 257) where a *Macrotus* was caught in a mouse trap set in the open desert and suggested that this species seeks some of its food on the ground inasmuch as the bat likely was caught while attempting to capture ants or beetles attracted to the trap bait. This account probably was the basis for Sanborn's (1954) mention of a specimen taken in a mousetrap. Additional reports on the food habits of *M. californicus* are also based on material gathered from under roosts in southern California. Howell (1920) found the wings of several diurnal butterflies, as well as parts of moths. Huey (1925) reported finding a willow leaf and the remains of grasshoppers

(*Trimerotropis* sp. and *Schistocerca* sp.), cicadas, beetles (Meloidae), Sphinx moths (*Celerio lineata* and *Smerinthus cerisyi*), a noctuid moth (*Peridroma margaritosa*), and a cossid moth below the roosts. He assumed that some of these insects were diurnal and suggested that they had been taken from their resting places on vegetation (willows) by the bats and then carried to the roost to be eaten. Vaughn (1959) noted the remains of moths, butterflies, and dragonflies found under roosts. He also found fragments of orthopteran insects, noctuid moths, caterpillars, and beetles (Scarabaeidae and Carabidae) in the stomachs of several *M. californicus* and concluded that this species was totally insectivorous, a supposition echoed by Novick (1963), Villa-R. (1967), Anderson (1969), and Barbour and Davis (1969). Supported by information in earlier reports and by finding the remains of caterpillars in stomachs, Vaughn (1959) also contended that *Macrotus* mainly takes insects that are on sparsely foliated vegetation or on the ground.

Burt (1938) reported on the stomach contents of five *Macrotus* taken in Sonora, México. Two had fruit and insects in their stomachs and three contained only fruit. Park and Hall (1951) treated *Macrotus* as a frugivore in their report on the tongue and stomach anatomy of several New World bats. Ross (1967: 214) cited observations which mentioned that *M. californicus* feeds on various cactus fruits. He also reported on the insect remains gathered beneath night roosts and on his analyses of 41 digestive tracts, mostly from bats collected in the vicinity of Tucson, Pima County, Arizona, but including a few from Sonora, México. The insect remains associated with roosts represented desert short-horned grasshoppers (Acrididae: *Trimerotropis* sp.), long-horned grasshoppers (Tettigoniidae: *Microcentrum californicus*, *Schistocerca vaga*, and other species), long-horned beetles (Cerambycidae: *Derobrachus geminatus*), Sphinx moths (Sphingidae: *Celerio lineata*), and underwing moths (Phalaenidae: *Catocala* sp.). The stomach contents varied from purely insect remains to purely vegetable matter. Some stomachs from winter-taken *M. californicus* contained what appeared to be green vegetative parts of plants.

Macrotus californicus feeds primarily on the abdomens of larger night-flying insects within an average size range of 40 to 60 millimeters in length and, to a lesser extent, on lepidopterous larvae and other small insects approximately 20 millimeters in length, such as short-horned grasshoppers (Acrididae) and June beetles (Scarabaeidae) (Ross, 1967:211). Ross, disagreeing with the conclusions expressed in earlier reports, claimed that most, if not all, of the insects preyed upon by this bat are nocturnally active forms. He also asserted that no truly ground dwelling forms of insects were found in any of the digestive tracts he examined.

Vaughn's (1959:34) observation that *Macrotus* regularly forages close to the ground, seems to hover easily, and is able to hover for several seconds at a time, suggests that these bats may glean insect prey from the ground and from vegetation, as well as capture flying insects. Therefore, *M. californicus* probably does include some flightless, ground-dwelling, or diurnal insects in its diet, as appears obvious from finding caterpillars in digestive tracts.

Genus LONCHORHINA Tomes

Lonchorhina aurita

Insects and plant material.

Ruschi (1953e) stated that *L. aurita* eats insects exclusively. An examination of the stomach contents of two specimens from Trinidad only revealed the remains of insects (Goodwin and Greenhall, 1961). Duke (1967), citing unpublished information from Edwin Tyson, stated that this species probably eats nectar, some insects, and overripe fruit in Panamá. Fleming *et al.* (1972) examined two stomachs of Panamanian *L. aurita*. One contained about equal quantities of fruit pulp and insect remains. Nevertheless, Fleming *et al.* (1972: 560) considered *L. aurita* to be primarily insectivorous. Howell and Burch (1974) agreed after finding the remains of Lepidoptera in a Costa Rican specimen.

Lonchorhina orinocensis

The food habits are unknown, but the diet is probably similar to that of *L. aurita*.

Genus MACROPHYLLUM Gray

Macrophyllum macrophyllum

A variety of insects.

Quelch (1892) believed *M. macrophyllum* to consume insects; however, on the basis of the large incisors, he also suggested that this species may supplement its diet with blood. Insects and fruit were mentioned by Ruschi (1953f) as foods eaten by Brazilian *M. macrophyllum*. Davis *et al.* (1964:378-379), commenting on the foraging behavior, body weight, and proportional size of the feet of this species in Nicaragua, suggested that aquatic insects or small fish were included in its diet. The stomachs of the specimens they collected were empty. Duke (1967) stated that Edwin Tyson thinks *Macrophyllum* eats swimming insects. Harrison and Pendleton (1974:691) reported finding the stomachs of four Salvadoran *Macrophyllum* "full of dark brownish, finely masticated material." Wing fragments, which they suggested represented lepidopterans and dipterans, as well as many lepidopteran wing scales were found among the stomach contents. The stomach contents of two *Macrophyllum* that I examined from Panamá primarily consisted of the remains of water striders (Hemiptera, Gerridae: *cf. Trepobates*), which also appeared as brownish, finely chewed insect remains.

Genus TONATIA Gray

Tonatia bidens

Fruit and insects.

The diet probably includes fruit and insects as was reported by Ruschi (1953b) for this species in Brazil. Goodwin and Greenhall (1961) stated that it eats fruit.

Tonatia brasiliensis

Probably fruit and insects.

A diet of fruit and insects was proposed by Ruschi (1953c); however, the identification of his specimens is open to question because the "*Tonatia brasiliensis*" illustrated clearly is a *Carollia.*

Tonatia sylvicola

Fruit and insects.

Only 11 stomachs of the 22 Panamanian *T. sylvicola* reported on by Fleming *et al.* (1972) contained food, all of which was the remains of insects. Howell and Burch (1974) recovered legume pollen and the remains of fruit (*Stemmadenia*) from two Costa Rican representatives of this species.

Summary.—The diets of *Tonatia carrikeri*, *T. nicaraguae*, and *T. venezuelae* are not known. I suspect that species of *Tonatia* consume a large variety of arthropods, both flying insects and those gleaned from vegetation and other substrates. Tyson (quoted by Duke, 1967:8) believed *Tonatia* to be insectivorous, and thought that it probably gleans insects "off twigs about which they hover." *Tonatia* may consume a variety of fruits as well (see Howell and Burch, 1974) and probably has food habits similar to those of *Micronycteris.*

Genus MIMON Gray

Mimon bennettii

Fruit and insects.

The diet is reportedly insects and fruit (Ruschi, 1953e).

Mimon cozumelae

Plant material and various arthropods.

Dalquest (1957:46), commenting on several *M. cozumelae* he saw flying around half-spoiled fruit in an orange grove in southern Veracruz, México, suggested "they may have been eating the fruit, fermented juice, or insects stupefied by the juice." Hall and Dalquest (1963), perhaps reporting on the same incident, stated that *M. cozumelae* ate only very ripe, sometimes spoiled oranges, or possibly the insects that were feeding on the overripe fruit. They commented that the white droppings littering the floor in caves inhabited by *M. cozumelae* and *Trachops cirrhosus* resembled the droppings of hawks and owls, and concluded that both genera of bats are probably somewhat carnivorous. Villa-R. (1967) reported that *M. cozumelae* apparently eats fruit.

Mimon crenulatum

Insects.

Dobson (1878) reported finding portions of small coleopterous insects in the mouth and throat of a specimen. This information was apparently repeated without citation by Walker *et al.* (1964).

Summary.—There is no information on the food habits of *Mimon koepckeae.* Species of the genus *Mimon* probably consume a variety of arthropods and fruits.

Genus PHYLLOSTOMUS Lacépéde

Phyllostomus discolor

Insects, fruit, pollen, nectar, and vegetative parts of flowers.

Van der Pijl (1957:294, citing correspondence from Heinz Felten) noted that remnants of the fruit of *Spondias purpurea* were commonly found under the roosts of *P. discolor* in caves in El Salvador. Observations on bats visiting flowers in the Parque do Museu Goeldi, Belem, Brazil, reported by de Carvalho (1960, 1961), revealed that *P. discolor* consumes droplets of nectar secreted by the flowers of *Parkia gigantocarpa* and *P. pendula* as well as the pollen and vegetative flower parts of these species and of *Ceiba pentandra.* Digestive tracts examined by de Carvalho contained flower parts, pollen, fruit, nectar, and insects. Goodwin and Greenhall (1961:238) stated: "This is a fruit-eating bat; in captivity . . . will not eat flesh. It has a long extendible tongue, with a deep groove on the upper surface which is used to scoop out fruit pulp." Valdivieso and Tamsitt (1962), misinterpreting Goodwin and Greenhall (1961), included small vertebrates among the foods eaten by this species. Tamsitt and Valdivieso (1965) considered *P. discolor* to be frugivorous although they had once reported it to be a consumer of both flowers and fruit (Tamsitt and Valdivieso, 1961). Villa-R. (1967) remarked that this species was a frugivore in México and included *Ficus* sp., *Diospyros ebenaster*, and *Achras sapota* among those fruits consumed. The stomach of a Colombian specimen contained plant material and insects (Arata *et al.*, 1967). The stomach contents of 128 Costa Rican and Panamanian *P. discolor* were reported on by Fleming *et al.* (1972). They found 73 containing approximately one per cent fruit and 99 per cent insect remains, by volume. Only one kind of seed was noted in the plant material suggesting that a single fruit type had been consumed. The stomachs of the remaining 55 bats were empty. Heithaus *et al.* (1974) found *P. discolor* carrying *Bauhinia* and *Crescentia* pollen on their fur and observed this species feeding at the flowers of *Bauhinia pauletia* in Costa Rica. Later, Heithaus *et al.* (1975) reported the recovery of *Ceiba pentandra, Crescentia* spp., *Ochroma lagopus, Pseudobombax septinatum, Manilkara zapota*, and *Hymenaea courbaril* pollen from the fur of Costa Rican *P. discolor.* They concluded that this species was primarily nectarivorous, at least during the dry season, and utilized a broad range of potential floral resources (79 per cent of the pollen loads were mixed). Fleming *et al.* (1972) were cited as the authority for including insects in the diet; nevertheless, Heithaus *et al.* (1975) found no remains of insects or fruit seeds and pulp in the feces. The diets of Costa Rican *P. discolor* reported on by Howell and Burch (1974) included vesiculate plant material, fruit (*Piper, Acnistus*, and *Musa*), pollen (*Hymenaea* and *Ceiba*), and insects (Coleoptera, Hymenoptera, Diptera, and Lepidoptera). McNab (1969) stated that *P. discolor* is a fruiteater; but in captivity, requires a small, but regular intake of meat. Power and Tamsitt (1973) remarked that this species is known to feed on fruit, insects, pollen, and nectar.

Phyllostomus hastatus

A variety of insects, small vertebrates, and plant material including fruit, pollen, nectar, and flower parts.

Authors of early accounts on South American bats often confused this species with *Vampyrum spectrum* as well as attributing to it the "blood-sucking" habits of vampire bats. Bat species are difficult to recognize in some of these early narratives. Husson (1962:126) interpreted Waterton's (1825) and Quelch's (1892) observations on the habits of large Guianan bats they identified as *Vampyrum* as being correctly ascribed. Waterton (1825:175), while discussing *Vampyrum*, stated: "He does not always live on blood. When the moon shone bright, and the fruit of the Banana-tree was ripe, I could see him approach and eat it. He would also bring into the loft, from the forest, a green round fruit, something like the wild Guava, and about the size of a nutmeg. There was something also, in the blossom of the Sawarri nut-tree, which was grateful to him; for on coming up Waratilla Creek, in a moonlight night, I saw several Vampires fluttering round the top of a Sawarri tree, and every now and then the blossoms, which they had broken off, fell into the water, they certainly did not drop off naturally, for on examining several of them, they appeared quite fresh and blooming. So I concluded the Vampires pulled them from the tree, either to get at the incipient fruit, or to catch the insects which often take up their abode in flowers." Quelch (1892:99), also relating observations on bats he believed to be *Vampyrum*, reported: "It had been tantilising the evening before to witness a continuous stream of these great winged creatures pouring out of one central hole high up in the trunk, and darting and wheeling, fluttering and hovering, about the fruit trees around the house, and helping themselves, no doubt, to the ripest fruits on the small branches, as they listed; but it was infinitely more tantilising to know that the same stream would issue undiminished next evening, after our departure.

"Though these bats are to a great extent insectivorous, yet from their size they must devour a large quantity of the mangoes, star-apples, sapodillas and other soft fruits where they occur, since their stomachs, when full, contain a considerable amount of pulpy matter. And indeed their great canine teeth, as in our bats generally, seem especially adapted for piercing and tearing open the skin, rind and fleshy parts of fruits, the power for the tear being derived from the force of their flight after they have seized the fruit with their teeth." When these accounts by Waterton and Quelch are critically examined, however, they obviously apply to *Phyllostomus hastatus*, and perhaps to *Artibeus lituratus* as well, but not to *Vampyrum spectrum*.

Bates (1875:338) observed bats, which he called vampires, at Ega on the upper Amazon in Brazil. He discussed their habits and referred to their large numbers, frugivorous diet, and blackish and reddish color phases (he considered each color pattern to represent a distinct species)—characters identifying them as *P. hastatus*. Bates opened the stomachs of several and found a few remains of insects intermingled with masses of fruit pulp and seeds. Alston (1879-1882:39) and Goldman (1920:189), perhaps misled by Bates' (1875:337) reference to their large size, assumed that these bats represented the species *Vampyrum spectrum*.

Dobson (1878) noted that the stomach of a *P. hastatus* was filled with the remains of insects. However, he also assumed that they occasionally fed on bats and other small mammals. Ruschi (1953*b*) claimed that some of the feces of *P. hastatus* were like those of vampires and, therefore, presumed them to feed on blood. Nonetheless, Ruschi (1953*d*) gave the diet of this species in Brazil as insects, small birds and mammals (including bats), and the fruits of *Musa paradisiaca, Carica papaya, Psidium guajava, Eriobotrya japonica, Cecropia* sp., *Solanum paniculatum, Terminalia catappa, Livistona chinensis, Mangifera indica, Achras sapota, Lucuma caimito, Eugenia uniflora, Myrcia jaboticaba, Vitis vinifera, Passiflora quadrangularis, Annona muricata, Pilocarpus pinnatifolius, Artocarpus integrifolia, Rubachia glomerata, Diospyros kaki,* "etc." In Belem, Brazil, de Carvalho (1960, 1961) found *P. hastatus* feeding on the inflorescences of *Parkia gigantocarpa, P. pendula,* and *Ceiba pentandra.* He reported finding agglutinated masses of pollen, anthers, parts of the corolla, and a yellowish clear liquid, possibly nectar, in the stomach. De Carvalho described the diet of this species as insects, fruit, birds, other bats, blood, and flower parts. The inclusion of blood in the diet may have been prompted by Ruschi's (1953*b*) comments on the desmodontinelike feces found in roosts.

Goodwin (1946) stated that the diet of Costa Rican *P. hastatus* included various kinds of fruit, birds, small bats, mice, and insects. This is essentially the same diet suggested by Williams *et al.* (1966) and Duke (1967). Goodwin and Greenhall (1961) noted the remains of fruit, fur, and feathers at the bases of roosts in Trinidad, and the inclusion of both fruit and flesh in the stomach contents. They mentioned that *P. hastatus* eats the fleshy funiculus of the Sapucaia nut (*Lecythis zabucajo*), a habit reported on in greater detail by Greenhall (1965). Greenhall (1966) reported *P. hastatus* feeding on ripe Valencia oranges in Trinidad. De la Torre (1961:37) remarked that several *P. hastatus,* captured as they attempted to enter a cave, were carrying large guava fruit. Bloedel (1955) reported on a group of about 30 *P. hastatus* that he observed several times at twilight following late afternoon rains as they fed on swarming termites at Juan Mina in the Panama Canal Zone. A Costa Rican specimen examined by Starrett and de la Torre (1964) contained fruit pulp, insect remains, a few bird feathers, and a partially digested tick in its stomach. The latter was probably consumed with its vertebrate host or was gleaned during grooming.

Arata *et al.* (1967) listed six stomachs of *P. hastatus* from Colombia as containing plant material and three with insect remains out of seven they examined. Fleming *et al.* (1972) gave the stomach contents of 19 of the 25 Costa Rican and Panamanian specimens they examined as 4 per cent plant material and 96 per cent insect remains, by volume; the remaining digestive tracts were empty. Tuttle (1970), reporting on Peruvian bats, mentioned that netted specimens were frequently dusted with pollen. I have noted this in *P. hastatus* netted in Costa Rica and eastern Perú. Howell and Burch (1974) did not report pollen from Costa Rican *P. hastatus,* but they did find the remains of fruit (*Cecropia* and *Piper*) and insects (Coleoptera, Hemiptera, Lepidoptera, and Diptera including Culicidae) in the feces and stomach contents.

Summary.—The food habits of *Phyllostomus elongatus* and *P. latifolius* are not known. Their diets, however, likely include flower parts, fruits, insects, and small vertebrates such as anoles and geckos gleaned from vegetation. As noted for *P. hastatus*, Tuttle (1970) frequently found the heads of netted *P. elongatus* covered with yellow pollen.

Bats of the genus *Phyllostomus* are omnivorous. Both *P. discolor* and *P. hastatus* feed on animal matter, but in the former this is probably restricted to insects, whereas *P. hastatus* preys on a variety of small vertebrates as well. Fruits, pollen, nectar, and insects caught in flowers probably are the major food items of *P. discolor*. The inclusion of blood in the diet of *P. hastatus* is without basis. The only blood consumed by this species is that of its vertebrate prey.

Genus PHYLLODERMA Peters

Phylloderma stenops

Plant material and insects.

The only reference to the food habits of this species is that by Jeanne (1970) who captured a male in the act of eating the larvae and pupae from an active nest of a social wasp (*Polybia sericea*) near Santarem, Pará, Brazil. The stomach of this bat contained the well-masticated remains of both larvae and pupae, but no evidence of adults.

Genus TRACHOPS Gray

Trachops cirrhosus

Insects, small vertebrates, and possibly some fruit.

Ruschi (1953c) recorded a diet of fruits, insects, and small reptiles for *T. cirrhosus* in Brazil. Burt and Stirton (1961) stated that the stomachs of several specimens collected in El Salvador contained hair and flesh. Goodwin and Greenhall (1961) reported finding flesh and small sharp bones in the stomach of a *T. cirrhosus* from Trinidad and commented on finding the remains of a gecko (*Thecadactylus rapidicaudus*) in the stomach of a specimen from Panamá. Duke (1967) noted that Edwin Tyson had observed *Trachops* hovering up and down tree trunks in a manner suggestive of an insect gleaner. In Honduras, Valdez and LaVal (1971) found a freshly killed anole (*Anolis lemurinus*) in the same net pocket containing a *T. cirrhosus*. They suggested that *Trachops* feeds on a variety of lizards. Only two of the eight stomachs of Panamanian *T. cirrhosus* reported on by Fleming *et al.* (1972) contained food. The contents of both consisted entirely of insect remains. Howell and Burch (1974) recovered a mixture of Lepidoptera and bat hair from each of four Costa Rican specimens.

I found *T. cirrhosus* commonly entering the houses of Cashinahua Indians at Balta, Departamento de Loreto, Perú, to feed on cockroaches during the evening. The bats were considered a nuisance because the sound of their flight as they moved along the walls and roof, the chewing noise as they consumed their prey, and the rain of urine, feces, and insect parts falling upon the mosquito nets below, disturbed the Cashinahua in their sleep.

Genus CHROTOPTERUS Peters

Chrotopterus auritus

Small vertebrates, insects, and fruit.

Goodwin (1946) was among the first to comment that *Chrotopterus* is probably carnivorous. Ruschi (1953b) reported finding many bird vertebrae, solanaceous seeds (*Solanum*?), and blood in the feces as well as fragments of fruit, fruit seeds, and scattered vertebrae under a cave roost of *C. auritus* in Brazil. He also claimed to have witnessed a *Chrotopterus* land and commence feeding on the back of a calf. This observation was alluded to by Ruschi and Bauer (1957:41). Ruschi (1953f) listed the diet of *Chrotopterus* as small mammals, young birds, fruit, insects, and blood. The bat on the calf most likely was a *Desmodus*, and the only blood in the diet of *C. auritus* probably is that of the small birds and mammals preyed on by this bat. At least some of the seeds in the feces mentioned by Ruschi may have been in the stomachs and crops of birds eaten by *Chrotopterus*. Hall and Dalquest (1963) commented that the white stains beneath the roosts of these bats in Veracruz, México, resembled those left by the excreta of hawks and owls. They also presumed *C. auritus* to be carnivorous, an opinion repeated by Villa-R. (1967) and McNab (1969). Villa-R. and Villa Cornejo (1969, 1971) reported finding the fragments of skeletons, skin, and hair below a roost of *C. auritus* in a mine in northern Argentina. Their suggestion that these fragments were the remains of *Ctenomys* is unlikely because of the fossorial habits of these rodents. Tuttle (1967) reported finding the remains of a gecko (*Thecadactylus rapidicaudus*) in the stomach of a Venezuelan specimen. Olrog (1973) reported finding the remains of a mouse opossum (*Marmosa*) and a bird among the stomach contents of Argentinian *Chrotopterus*. Because the bird was being eaten in a mist net, Olrog concluded that *Chrotopterus* had been eating his mist-netted bats and birds.

Genus VAMPYRUM Rafinesque

Vampyrum spectrum

Birds, bats, rodents, and possibly some fruits and insects.

Vampyrum spectrum figured prominently in many of the early narratives on the South American fauna because of its awesome proportions and erroneously ascribed blood-feeding habits. Husson (1962:14, 122-126) discussed those accounts dealing with Guianan bats. Many of the early travelers, however, confused *V. spectrum* with *Phyllostomus hastatus* (see account of *P. hastatus*) and possibly with *Artibeus lituratus*.

Dobson (1878:471) remarked on finding "some vegetable matter of rather firm consistence, apparently [a] portion of the rind of some large fruit" in the stomach of a *V. spectrum*. His remark (p. 471) that this species has been "shown by the observations of modern travellers to be mainly frugivorous" may have been influenced by Bates (1875, see acount of *Phyllostomus hastatus*). Goodwin (1946) reported the diet of Costa Rican *Vampyrum* to be small birds, rodents, smaller bats, some fruit, and probably insects. Wehekind (1956:20) presented in-

formation on the food habits of *V. spectrum* in Trinidad. He found fur, feathers, and bone in the stomachs of three he collected and the remains of "blue birds," doves, and rodents at the base of a roost in a silk cotton tree (*Ceiba pentandra*). Two Costa Rican *V. spectrum* were reported on by Casebeer *et al.* (1963) who found the remains of a passerine bird in the digestive tract of one. Brosset (1966:54) and Goodwin and Greenhall (1961) noted that *Vampyrum* is largely, if not entirely, carnivorous, and the latter mentioned finding fur and feathers in the stomach of this bat and bat bones at the base of a roost. Greenhall (1968) also said these bats were carnivorous and mentioned that a variety of fruits offered to *V. spectrum* in captivity were never eaten. Duke (1967), however, listed *Anacardium* sp. and *Psidium* sp. as examples of fruits eaten by this species in Panamá in addition to bats, rodents, birds, and insects. Peterson and Kirmse (1969) reported on finding the remains of bats and an oryzomyine rodent in the stomach of a Panamanian *Vampyrum*. They surmised that this bat had been eating other bats caught in mist nets without having become caught itself. However, their statement (p. 140) "that these bats were virtually eaten *in situ* in the net negated any evidence for birds of prey being responsible" is not necessarily correct. In Chiapas, México, I saw a barred forest-falcon (*Micrastur ruficollis*) in the act of eating small bats in a mist net at daybreak. The hawk hit a bat in the net, rebounded, and ate parts of it while hanging nearly upside down and free from the net. As I approached, the hawk released the bat (a *Sturnira lilium*) and flew off. The net contained other bats including some for which heads and upper parts of the body were missing. Later in the day, the hawk returned to the net and was captured while hanging and feeding on a small bird.

SUBFAMILY GLOSSOPHAGINAE

Genus GLOSSOPHAGA É. Geoffroy St.-Hilaire

Glossophaga soricina

Insects, fruits, pollen, nectar, and flower parts.

This species, which figured prominently in many early accounts of tropical American bats, was assumed to feed on blood. For example, Quelch (1892:101) stated: "It seems likely . . . that these bats supplement their ordinary insect diet, with the blood of the domestic animals." He noted, however, that the tongue seemed to be modified to lick out the pulpy matter of fruits. Gaumer (1917) stated that *G. soricina* feeds on insects and small or soft fruits in Yucatán, México, and mentioned the fruit of *Cordia dodecandra*. He remarked (p. 297) that they open holes in the fruit and lick the juice, and "aunque son vampiros nunca chupan sangre."

One of the earliest reports on the flower-feeding habits of *G. soricina* was by Porsch (1931), who observed this species at the flowers of *Crescentia cujete* and *Parmentiera alata* in Costa Rica. Vogel (1958) reported that they feed on flowers of *Kigelia aethiopica* and noted finding the pollen of *Marcgravia* sp. on the heads of some specimens. Baker (1970) presented information on flowers visited by bats at the botanical gardens of the Tela Railroad Company, Lancetilla, Honduras,

and at Finca Lornessa, Santa Ana, Costa Rica. Even though the bats were not identified, examination of his photographs (figs. 1-4, 6-11) show *G. soricina* visiting the flowers of *Durio zibethinus* in Honduras. Those bats visiting the flowers of *Mucuna andreana* in Costa Rica are almost certainly this species as well, inasmuch as this is the only glossophagine I have ever netted at Finca Lornessa despite extensive collecting, and the species proved to be common there. Heithaus *et al.* (1974) reported capturing *G. soricina* dusted with *Bauhinia* and *Crescentia* pollen and mentioned observing this species at the flowers of *Bauhinia pauletia* near Cañas, Costa Rica. Heithaus *et al.* (1975) noted that 59.6 per cent of the 146 *G. soricina* they examined from the same region in Costa Rica carried pollen on the fur. The six most common plants represented by the pollen were *Ochroma lagopus*, *Pseudobombax septinatum*, *Ceiba pentandra*, *Hymenaea courbaril*, *Manilkara zapota*, and *Crescentia* sp. They also found that these bats had fed on the fruits of *Piper tuberculatum*, *Muntingia calabura*, *Solanum* sp., and *Ficus* sp. as well as on other fruits, the remains of which they could not identify. When contrasting frugivory and nectarivory in this species, Heithaus *et al.* (1975) remarked that *G. soricina* was primarily nectarivorous in both the wet and dry seasons in Costa Rica. The insect-eating habits of *G. soricina* were acknowledged, however; they cited Fleming *et al.* (1972) as the source for this information.

Test (1934) reported *G. soricina* feeding on ripening bananas in Honduras, and Tamsitt and Valdivieso (1965) considered this species to be frugivorous. *Glossophaga soricina* was thought to be nectarivorous by Park and Hall (1951), Wille (1954), Tamsitt and Valdivieso (1961, 1963), and McNab (1969). Goodwin (1946) also thought it was a nectar feeder and mentioned flowers of the calabash tree and night-blooming cacti as food sources. Piccinini (1971) noted that Brazilian *G. soricina* eat pollen and nectar. Dalquest (1953), reporting on mammals from San Luis Potosí, México, suggested that *G. soricina* feeds principally on nectar but consumes fruit juices and pulp as well. Hall and Dalquest (1963) stated that it was a nectar and fruit eater and mentioned catching a specimen in a banana-bated snap trap placed in a tree in Veracruz, México. A nectar and fruit diet was cited for *G. soricina* by Novick (1963) and Hall and Kelson (1959). Duke (1967), relating Edwin Tyson's information on Panamanian *G. soricina*, stated that they feed on overripe bananas and guavas and drink from the flowers of Musaceae, Bignoniaceae, and Bombacaceae. Pollen, nectar, and soft fruits were noted in the diet of this species in México by Villa-R. (1967), who also reported finding some specimens with their heads covered with *Ipomoea arborea* pollen.

Wied-Neuwied (1826) reported finding insects in the stomach of a *G. soricina* from Brazil. Alston (1879-1882:43) also stated that *G. soricina* preys on insects but mentioned that this species "feeds largely on fruits, lapping up the juices and soft pulp with their extensile tongues." Brosset (1965), on the basis of tongue structure, suggested that *G. soricina* may capture insects at flowers as well as drink the nectar. Felten (1956) reported this species feeding on flowers (especially *Crescentia*) in El Salvador; however, on the basis of observations on captive individuals, he said they prefer insects. Fruit juices and small insects were found in the stomachs of Trinidadan *G. soricina* (Goodwin and Greenhall,

1961). Ruschi (1953g) listed insects, fruits, nectar, and pollen in the diet of Brazilian *G. soricina*. He noted that this species consumes nectar from many kinds of flowers, including *Crescentia cujete* and *Vochysia* sp., as well as eating the fruits of *Musa paradisiaca*, *Carica papaya*, and *Solanum paniculatum*. De Carvalho (1960) reported on the stomach contents of *G. soricina* from Belem, Brazil. One stomach contained the remains of insects, a large quantity of reddish fragments, presumably flower parts, and yellowish and whitish masses, probably pollen. Another contained scales of lepidopterous insects and a gelatinous mass of proteinaceous material, presumably pollen. According to de Carvalho (1961) *G. soricina* eats fruit, flowers, nectar, and insects. Based on observations in the Parque do Museu Goeldi, Belem, he cited a variety of flowering plants of which the nectar, pollen, and sometimes the flower parts are eaten: *Crescentia cujete*, *Crescentia amazonica*, *Alexa grandiflora*, *Hymenaea courbaril*, *Bougainvillea spectabilis*, *Crataeva benthami*, and *Elizabetha paraense*. Also cited were the fruits of *Cecropia bureaniana*, *Cecropia* sp., *Piper* sp., and *Achras sapota* as foods consumed during periods of annual fruiting maxima (December to January). Starrett and de la Torre (1964) reported on *G. soricina* from El Salvador, Honduras, Nicaragua, and Costa Rica. They wrote (p. 57): "Fruit 'pulp' and seeds of a number of different kinds of plants were present to some extent in the digestive tracts of every *Glossophaga*. No pollen was found in any individual. Eight . . . had insect remains in their digestive tracts. In two cases the insect parts made up the bulk of the contents of the tract. The insects had been finely chewed but lepidopteran scales were readily recognizable, as well as portions of the wings of Diptera and Hymenoptera." They also observed *G. soricina* feeding on ripe bananas at Los Diamantes, Costa Rica. Fleming *et al.* (1972) classified *G. soricina* as an omnivore after examining the stomachs of 217 specimens from Costa Rica and Panamá. Of these, only 38 stomachs contained food—34 per cent plant material (including 5 per cent pollen) and 66 per cent insect remains, by volume. Two collected in January and one in May contained insects exclusively. One taken in March only contained pollen, and two caught in September only held fruit. Two captured in February and six from December contained insects, fruit, and pollen, whereas the stomachs of bats in June, July, August, and October, contained fruit and insects. At least seven seed types were found in the plant matter recovered from these stomachs. Howell and Burch (1974) reported finding the pollen and nectar of *Cresentia*, *Inga*, *Hymenaea*, *Mucuna*, *Musa*, *Pitcairnia*, and an unidentified Bombacaceae in Costa Rican *G. soricina*. They also found the remains of fruit (*Acnistus*, *Muntingia*, *Musa*, and an unidentified Melastomaceae) and Lepidoptera in the feces or stomach contents. Lepidopterous insects were the only food items recovered from 24 of the 62 *G. soricina* they examined.

Alvarez and Gonzalez Q. (1970) presented information on their analyses of 174 *G. soricina* from the Mexican states of Veracruz, Oaxaca, Guerrero, and Morelos. Of these, 107 (61.6 per cent) did not contain pollen in their digestive tracts. Nevertheless, *G. soricina* contained the greatest diversity of pollen grains (at least 34 species recognized—see Table 2) of any of the other glossophagines studied (*Anoura geoffroyi*, *Choeronycteris mexicana*, *Leptonycteris sanborni*,

TABLE 2.—*Plants identified by pollen grains in the stomachs of* Glossophaga soricina, Anoura geoffroyi, Choeronycteris mexicana, Leptonycteris sanborni, L. Nivalis, *and* Hylonycteris underwoodi *from México (modified from table 5* in *Alvarez and Gonzalez Q., 1970:165).*

Pollen	G. soricina	A. geoffroyi	C. mexicana	L. sanborni	L. nivalis	H. underwoodi
Acacia	+	+	+	+		
Acanthaceae			+			
Agave	a	a	a	a, b	a, b	+
Albizzia	+					
Alnus	+	+		+		
Amaranthaceae				+		
Anoda					+	
Apocynaceae					+	
Arbutus	+					
Aristolochia	+					
Bauhinia	+	+		+		
Berberis				+		
Bombax	+	+	+	+	a, b	
Bursera			+			
Caesalpinia	+					
Calliandra	+	a		+	a	
Ceiba	a, b	a, b	a	a	a, b	
Citharexylum	+					
Compositae	+	a	a	+	a	
Conzattia	+					
Cordia	+		+			
Crescentia				+	+	
Croton	+					
Echinocactus	+					
Eucalyptus	+	a	+	+	a	
Ficus	+	+	+	+	+	
Gentiana				a		
Geranium		+				
Graminae	+	+	+	+	a	
Hibiscus		+				
Ipomoea	a	a	a	a	a	
Labiateae					+	
Lantana	+		+			
Leguminosae	+				+	
Liliaceae					+	
Lonchocarpus						c
Malvaceae	+	+		+	+	
Mimosa				+		
Musa	+			+		
Myrtillocactus d	a, b	a	a, b	a, b	a	
Oenothera				+	+	
Onagraceae	+			+		
Pinus	a	a	a	+	a	+
Platyopuntia	+		+	+		
Quercus		+				
Roupala	+					

TABLE 2.—*Continued.*

Salix	+			
Salvia	+	+	+	+
Solanaceae	+			
Urticaceae		+		
Zea	+		+	
Zingiber			+	

Symbols: *a*, occurring in over 20 per cent of all stomachs containing pollen; *b*, exceeding 25 per cent of total volume of pollen; *c*, 99.8 per cent of stomach contents; *d*, includes *Lemaireocereus*.

L nivalis, and *Hylonycteris underwoodi*). Alvarez and Gonzalez Q. (1970) considered *G. soricina* to be an opportunistic omnivore that utilizes pollen as a food source whenever nectar, fruits, or insects are not readily available. Their observations on this species extended from February to September, during which time the commonest pollen ingested varied seasonally from *Cordia, Acacia, Conzattia,* and *Albizzia* in the spring to *Ceiba, Ipomoea, Myrtillocactus,* and *Agave* in the summer, and *Conzattia* in September. The pollen grains in the diet were correlated with each habitat. For example, three samples of *G. soricina* collected in May from different localities on the Pacific versant of Michoacán demonstrated different pollen profiles. Specimens from the Tepalcatepec-Balsas Basin south of Nueva Italia principally contained the pollen of *Lemaireocereus* and *Echinocactus.* In the vicinity of Arteaga, the most abundant pollen found were *Roupala, Agave,* and *Ceiba*; however, in the Melchor Ocampo area on the coastal plain, the primary pollen grains consumed were *Ceiba* and *Cordia.*

Arata *et al.* (1967) presented data on the stomach contents of 16 Colombian *G. soricina.* They found that 15 contained plant material, and 6 contained the remains of insects. On the basis of a stomach containing matted hair, claws, and flesh, they ascribed carnivorous habits to this species. I suggest, however, that this observation not be interpreted as reflecting a normal aspect of the diet. As the authors noted (p. 653), the bats were collected at night and kept alive for processing the next day. According to Arata (personal communication), the bats were individually held in small cloth bags. Nevertheless, bats kept under these conditions sometimes will chew on themselves and, if pregnant, often abort and eat parts of the fetus. The finding of claws and flesh in the stomach of a *G. soricina* probably represents cannibalism induced by the treatment the bat received between the time it was caught and its death. Unfortunately, the sex and reproductive state of the bat was not presented. The information presented by Arata *et al.* (1967) may have prompted Phillips (1971) to include meat in the diet of *G. soricina.*

Goodwin (1934:9), commenting on *G. soricina* from Guatemala, said, "The single specimen taken at Barrillas was caught in a mousetrap hanging over a pile of raw sugar. Whether the bats were after insects drawn by the sugar or were there for the sweets, I cannot say, but I lean toward the former idea. The natives insist that bats eat the sugar." The owners of Finca Lornessa, Santa Ana, Costa Rica, often found dead bats hanging on the edge or floating in the large vats used to concentrate sap from sugar cane if these pots were left filled and uncovered during

the night. The Finca Lornessa sugar mill houses a large colony of *G. soricina,* and the owners believe the bats drink the concentrated sugar cane sap.

Glossophaga commissarisi

Insects, fruit, pollen, and nectar.

The remains of Lepidoptera, fruit (*Acnistus*), and the pollen and nectar of *Musa* and *Mucuna* were recovered by Howell and Burch (1974) from Costa Rican *G. commissarisi.*

Glossophaga longirostris

Insects, fruit, pollen, nectar, and possibly other flower parts.

Wille (1954) and Valdivieso and Tamsitt (1962) considered *G. longirostris* to be nectarivorous. Goodwin and Greenhall (1961) said it feeds on fruit pulp and fruit juices, occasional insects, and some nectar. Pirlot (1964) said *G. longirostris* is nectarivorous and frugivorous. He also cited correspondence from Goodwin and Novick, who suggested that insects found among stomach contents have come from the fruit these bats have eaten.

Summary.—The diet of *Glossophaga alticola* is not known; however, its food habits likely are similar to those of *G. soricina* and *G. commissarisi.* Villa-R. (1967) reported the diet of *G. morenoi* as nectar, pollen, and pulpy fruits. I am uncertain to which of the three species of *Glossophaga* occurring in México he was referring. The diet of *Glossophaga* includes a variety of plants and insects. Many of the insects may be consumed in conjunction with the flower-feeding habits of these species; however, some insects likely are caught away from flowers.

Genus MONOPHYLLUS Leach

Monophyllus redmani

Nectar and fruit.

Osburn (1865) reported finding yellow pulp in the intestines of two *Monophyllus redmani* taken in Jamaica. Wille (1954) reported that this species was "nectar-eating" on the basis of tongue structure. Tamsitt and Valdivieso (1970) also considered *M. redmani* to be nectarivorous.

Summary.—Nothing has been reported on the diet of *Monophyllus plethodon.* According to Walker *et al.* (1964), *Monophyllus* spp. are known to feed on the juices and pulp of fruits and presumably include insects in their diet.

Genus LEPTONYCTERIS Lydekker

Leptonycteris nivalis

Fruit, pollen, nectar, and insects.

Park and Hall (1951), on the basis of tongue and stomach anatomy, considered *L. nivalis* to be nectarivorous. Dalquest (1953:28) found *L. nivalis,* captured in

rooms of Hacienda Capulin, San Luis Potosí, México, with their stomachs filled "with thick, brilliant red fruit juice . . . almost certainly the juice of the fruit of the organ cactus." Novick (1963) believed that this species feeds on flowers and fruits. Barbour and Davis (1969) remarked that *L. nivalis* feeds on nectar and pollen. Phillips *et al.* (1969) mentioned nectar, pollen, and soft fruit in the diet of *L. nivalis* in their report on the macronyssid mites inhabiting the oral mucosa of these bats. The mites were found in *L. nivalis* but not in *L. sanborni*, even when both species were found in the same cave. They implied that the presence of the mites in *L. nivalis* indicated a diet differing from that of *L. sanborni* and suggested that abrasive diets of insects or plant fibers might prevent the mites from inhabiting the oral cavity of *L. sanborni*.

Alvarez and Gonzalez Q. (1970) reported on pollen found in the stomach contents of 13 specimens from the Mexican states of Michoacán and Hidalgo. Pollen grains representing 22 kinds of plants were found in 12 stomachs (Table 2); one stomach did not contain pollen. *Leptonycteris nivalis* consumed the pollen of *Agave*, *Ipomoea*, *Ceiba*, and *Myrtillocactus* in about the same proportions as did *L. sanborni*. Alvarez and Gonzalez Q. remarked on not finding any significant differences in the diets of the two species.

Leptonycteris sanborni

Fruit, nectar, pollen, and insects.

Wille (1954), on the basis of the throat musculature of specimens from Jalisco, México, considered *L. sanborni* to be nectarivorous. Hoffmeister and Goodpaster (1954) presumed *L. sanborni* to feed heavily on pollen and nectar after observing that nearly every specimen they collected in the vicinity of the Huachuca Mountains in southern Arizona had yellow pollen covering the head. An analysis of the stomach contents of six specimens revealed an average of 92 per cent pollen and 8 per cent insect remains. Hoffmeister and Goodpaster (1954) surmised that the pollen came from jimsonweeds (*Datura*), which have yellow pollen, are open at night, and are abundant in the area.

Alcorn *et al.* (1961) and McGregor *et al.* (1962) reported on experiments they conducted in southern Arizona with caged *L. sanborni* exposed to flowering saguaros (*Carnegiea gigantea*) and century plants (*Agave schottii*). They found 62 per cent of the saguaro flowers setting seed when pollinated by *L. sanborni* as opposed to 52 per cent for bees and 45 per cent for white-winged doves. Hayward and Cockrum (1971) presented information on analyses of digestive tracts collected from *L. sanborni* between 15 May and 2 September over a four-year period in southeastern Arizona. They found the tracts to contain 100 per cent saguaro pollen in mid-May. The pollen content shifted with increasing percentages of *Agave* pollen beginning in late May to early July and thereafter to early September, when the pollen content was 100 per cent *Agave*. The stomach of one bat taken on 7 November near Carbo, Sonora, México, contained a few grains of saguaro pollen. Hayward and Cockrum (1971) expressed the opinion that *L. sanborni* is a nectarivorous species in the United States and accidentally ingests pollen while feeding at flowers. They believed pollen to comprise the major proteinaceous portion of the diet and mentioned that, when nectar is not available,

L. sanborni eats soft juicy fruits. Barbour and Davis (1969) gave a diet of nectar, pollen, insects, and fruit.

Alvarez and Gonzalez Q. (1970) reported on the pollen found in the stomachs of *L. sanborni* over a six-month period in the Mexican states of Hidalgo and Guerrero. Fecal samples were collected in a cave in Xoxafi, Hidalgo, from February to September. Of the 279 stomachs examined, 249 contained identifiable pollen grains representing 28 kinds of plants (Table 2). The results from the fecal analyses duplicated the information obtained from the stomach contents. *Leptonycteris sanborni* first arrived at the cave in Xoxafi in February and, since their stomachs contained pollen grains of *Bombax* and *Ipomoea*, were presumed to have come from subtropical habitats. The pollens found in the stomachs of these bats reflected the plants that were flowering at the time as well as the changes in the flowering times of the flora from one season to another. For example, in the vicinity of Juxtlahuaca, a subtropical locality in Guerrero, bats contained large amounts of the pollen of *Bombax*, *Ipomoea*, *Ceiba*, and *Agave* on 3 February, as well as very small quantities of the pollen of *Myrtillocactus*. On 20 July, however, *L. sanborni* stomachs contained nearly 90 per cent *Myrtillocactus* pollen, no *Bombax* pollen, and greatly reduced amounts of *Ceiba*, *Ipomoea*, and *Agave* pollens. Comparisons of pollens found in the digestive tracts of *L. sanborni* taken in late July from Xoxafi and Juxtlahuaca demonstrated differences in the foods available in these two contrasting habitats. *Agave* pollen predominated (98.7 per cent) in the stomachs from Xoxafi, whereas the pollen of *Lemaireocereus* was commonest (87.7 per cent) in bats from Juxtlahuaca. No significant differences were noted in the pollens consumed by *L. sanborni* and *L. nivalis*.

Howell (1974) reported finding fragments of thrips (*Carpophilus*) and a bee (*Halictus*) in some stomachs of *L. sanborni* from southern Arizona. However, she suggested that, because these insects are associated with batflowers, they were consumed incidental to nectar feeding and are not actively pursued. Thirty stomachs contained an average of 4 grams of material each, of which about 25 per cent was pollen; the remainder, nectar. Howell's thesis is that *L. sanborni* is nectarivorous, prefers *Agave* and *Carnegiea* flowers as food sources while in Arizona, and that pollen supplies all of the dietary proteins. She supports her contention regarding the dietary role of pollen by pointing out the higher nitrogen content of pollen from chiropterophilous plants (when compared against anemophilous and entomophilous pollen) and demonstrating the array of "essential" amino acids present in *Agave* and *Carnegiea* pollen, two of which (proline and tyrosine) are recommended as being of special importance to bats.

Summary.—The food habits of *Leptonycteris curasoae* are unknown; however the diet likely is similar to those of *L. nivalis* and *L. sanborni*.

There have been several reports concerning the food habits of *Leptonycteris*; however, it is nearly impossible at this time to determine to which North American species this information applies. Duges (1906) reported on finding an *Ichnoglossa* (= *Leptonycteris*) in Guanajuato, México, the fur of which was covered and stomach filled with the pollen of *Malvaviscus acerifolius*.

Palmer (1954) stated that *Leptonycteris* probably feeds on flowers. Sanborn (1954) maintained that these bats feed on insects from night-blooming flowers because cactus pollen has been found in some of the stomachs examined. Hoffmeister (1957) gave the diet as nectar, pollen, and insects. According to Walker *et al.* (1964), *Leptonycteris* is known to visit the flowers of *Malvaviscus* and perhaps jimsonweed (*Datura*) and to eat the fruits of cacti.

Genus LONCHOPHYLLA Thomas

Lonchophylla mordax

Insects, fruits, nectar, and pollen.

Ruschi (1953*i*) recorded the diet as insects, succulent fruit, nectar, and pollen.

Lonchophylla concava

Pollen, nectar, and insects.

Howell and Burch (1974) reported the following food materials recovered from six Costa Rican specimens of *L. concava*: one with nectar and *Mucuna* pollen, two with nectar and *Musa* pollen, and three with the remains of Lepidoptera.

Lonchophylla robusta

Pollen, nectar, fruit, and insects.

Wille (1954) considered *L. robusta* to be a nectar-eating bat. Fleming *et al.* (1972) examined the stomachs of 17 specimens from Costa Rica and Panamá. Ten per cent plant material and 90 per cent insect remains were found in the only stomach containing food items. Howell and Burch (1974) did not find any plant material in their three *L. robusta* from Costa Rica; however, they did find the remains of Lepidoptera, Coleoptera, and Streblidae.

Summary.—Nothing has been published on the food habits of *Lonchophylla hesperia* and *L. thomasi*. Walker *et al.* (1964) remarked that *Lonchophylla* feeds on flowers and the diet may consist of nectar, pollen, insects, and fruit. Duke's (1967) mention of nectar and possibly overripe fruit, pollen, and insects in the diet of Panamanian species of *Lonchophylla* may apply to all species in the genus. Goodwin (1946:312) wrote that "*Lonchophylla* . . . is to some extent a nectar feeder, and uses its long tongue to lap up the honeyed liquid from the large night-blooming flowers." I have seen *L. thomasi* feeding at banana flowers in eastern Perú and many of these bats had their heads and shoulders dusted with pollen.

Genus LIONYCTERIS Thomas

Lionycteris spurrelli

The diet is unknown; however, the food habits of *Lionycteris* likely are similar to those of *Lonchophylla*.

Genus ANOURA Gray

Anoura geoffroyi

Fruit, pollen, nectar, and insects.

Perhaps the earliest account providing information on the food habits of *A. geoffroyi* is that of Tschudi (1844:73), who recorded the remains of Diptera in the stomach of a specimen from Perú. Ortiz de la Puente (1951) also found insects in the stomachs of Peruvian *A. geoffroyi*. According to him (p. 12), an examination of stomach contents revealed the remains of two species of small coleopterans, one of which is a member of the family Nitidulidae.

Knuth (1906:73) related J. H. Hart's observations (*in litt.*) on visits by *Glossonycteris Geoffroyi* (= *A. geoffroyi*) to the flowers of *Eperua falcata* in Trinidad. This information was mentioned by Baker and Harris (1957:449) and given without citation by Walker *et al.* (1964). According to Goodwin (1946:312), "*Anoura* is in part a nectar feeder, and its long tongue is adapted for reaching into the corolla of various night-blooming tropical flowers. It is known also to visit blossoms where there is no secretion of nectar, and it may be supposed that there they are attracted by the insects drawn in by the perfume of the flowers." Ruschi (1953*g*) mentioned visits to flowers of *Vochysia* sp. by *A. geoffroyi* in Brazil and listed insects, fruit, nectar, and pollen in the diet of this bat. Wille (1954) considered this species as nectarivorous. Vogel (1958) noted that *A. geoffroyi* visits the flowers of *Symbolanthus latifolius* and *Purpurella grossa*. Goodwin and Greenhall (1961) reported that *Anoura* feeds on nectar and the soft pulp of ripe fruit. Villa-R. (1967) gave nectar and pollen as the foods of *A. geoffroyi* in México. Duke (1967) stated that this species is a nectar feeder in Panamá that also eats overripe fruit. Goodwin (1934) remarked on catching an *A. geoffroyi* in Guatemala in a mousetrap hanging over a pile of raw sugar.

The high incidence of insect remains and the numerous stomachs without pollen prompted Alvarez and Gonzalez Q. (1970) to suggest that *A. geoffroyi* is a facultative pollen eater. Alvarez and Gonzalez Q. reported on 69 *A. geoffroyi* from the Mexican states of Michoacán, México, Guerrero, and Oaxaca. Of these bats, 34 contained identifiable pollen grains, representing 20 kinds of plants, in their stomachs (Table 2). The kinds of pollen present were similar to those found in other species and reflected the flora in the different habitats where the bats were found. The major differences noted between *A. geoffroyi* and the other species Alvarez and Gonzalez Q. (1970) studied were the increased representation of entomophilus plant pollen (for example, Compositae) and the high frequency of insects in the stomach contents. According to them, *A. geoffroyi* behaves like an insectivorous species with a partiality for pollen. This observation is supported by Howell and Burch (1974) who found only Lepidoptera in the specimen they examined from Costa Rica.

Anoura caudifer

Fruit, nectar, pollen, and insects.

Wied-Neuwied (1826:217) mentioned finding the remains of insects in the stomach of an *Anoura ecaudata* (= *A. caudifer*) from Brazil. Ruschi (1953*h*)

claimed that Brazilian *A. caudifer* eat insects, soft juicy fruits, nectar, and pollen.

Anoura cultrata

Insects, pollen, and nectar.

The six *A. cultrata* examined by Howell and Burch (1974) contained only the remains of Lepidoptera. However, I collected several *A. cultrata* in Costa Rica, the heads and shoulders of which were dusted with pollen.

Anoura werckleae

Pollen and probably nectar, fruit, and insects.

Starrett (1969) reported *A. werckleae* visiting the flowers of *Wercklea lutea*, as he determined by finding *Wercklea* pollen on the fur of the head and shoulders.

Summary.—Very little is known of the food habits of *Anoura werckleae* and *A. cultrata*; the diet of *A. brevirostrum* is unknown. However, these species probably have diets similar to that of *A. geoffroyi*, which is a highly insectivorous glossophagine.

Genus SCLERONYCTERIS Thomas

Scleronycteris ega

Probably fruit, pollen, nectar, and insects.

Nothing has been reported on the diet of this species.

Genus LICHONYCTERIS Thomas

Lichonycteris obscura

Pollen, nectar, and insects.

Goodwin (1946:315) wrote: "*Lichonycteris* is probably a nectar feeder as is indicated by its weak teeth and absence of lower incisors, to give the long tongue free play." Tamsitt and Valdivieso (1961) included *L. obscura* among species that consume flowers and fruits. Carter *et al.* (1966) reported on two specimens netted near a plant bearing night-blooming flowers in Guatemala. They noted pollen on the rump and uropatagium of these bats.

Summary.—Nothing is known of the diet of *Lichonycteris degener* and little is known of the food habits of *L. obscura* other than the fact that these bats visit flowers.

Genus HYLONYCTERIS Thomas

Hylonycteris underwoodi

Insects, pollen, and nectar.

Goodwin (1946) believed *Hylonycteris* to be a flower visitor and Hall and Kelson (1959) stated that it is a nectar feeder. Hall and Dalquest (1963:228) re-

porting on this species in Veracruz, México, wrote: "Beneath their resting place was a pile of guano about three inches high by six in diameter. There were several pits of jobo plums [*Spondias lutea*] on the pile, showing that some of this fruit is taken to the cave to be eaten." Carter *et al.* (1966) reported a specimen with pollen grains on the rump and uropatagium netted near night-blooming flowers in Guatemala. Villa-R. (1967) stated that *Hylonycteris* feeds on nectar and pollen. He cited a specimen from Tabasco, México, with pollen that he suspected to be cacao (*Theobroma cacao*) on the vibrissae and hairs around the mouth. Walker *et al.* (1964) reported the diet as probably nectar, fruit, and some insects. Alvarez and Gonzalez Q. (1970) reported on the pollen found in the stomachs of two specimens from Chiapas, México. The stomach contents were composed almost entirely of the pollen of *Lonchocarpus* (99.8 per cent). Pollen of *Agave* and *Pinus* were also present but in minute amounts (Table 2). Apparently, Howell and Burch (1974) were the first to demonstrate insectivory in *H. underwoodi*. They recovered the remains of Lepidoptera from a specimen in Costa Rica.

Genus PLATALINA Thomas

Platalina genovensium

Probably pollen, nectar, and insects.
The food habits are unknown.

Genus CHOERONISCUS Thomas

Choeroniscus godmani

Probably pollen, nectar, and insects.
Goodwin (1946:313), commenting on Costa Rican *C. godmani*, wrote: "Tip of tongue has numerous thread-like papillae forming a brush, especially adapted for reaching the nectar at the base of the corolla in large blossoms." Villa-R. (1967), while discussing *C. godmani* in México, cited the stomach contents given by Goodwin and Greenhall (1961) for *C. intermedius* from Trinidad.

Choeroniscus intermedius

Pollen, nectar, and insects.
Goodwin and Greenhall (1961:248) stated: "Microscopical examination of the stomach contents of one specimen [from Trinidad], however, revealed some minute particles that are possibly honey or fruit juice, many fragments of a coleopterous insect, and numerous brown and white, hair-like strands, probably either from insects or from fruit. This specimen, at least, had fed to a large extent on insects."

Summary.—Nothing is known of the food habits of *Choeroniscus minor*, *C. inca*, and *C. periosus*. Their diets, however, probably include pollen, nectar, insects, and small juicy fruits.

Genus CHOERONYCTERIS Tschudi

Choeronycteris mexicana

Fruits, pollen, nectar, and probably insects.

Dalquest (1953) expressed the opinion that in San Luis Potosí, México, *C. mexicana* feeds principally on the nectar of desert flowers, probably of cacti. Park and Hall (1951), Wille (1954), and Hall and Kelson (1959) considered *C. mexicana* to be nectarivorous. Hoffmeister and Goodpaster (1954) noted several specimens from the Huachuca Mountains in southern Arizona that had yellow pollen on the fur around the face. Huey (1954) mentioned *C. mexicana* from San Diego, California, with yellow matter in their stomachs and pollen on their faces. Sanborn (1954) suggested that this species may have the same feeding habits as *Leptonycteris nivalis*. Villa-R. (1967:263) reported capturing four *C. mexicana* in Bahia de San Carlos, Sonora, México, the mouths of which contained remains of the fruit of pitahayas (*Lemaireocereus*) or garambullas (*Myrtillocactus*). He also mentioned observing this species flying with *Leptonycteris* around fruiting cacti. In Guerrero, Villa-R. (1967) caught five specimens that had their heads and shoulders covered with *Ipomoea arborea* pollen. Walker *et al.* (1964) suggested a diet of nectar, pollen, fruit juices, and insects for this species. Barbour and Davis (1969) stated that *C. mexicana* probably feeds on nectar and mentioned individuals for which the heads and faces were covered with pollen when captured.

Alvarez and Gonzalez Q. (1970) reported on the pollen found in the stomachs of 16 *C. mexicana* from the Mexican states of Hidalgo, Guerrero, and Morelos. All stomachs contained pollen grains, and 17 pollen types were identified (Table 2). Noting that the major percentages of pollen were from *Lemaireocereus*, *Ceiba*, *Ipomoea*, *Agave*, and *Myrtillocactus* (plants that are especially attractive to pollenophagus bats), Alvarez and Gonzalez Q. (1970:156) expressed the opinion that *C. mexicana* is an obligate pollen feeder.

Genus MUSONYCTERIS Schaldach and McLaughlin

Musonycteris harrisoni

Probably pollen, nectar, and insects.

Schaldach and McLaughlin (1960) remarked on *M. harrisoni* feeding on the nectar of banana flowers in Colima, México. I noted pollen on the heads and faces of several *M. harrisoni* caught in a small banana grove in Colima (some of these specimens were included in the report by Schaldach and McLaughlin, 1960). Villa-R. (1967) stated that this species feeds on pollen, nectar, and insects found in banana flowers.

SUBFAMILY CAROLLIINAE

Genus CAROLLIA Gray

Carollia castanea

A variety of fruits and insects.

Because *C. castanea* has been confused with *C. subrufa* and *C. brevicauda* by many investigatiors, it is difficult to ascribe correctly the information on food habits in many of the accounts on *Carollia* to this species even when the name *C. castanea* was cited. A notable exception is the report by Fleming *et al.* (1972) on bats from Costa Rica and Panamá. Sixty-nine of the 102 stomachs of *C. castanea* they examined were empty. The other 33 stomachs contained approximately 92 per cent plant material (fruit) and 8 per cent insect remains. Included among the plant matter were 10 kinds of seeds. The stomachs of 28 *C. castanea* from Costa Rica and Panamá collected during all months of the year, except July and September, contained plant material exclusively. The stomach of a bat collected in July contained only insect·matter. No information was given on the stomach contents for September-caught *C. castanea*. The eight May-caught *C. castanea* from Costa Rica reported on by Howell and Burch (1974) had been feeding on *Piper*. They were able to identify *Piper auritum* in three of the bats.

Carollia subrufa

Probably fruit, flowers, and insects.

Many investigators have confused *C. perspicillata*, *C. brevicauda*, and *C. castanea* with this species. Information, however, in the accounts by Sanborn (1936) and Starrett and de la Torre (1964) probably apply to this species. Starrett and de la Torre (1964:58-59) stated: "Several types and colors of fruit pulp were taken from the digestive tracts of both specimens [from El Salvador], along with bat hairs. A small stalked inflorescence was also found in the small intestine of one, and a segment of an insect leg in the tract of the other." Sanborn (1936) related catching a *C. subrufa* in a steel trap set on a bunch of bananas in Escobas, Guatemala.

Carollia brevicauda

A variety of fruits and probably insects as well.

According to Dalquest (1953:30), in San Luis Potosí, México, "*Carollia perspicillata* [= *C. brevicauda*—see Pine, 1972:35, 38] feeds entirely on fruit. It does some damage to stored bananas, but wild figs and other wild fruits constitute its principal food." Hall and Dalquest (1963:231) reported that the stomachs of *C. perspicillata* (= *C. brevicauda*—see Pine, 1972:35, 38) taken in Veracruz, México, "held a semi-liquid mass of yellow pulp, probably of the wild sweet-lemon or wild orange." They also referred to four occasions when *C. brevicauda* were caught in banana-baited snap traps. Three were taken in traps on the ground and the fourth was caught in a trap suspended above a stem of ripe bananas hanging in a tree. Villa-R. (1967-269) reported that he observed this species in San Luis Potosí, México, eating cakes of raw sugar that were hanging high up in the eaves of a house.

Carollia perspicillata

A variety of fruits, flowers, and insects.

Many reports on *C. perspicillata* simply call it a frugivore (Park and Hall, 1951; Goodwin, 1946; Valdivieso and Tamsitt, 1962; Tamsitt and Valdivieso, 1965; McNab, 1969). Davis (1945) recorded instances in Brazil where *C. perspicillata* were caught in banana-baited snap traps set on the ground. Tuttle (1970) also reported catching several of this species in rat traps (baited with bananas) set on the ground and mentioned that in Perú these bats entered Indian houses to eat bananas. Ruschi (1953*i*) gave the diet of Brazilian *C. perspicillata* as fruit and insects. Goodwin and Greenhall (1961) and Greenhall (1956, 1957) cited the fruits of 23 species of plants consumed by this species in Trinidad (see Table 3). Goodwin and Greenhall (1961:250) also stated: "If the fruit is large, the bat eats it while hanging in the tree; if small, the fruit is plucked and carried by the bat to a temporary roost, called 'digesting place' to be eaten. . . . Some fruit is carried to the regular daytime roost."

Starrett and de la Torre (1964:58) described the contents of the digestive tracts of four *C. perspicillata* from Honduras and Costa Rica as "several types of fruit pulp, seeds and vegetable fibers." Arata *et al.* (1967) reported on the stomach contents of 74 Colombian *C. perspicillata*. They found 71 with plant material, 16 containing insects, and 6 with matted hair, claws, and flesh. The remains of bats (claws and flesh) in the stomachs could be the result of holding the bats together for a period of time after they were caught and may not represent normal food items for this species (see account of *Glossophaga soricina* for the discussion of a similar situation). Howell and Burch (1974) reported recovering the following food items from Costa Rican *C. perspicillata*: the fruits of *Piper, Cecropia, Heisteria, Licania, Acnistus, Solanum, Mangifera*, an unidentified large-seeded Solanaceae, and the remains of unidentified insects as well as those of Coleoptera.

Summary.—Many of the reports on *Carollia* confused the species *C. castanea, C. subrufa, C. perspicillata*, and *C. brevicauda*. In some instances, species can be recognized because only one is known to occur in the region discussed; for example, *C. brevicauda* in San Luis Potosí, México (Pine, 1972:38). Villa-R. (1967:269) stated that *Carollia* eat *Musa* sp., *Diospyros ebenaster, Achras sapota, Casimiroa edulis, Ficus* spp., and pitahayas (*Lemaireocereus*) in México. Duke (1967) remarked that *Carollia* eat almost any fruit in Panamá, and he cited, as examples, *Cecropia, Ficus, Mangifera, Musa, Piper*, and *Psidium*. Fleming *et al.* (1972) acknowledged that their sample of *Carollia* from Costa Rica and Panamá included *C. brevicauda* and *C. perspicillata*. They examined 760 stomachs and found 272 with food items that consisted of about 87 per cent plant matter and 13 per cent insect remains, by volume. The plant material included a wide variety of fruits as determined from the 22 kinds of seeds present in the stomachs analyzed. Stomachs either contained all plant matter or a combination of plant and insect remains.

Heithaus *et al.* (1975) also pointed out that their *C. "perspicillata"* from Costa Rica probably included more than one species. Nevertheless, they concluded that these bats were primarily frugivorous but utilized nectar during the dry

TABLE 3.—*Plants utilized in the diets of* Carollia perspicillata, Artibeus jamaicensis, *and* Artibeus lituratus.

| Plant species | Part eaten* | References** | | |
		C. perspicillata	A. jamaicensis	A. lituratus
Achras sapota	SP	2, 3, 4	2, 3, 4, 5, 6	1, 2, 3, 4
Acnistus sp.	fruit	7		
Acrocomia aculeata	P		4	4
Anamomis umbellulifera	P		2, 3, 4	2, 3, 4
Andira inermis	SP		2, 3, 4	2, 3, 4
Annona muricata	P		2, 3, 4	2, 3, 4
Annona pisonis	fruit			1
Annona squamosa	P		2, 3, 4	2, 3, 4
Anthurium sp.	fruit		9	
Artocarpus integrifolia	fruit			1
Bactris sp.	SP		2, 3, 4	2, 3, 4
Bombax sp.	F		7	
Brosimum alicastrum	fruit		7, 9	
Byrsonima spicata	SP		2, 3, 4	4
Calocarpum mammosum	P	2, 3, 4	2, 3, 4, 6	2, 3, 4
Calophyllum brasiliense	fruit		9	
Carica papaya	E	2, 3, 4	2, 3, 4	1, 2, 3, 4
Casimiroa edulis	P		6	
Cecropia bureaniana	E		5	
Cecropia obtusifolia	E		9	
Cecropia peltata	E, F	2, 3, 4	2, 3, 4	1, 2, 3, 4
Cecropia spp.	E, F	7	7	1
Ceiba pentandra	F	8	6, 7, 8	8
Cereus hexagonus	SP		4	2, 3, 4
Cerocarpus disticus	E		5	
Chlorophora tinctoria	E	2, 3, 4	2, 3, 4	2, 3, 4
Chrysalidocarpus lutescens	fruit			1
Chrysobalanus icaco	P		2, 3, 4	2, 3, 4
Chrysophyllum cainito	SP	2, 3, 4	2, 3, 4	2, 3, 4
Coccoloba uvifera	P	2, 3, 4	2, 3, 4	2, 3, 4
Coccothrinax sp.	SP		4	2, 3, 4
Coffea sp.	SP	2, 3, 4	2, 3, 4	2, 3, 4
Cordia bicolor	S		2, 3, 4	2, 3, 4
Cordia collococca	P		2, 3, 4	2, 3, 4
Crescentia cujete	F	8	8	8
Cynometra retusa	fruit		9	
Dendropanax arboreus	fruit		9	
Diospyros digyna	P		6	
Diospyros mabola	P		2, 3, 4	2, 3, 4
Dipteryx odorata	SP	2, 3, 4	2, 3, 4	2, 3, 4
Epiphyllum hookeri	P		2, 3, 4	2, 3, 4
Eugenia jambos	SP	2, 3, 4	2, 3, 4	2, 3, 4
Eugenia malaccensis	SP	2, 3, 4	2, 3, 4	2, 3, 4
Eugenia uniflora	fruit			1
Ficus benjamina	E	2, 3, 4	2, 3, 4	1, 2, 3, 4
Ficus glabrata	E		8, 9	

TABLE 3.—*Continued.*

Ficus obtusifolia	E		9	
Ficus radula	E		5	
Ficus religiosa	E, L		4	2, 3, 4
Ficus retusa	E		5	
Fisuc spp.	E	8	5, 6, 7, 8, 9	1
Flacourtia indica	E		2, 3, 4	2, 3, 4
Genipa sp.	fruit		7	
Heisteria sp.	fruit	7		
Hylocereus lemairei	P		2, 3, 4	2, 3, 4
Hymenaea courbaril	F	8	7, 8	
Iriartea exorrhiza	E		5	
Jambosa vulgaris	SP		5	
Lemaireocereus sp.	fruit		6	
Licania sp.	fruit	7	7, 9	
Livistona chinensis	fruit			1
Lucuma caimito	fruit			1
Madhuca latifolia	F		4	4
Malpighia glabra	SP		2, 3, 4	2, 3, 4
Mammea americana	P		2, 3, 4	2, 3, 4
Mangifera indica	SP	2, 3, 4, 7	2, 3, 4	2, 3, 4
Manilkara bidentata	SP	2, 3, 4	2, 3, 4	2, 3, 4
Manilkara zapota	F	8	8	8
Melicocca bijuga	P	2, 3, 4	2, 3, 4	2, 3, 4
Mimusops elengi	SP		2, 3, 4	2, 3, 4
Muntingia calabura	fruit	8	7, 8, 9	
Musa paradisiaca	E			1
Musa spp.	E	2, 3, 4	2, 3, 4, 6	2, 3, 4
Myrcia jaboticaba	fruit			1
Ochroma lagopus	F	8	8	8
Passiflora quadrangularis	P		4	1, 2, 3, 4
Persea americana	P		2, 3, 4	2, 3, 4
Pimenta racemosa	E	2, 3, 4	2, 3, 4	4
Piper amalago	E		9	
Piper auritum	E		9	
Piper hispidum	E		9	
Piper sanctum	E		9	
Piper tuberculatum	E	8	8	
Piper spp.	E	2, 3, 4, 7	2, 3, 4	4, 7
Poulsenia armata	fruit		9	
Pouteria multiflora	SP	2, 3, 4	2, 3, 4	2, 3, 4
Pseudobombax septinatum	F	8	8	
Pseudolmedia oxyphyllaria	fruit		9	
Psidium guajava	E	2, 3, 4	2, 3, 4, 5	1, 2, 3, 4
Psidium mediterraneum	E			1
Putranjivora roxburghii	SP		3, 4	2, 3, 4
Quararibea funebris	fruit		9	
Rheedia edulis	fruit		9	
Roystonea oleracea	E		4	2, 3, 4
Sapindus saponaria	P	2, 3, 4	2, 3, 4	4
Sideroxylon quadrioculare	SP		2, 3, 4	2, 3, 4

TABLE 3.—*Continued.*

Solanum paniculatum	fruit			1
Solanum spp.	fruit	7, 8	8, 9	
Spondias cytherea	P		2, 3, 4	2, 3, 4
Spondias mombin	SP	2, 3, 4	2, 3, 4, 9	2, 3, 4
Spondias sp.	SP		6	
Terminalia catappa	SP	2, 3, 4	2, 3, 4	2, 3, 4
Turpinia pinnata	fruit		9	
Vitis vinifera	E		2, 3, 4	1, 2, 3, 4

*Part eaten: E, entire fruits; S, skin only; P, pulp only; SP, skin and pulp; F, flowers (includes pollen and nectar; L, leaves; fruit, no information on part of fruit consumed.

**References: 1) Ruschi, 1953*j*; 2) Greenhall, 1956; 3) Greenhall, 1957; 4) Goodwin and Greenhall, 1961; 5) Carvalho, 1961; 6) Villa-R., 1967; 7) Howell and Burch, 1974; 8) Heithaus *et al.*, 1975; 9) Vázquez-Yáñes *et al.*, 1975.

season. The six most common pollens found on these bats were *Ochroma lagopus*, *Hymenaea courbaril*, *Pseudobombax septinatum*, *Crescentia* sp., *Manilkara zapota*, and *Ceiba pentandra*. Identifiable fruit remains recovered in the feces of these bats included *Ficus* sp., *Muntingia calabura*, *Solanum* sp., and *Piper tuberculatum*. They reported 38.2 per cent of 186 bats with pollen, 32.4 per cent of which carried two or more species of pollen; 44.9 per cent of 316 bats with seeds in their feces; and 13.0 per cent of 272 bats had consumed insects (percentage by volume; data from Fleming *et al.*, 1972).

Klite (1965) reported on the transit time through the digestive tract of dyed fruits in three Neotropical bat species from Panamá including three individuals he identified as *C. perspicillata*. When India ink was used as a marker, two of the three *Carollia* passed stools containing the ink after a time lapse of 30 minutes. These results indicate that some frugivorous species are able to extract the nutritive components of their food in a very short time and may consume several times more fruit in a single night than the holding capacity of the stomach would suggest.

Genus RHINOPHYLLA Peters

Rhinophylla pumilio

Presumedly fruit.

McNab (1969) considered *R. pumilio* to be frugivorous. Tuttle (1970) recorded capturing a male in a banana-baited trap set on the ground beneath ferns in dense mature forest in Perú.

Summary.—The food habits of *Rhinophylla alethina* and *R. fischerae* are not known. Bats of this genus are probably all frugivores, although they may consume insects as well.

SUBFAMILY STENODERMINAE

Genus STURNIRA Gray

Sturnira lilium

A variety of fruits and possibly pollen and nectar as well.

Most accounts on *S. lilium* simply state that the species is frugivorous (Goodwin, 1946; Tamsitt and Valdivieso, 1961; Villa-R., 1967; McNab, 1969). Several investigators have mentioned finding the remains of fruit in the digestive tracts of these bats (Dalquest, 1953; Goodwin and Greenhall, 1961; Starrett and de la Torre, 1964; Arata *et al.*, 1967; Fleming *et al.*, 1972). Cockrum and Bradshaw (1963) reported on a *S. lilium* shot from among several bats observed feeding on wild figs (*Ficus*) growing along the Río Cuchajaqui in southern Sonora, México. Villa-R. and Villa Cornejo (1969, 1971) remarked that *S. lilium* take the fruit of the date palm and are attracted to ripe bananas in northern Argentina. Sanborn (1936) referred to a specimen caught in a steel trap placed on a bunch of bananas in Escobas, Guatemala. Gaumer (1917) reported that *S. lilium* in Yucatán, México, eat insects, although he said their principal food was fruit. Ruschi (1953*k*) also gave the diet of *S. lilium* in Brazil as fruit and insects. I have collected *S. lilium* at Balta on the Río Curanja, Departamento de Loreto, in eastern Perú, the feces of which contained the seeds of *Cecropia* sp. and *Piper* sp. One entered a mist net while carrying a catkin of *Cecropia* sp. in its mouth.

Heithaus *et al.* (1974) reported recovering *Bauhinia pauletia* pollen from a specimen near Cañas, Costa Rica, and mentioned (p. 418) that "*S. lilium* visited other flowers in the study region." The latter observation was substantiated by Heithaus *et al.* (1975) who reported finding pollen on 41.8 per cent of 110 Costa Rican *S. lilium* of which 47.8 per cent carried two or more species of pollen. The six most common pollens they recovered were *Crescentia* sp., *Pseudobombax septinatum*, *Manilkara zapota*, *Hymenaea courbaril*, *Ochroma lagopus*, and *Ceiba pentandra*. Most of the fruit remains found in the feces were unknown; however, they were able to identify the seeds of *Piper tuberculatum*, *Muntingia calabura*, and *Solanum* sp. Howell and Burch (1974) reported the following food items recovered from *S. lilium* in Costa Rica: insects (Lepidoptera), pollen (*Ceiba*), and fruit (*Piper*, *Licania*, *Muntingia*, *Acnistus*, *Solanum*, melastomaceous fruit, and large-seeded solanaceous fruit).

Sturnira tildae

Fruit.

Goodwin and Greenhall (1961) reported finding purplish fruit juice in the stomach of a *S. tildae* from Trinidad.

Sturnira mordax

Fruit.

Howell and Burch (1974) reported recovering the identifiable remains of the fruits of *Centropogon*, *Anthurium*, *Musa*, and *Cecropia* from *S. mordax* in Costa Rica.

Sturnira ludovici

Fruit.

Dalquest (1953) wrote that he observed *S. ludovici* feeding on tree fruits in San Luis Potosí, México. Tschudi (1844) mentioned that *S. oporophilum* (= *S. ludovici*) eats fruit, but he also believed that this species feeds on blood. Starrett and de la Torre (1964) remarked on *S. ludovici* from Costa Rica that had fruit pulp in their digestive tracts. Howell and Burch (1974) reported another specimen from Costa Rica that had consumed fruit.

Sturnira erythromos

Fruit.

The only account containing food habits information is that by Tschudi (1844), who stated that this species feeds on fruit. In addition, he (1844:67) related an incident where a bat he identified as this species bit a sleeping drunken Indian on the nose and became so engorged with blood that it could not fly. The bat was captured and taken back to Europe as a specimen. This bat was undoubtedly a desmodontine and not a *Sturnira*, and, inasmuch as Tschudi described the species *S. erythromos* in this publication (the holotype was not the same specimen mentioned above), he may not have witnessed the incident personally.

Summary.—No information has been published on the food habits of *Sturnira thomasi*, *S. magna*, *S. bidens*, *S. nana*, and *S. aratathomasi*; nevertheless, the diets of these species most likely include a wide variety of fruits. Duke (1967), relating information from Edwin Tyson, said the foods eaten by *Sturnira* in Panamá "consist mainly of fruits, e.g. *Piper*, *Psidium*." Gaumer (1917) and Ruschi (1953k) mentioned insects in the diet of *S. lilium*; however, the actual role of insects as food items of *Sturnira* is unknown.

Genus URODERMA Peters

Uroderma bilobatum

Various kinds of fruit and insects.

Most references that allude to the food habits of *U. bilobatum* simply state that this bat eats fruit or is a frugivore (Goodwin, 1946; Tamsitt and Valdivieso, 1965; Villa-R., 1967; Duke, 1967; Walker *et al.*, 1964; McNab, 1969). Bloedel (1955) reported *U. bilobatum* eating the pericarp of small unidentified palm fruits in Panamá. Fruits, particularly of three species of *Ficus*, were recorded by de Carvalho (1961) as food items for this species in Brazil. Goodwin and Greenhall (1961) mentioned finding the remains of *Psidium guajava* in the stomachs of two *U. bilobatum* in Trinidad. Fleming, *et al.* (1972) cited 405 stomachs of *U. bilobatum* they examined from Costa Rica and Panamá. Of these, 320 contained

food remains consisting of approximately 76 per cent plant matter, 13 per cent insects, and 11 per cent unclassified material, by volume. Howell and Burch (1974) reported finding *Brosimum* in one and an unidentifiable green fruit in the other of the two *U. bilobatum* they examined in Costa Rica.

Summary.—The diet of *Uroderma magnirostrum* has not been reported; however, it probably includes fruit, flower products, and insects. I collected several *U. magnirostrum* at Balta on the Río Curanja, Departamento de Loreto, Perú, the fur of which was stained yellow from flower pollen or the heads and shoulders of which were dusted with pollen.

Both species of *Uroderma* likely are frugivorous but many also consume quantities of pollen, nectar, and insects found in flowers and fruit as well.

Genus VAMPYROPS Peters

Vampyrops vittatus

Fruit.

Tuttle (1970) reported that he netted several *V. vittatus* in Perú that were carrying large figs (*Ficus*). Howell and Burch (1974) listed *Cecropia* and *Acnistus* as food items eaten by this species in Costa Rica.

Vampyrops dorsalis

Fruit and insects.

Arata *et al.* (1967) reported on the stomach contents of four Colombian *Vampyrops* identified as *V. dorsalis*. Three of the stomachs contained plant material and one contained insect remains. Their paper does not indicate whether the stomach containing insects was one of the three with fruit or was the fourth they examined.

Vampyrops helleri

Fruit.

Goodwin (1946), reporting on Costa Rican *V. helleri*, stated that it is a fruit-eating species. Villa-R. (1967) also reported that Mexican *V. helleri* are frugivorous.

The remains of fruit have been noted in most analyses of stomach contents (Goodwin and Greenhall, 1961; Starrett and de la Torre, 1964; Arata *et al.*, 1967; Fleming *et al.*, 1972); however, Howell and Burch (1974) reported two Costa Rican *V. helleri* that had eaten both fruit (*Cecropia*) and insects (Lepidoptera). The other eight they examined had been feeding on the fruit of *Acnistus*.

Vampyrops lineatus

A variety of fruits and insects.

Ruschi (1953*j*) recorded the foods of Brazilian *V. lineatus* as various fruits and insects (especially lepidopterans of the family Sphingidae). McNab (1969) reported the diet as fruit.

Summary.—Nothing has been reported on the food habits of *Vampyrops infuscus, V. aurarius, V. nigellus, V. brachycephalus,* and *V. recifinus.* The diets of these and other species of *Vampyrops* probably consist of a variety of fruits, some insects, and possibly some flower products. Walker *et al.* (1964) and Duke (1967) presumed *Vampyrops* to be frugivorous.

Genus VAMPYRODES Thomas

Vampyrodes caraccioloi

Fruit.

Vampyrodes caraccioloi is considered to be a frugivore (Goodwin, 1946; Walker *et al.,* 1964; Duke, 1967). Goodwin and Greenhall (1961) and Fleming *et al.* (1972) reported the contents of the stomachs they examined as consisting entirely of the remains of fruit.

Genus VAMPYRESSA Thomas

Vampyressa pusilla

Fruit.

Goodwin (1946) considered Costa Rican *V. minuta* (= *V. pusilla*) to be frugivorous. Starrett and de la Torre (1964) reported finding a small amount of fruit pulp in the digestive tract of a *V. thyone* (= *V. pusilla*) from Nicaragua. Fleming *et al.* (1972) reported the stomach contents of one *V. pusilla* out of the eight they examined from Panamá as 100 per cent plant material. The others apparently were empty. Howell and Burch (1974) listed five from Costa Rica that had fed on the fruit of *Acnistus.*

Summary.—The diets of *Vampyressa melissa, V. nymphaea, V. brocki,* and *V. bidens* are not known. These species probably subsist primarily on fruits as was suggested for the genus by Walker *et al.* (1964) and Duke (1967).

Genus CHIRODERMA Peters

Chiroderma villosum

Fruit.

This species is presumed to be frugivorous (Goodwin, 1946; Goodwin and Greenhall, 1961; Villa-R., 1967).

Chiroderma salvini

Fruit.

Fruit-eating habits were reported by Goodwin (1946). Jones *et al.* (1972) implied that *C. salvini* eats figs inasmuch as they mentioned catching one along with *Artibeus* and *Sturnira* in a net under a fig tree replete with ripe fruit in Sinaloa, México.

Chiroderma trinitatum

Fruit.

A diet of fruit was suggested by Goodwin and Greenhall (1961).

Summary.—Nothing has been reported on the diets of *Chiroderma doriae* and *C. improvisum.* Although the fruit diets of *C. villosum, C. salvini,* and *C. trinitatum* are based only on conjecture, these species probably do subsist primarily on fruits as suggested by Walker *et al.* (1964) and Duke (1967).

Genus ECTOPHYLLA H. Allen

Ectophylla alba

Presumedly fruit.

Casebeer *et al.* (1963) reported finding small amounts of unidentified green vegetable matter in the lower intestine of *E. alba* from Costa Rica. I also found similar material in the digestive tracts of five Costa Rican specimens.

Summary.—The food habits of *Ectophylla macconnelli* are not known; however, this species most likely is frugivorous. Duke (1967) mentioned that the food habits were not known for species of *Ectophylla* and attributed to Edwin Tyson the opinion that Panamanian species are insectivorous.

Genus ARTIBEUS Leach

Artibeus cinereus

Fruit and insects.

Goodwin and Greenhall (1961) stated that *A. cinereus* eats a variety of fruits in Trinidad, and Piccinini (1971) mentioned that this species is frugivorous in Brazil. Arata *et al.* (1967) noted that the stomachs of five Colombian specimens contained plant material and one of these held insect remains as well.

Artibeus watsoni

Fruit.

Fleming *et al.* (1972) reported only finding plant matter in two of the 53 stomachs of *A. watsoni* they examined from Costa Rica and Panamá. The other 51 stomachs were empty. Howell and Burch (1974) were able to identify *Cecropia* as the fruit eaten by the two *A. watsoni* they examined in Costa Rica.

Artibeus phaeotis

Fruit.

Villa-R. (1966) reported that *A. turpis* (= *A. phaeotis*) is frugivorous in México. Fleming *et al.* (1972) examined the stomach contents of 90 *A. phaeotis* from Costa Rica and Panamá. Of these, only two contained food, which was 100 per cent fruit pulp in each case. Heithaus *et al.* (1975) determined that 40 per

cent of 15 *A. phaeotis* in Costa Rica were carrying pollen when captured. Of these, 33.3 per cent carried two or more species of pollen. They found seeds in the feces of 8 per cent of 25 of these bats but did not identify any of the fruits consumed. The five most common pollens recovered were *Ceiba pentandra, Crescentia* sp., *Ochroma lagopus, Pseudobombax septinatum,* and *Hymenaea courbaril.*

Artibeus toltecus

Fruit.

Villa-R. (1967) reported observing *A. toltecus* eating the fruits of "amate prieto" (*Ficus padifolia*) in México. *Cecropia* was listed by Howell and Burch (1974) as the food eaten by the six they examined in Costa Rica.

Artibeus hirsutus

Presumedly fruit.

Jones *et al.* (1972:13) wrote: "A specimen from . . . [Sinaloa, México] was shot as it sought food in a strangler fig [*Ficus cotinifolia*]." Villa-R. (1967) suggested that the food habits are similar to those of *A. jamaicensis.*

Artibeus jamaicensis

Insects and a variety of plant materials such as fruits, flower products, and leaves.

Osburn (1865) reported finding the kernels of *Brosimum* strewn on the floor of a cave in Jamaica inhabited by *Arctibeus carpolegus* (= *Artibeus jamaicensis*): Some of the nuts (p. 64) had "germinated into young blanched trees on the thick deposit of dung." In other Jamaican caves used by this species he found dried seeds, berries of *Cordia collococca,* and husks that included gnawed fragments of unripe mangoes and the fruit of the rose-apple (*Eugenia jambos*). He (1865:66) also mentioned finding yellow juice and small seeds that he suspected were those of the fustic (*Morus tinctoria*) in the digestive tract of a specimen. Ortiz de la Puente (1951) related finding the male inflorescences of maize and, occasionally, seeds of *Eriobotrya japonica* under roosts of *A. jamaicensis* in caves in western Perú. Van der Pijl (1957:294) referred to Heinz Felten's observations (personal communication) on regularly finding remnants of *Spondias purpurea* under colonies in caves in El Salvador. Bond and Seaman (1958) remarked that seeds and partly eaten fruits of mango, East Indian almond, hogplum, and other easily recognized food items were abundant under *A. jamaicensis* roosts in the Virgin Islands. Goodwin (1970:575) stated that the presence of *A. jamaicensis* in caves in Jamaica is usually indicated by a "garden" of pale, spindly, seedling plants growing on the floor beneath the roosting site. He identified the plants from two caves as *Andira inermis* and observed that the fruits of this tree are a staple food of *Artibeus.* Allen (1939) mentioned the presence of sprouted nuts of *Acrocomia* in a cave in Puerto Rico and stated that *A. jamaicensis* was fond of the thin layer of pulp surrounding the small nutlike fruits of this palm. Tuttle

(1968) remarked on finding the remains of several kinds of fruit on a large pile of guano beneath an *A. jamaicensis* roost in Chiapas, México. The remains included many hard nuts, each of which had been chewed open at one end. Beneath the roost, Tuttle (1968) also found discarded leafy twigs of which many of the leaves were chewed and appeared to have been partly eaten. While conducting his reconnaissance on the roosting site, he recorded the following observations (p. 787): "While I sat quietly a few feet below them, the bats began to catch and eat large (about 6 mm long) blackflies. The bats would hang by one foot and rotate in nearly complete circles watching the flies. Whenever a fly flew within reach of one of the bats, the bat would capture it with a rapid thrust of one of its wings. Flies were caught in the wing-tips and were immediately eaten. This behavior was observed repeatedly."

Quelch (1892:102) described the foraging behavior of *A. jamaicensis* in British Guiana (Guyana): "During the fruiting season, when the sapodillas, star-apples, mangoes, and such like fruit are ready to be gathered, numbers of these large bats are to be observed at sunset, flitting in and out among the leaves and branches, picking out and feeding on the ripest fruit to be found. They dart up and down repeatedly at the same fruit, remaining momentarily almost stationary while their teeth are applied, and with the force of their flight they cause either the tearing away of part of the soft pulp, or of the whole fruit, according to its degree of ripeness." Jimbo and Schwassmann (1967) reported *A. jamaicensis* feeding on sapodilla plums (*Achras sapota*), guava (*Psidium guajava*), and figs (*Ficus* sp.) at Belem, Brazil. The fruits, some weighing as much as 50 grams, were carried off. If the fruit was dropped, the bat sometimes would drop to the ground and eat part of it before flying away. Tamsitt and Valdivieso (1961) mentioned two occasions in Costa Rica when *A. jamaicensis* entered mist nets while carrying pomarrosa fruit (*Syzigium jambos*) in their mouths. One of the fruits measured 34.8 millimeters in diameter. Tuttle (1970) related catching an *A. jamaicensis* in Perú that was carrying a large (about 30 millimeters in diameter) wild fig in its mouth. I recovered pomarrosa and guava fruit carried into a mist net by *A. jamaicensis* in Villavicencio, Colombia. One of the larger guavas measured 42 millimeters in its greatest diameter and weighed 35 grams. A second measured 48 by 42 millimeters and weighed 50 grams. The largest was not weighed but measured 64 by 50 millimeters. Jones *et al.* (1972:13) recorded observations on *A. jamaicensis* in Sinaloa, México, and stated, "individuals of this species were seen emerging from a hollow limb of a fig tree. They foraged higher in the tree, sometimes returning in approximately 10 minutes with cut green figs to the hollow." Dalquest (1953) recorded this bat feeding on fruits such as jobo plums (*Spondias* sp.) and green wild figs (*Ficus* sp.) in San Luis Potosí, México. He noted that the mouths of caves used as day roosts were commonly heaped with cores and seeds of fruit and small pellets of fruit skin and rind, which the bats eject when they eat. Hall and Dalquest (1963) also mentioned jobo plums and wild figs as foods of *A. jamaicensis* in Veracruz, México. Vázquez-Yáñes *et al.* (1975) reported the kinds and percentages by weight for each month of occurrence of the fruits they recovered from a cave inhabited by *A. jamaicensis* in the Tuxtlas region of Vera-

cruz, México. The fruits they identified are *Cecropia obtusifolia*, *Spondias mombin*, *Ficus* spp., *F. glabrata*, *F. obtusifolia*, *Poulsenia armata*, *Cynometra retusa*, *Calophyllum brasiliense*, *Brosimum alicastrum*, *Piper auritum*, *P. hispidum*, *P. amalago*, *P. sanctum*, *Turpinia pinnata*, *Solanum* spp., *Dendropanax arboreus*, *Quararibea funebris*, *Anthurium* sp., *Licania* sp., *Muntingia calabura*, *Pseudolmedia oxyphyllaria*, and *Rheedia edulis*. Dalquest *et al.* (1952) reported on the mucous salivary glands opening in the lips at the ventral angle of the lower jaw in *A. jamaicensis*. They interpreted the function of these glands as supplying the mucous that binds together the pelletized ejected unpalatable portions of the fruit these bats eat.

Greenhall (1956, 1957) and Goodwin and Greenhall (1961) presented nearly identical lists of foods eaten by *A. jamaicensis* (Table 3). Their information was based primarily on debris found beneath roosting sites in Trinidad. De Carvalho (1961) described a number of fruits utilized as food by *A. jamaicensis* in Brazil (Table 3). Villa-R. (1967) noted a number of fruits in the diet of Mexican *A. jamaicensis* as well as pollen and nectar from the flowers of *Ceiba pentandra* (Table 3). He also related having observed *A. jamaicensis* entering a small house in San Luis Potosí, México, to eat cakes of sugar that were stored near the ceiling. Goldman (1920) commented on catching several of this species at Gatún, Panamá, in traps placed about a bunch of ripening bananas. Starrett and de la Torre (1964) gave the stomach contents of *A. jamaicensis* from Nicaragua and Costa Rica as fruit pulp, plant fibers, and bat hairs. They also noted (p. 61) that a specimen "from Costa Rica also had an ant (Formicidae: Ponerinae) embedded in a reddish amber-like substance in its intestine." Arata *et al.* (1967) related finding only plant material in the stomach of a specimen they examined from Colombia. Fleming *et al.* (1972) reported on the 23 stomachs containing food material among the 916 digestive tracts they examined from Costa Rica and Panamá. The stomach contents, by volume, consisted of about 66 per cent plant matter, 25 per cent insect remains, and 9 per cent unclassified material. They also expressed the opinion that figs (*Ficus insipida*) were a favorite food of *A. jamaicensis* in the Panama Canal Zone. Howell and Burch (1974) identified insects (Coleoptera), pollen (*Hymenaea*, *Ceiba*, and *Bombax*), and fruit (*Licania*, *Genipa*, *Muntingia*, *Brosimum*, *Ficus*, *Cecropia*, and melastomaceous fruit) as the food items they recovered from *A. jamaicensis* in Costa Rica.

Palmer (*in* Miller, 1904:347), in reporting the habits of *A. jamaicensis* in Cuba, wrote that "they evidently capture much of their food among flowering trees, as their fur often contains pollen and parts of flowers. These are also found abundantly on the floors of caves where the bats roost." Silva Taboada and Pine (1969) implied that either Palmer's observations were unusual or were in error as they had never found flower parts in the fur of Cuban *Artibeus*. However, Piccinini (1971) noted that several *A. jamaicensis* collected in Brazil during October were stained yellow by the pollen of *Anacardium occidentale* and he assumed that these bats, although primarily frugivorous, eat pollen when fruits are not available. Heithaus *et al.* (1974) recovered *Bauhinia pauletia* pollen from the fur of two *A. jamaicensis* near Cañas, Costa Rica. Heithaus *et al.* (1975)

reported recovering pollen from the fur of 54.1 per cent of 477 individuals in Costa Rica of which 43 per cent were carrying two or more species of pollen. Only 8.6 per cent of 617 *A. jamaicensis* had seeds in their feces. The six most common pollens they recorded were *Crescentia* sp., *Manilkara zapota*, *Hymenaea courbaril*, *Pseudobombax septinatum*, *Ochroma lagopus*, and *Ceiba pentandra*. The identifiable fruit remains they recorded were *Piper tuberculatum*, *Solanum* spp., *Muntingia calabura*, and *Ficus* sp. Hall and Kelson (1959) described the food of *A. jamaicensis* as mainly ripe fruits, the small kinds of which are plucked and carried to the feeding sites. McNab (1969) and Tamsitt and Valdivieso (1970) merely stated that the species is a frugivore.

Artibeus lituratus

Insects and a variety of plant matter including fruit, flowers, and leaves.

Valdivieso and Tamsitt (1962), Tamsitt and Valdivieso (1965), and McNab (1969) considered *A. lituratus* to be frugivorous. Dalquest (1953) reported on finding the gound beneath the roosts of this species in San Luis Potosí, México, littered with the small, brown pellets of rind and skin of fruit ejected by the bats as they fed. Van der Pijl (1957:294) quoted Heinz Felten (personal communication) who told him of regularly finding remnants of *Ficus* sp. under colonies in caves in El Salvador. Bloedel (1955:235), writing about Panamanian bats, mentioned that *A. lituratus* "dropped many spave beans below their habitual roosting place." Villa-R. and Villa Cornejo (1969, 1971) reported that they observed numbers of *A. lituratus* taking either ripe palm fruit or pollen from flowers in northern Argentina. Tamsitt and Valdivieso (1963) commented on twice netting *A. lituratus* that were carrying ripe almond fruits in their mouths. Greenhall (1956, 1957) and Goodwin and Greenhall (1961) listed a number of plant species utilized in the diet of this species (Table 3). The plant foods listed by Goodwin and Greenhall (1961) were cited as foods for both *A. lituratus* and *A. jamaicensis*. Villa-R. (1967) also stated that these two species have similar food habits in México.

Ruschi (1953a) presented information on the stomach contents of *A. jamaicensis lituratus* (= *A. lituratus?*) from Brazil. He claimed (p. 3) to have found coagulated blood in addition to fragments of fruit in the stomachs of these bats. Ruschi (1953j), in addition to listing a number of the principal fruits eaten by these bats (Table 3), elaborated on his earlier report on finding blood among the stomach contents. He referred to capturing several *A. lituratus* alive in a palm tree and later finding blood in their stomachs. I recommend, however, that blood not be considered a normal food for *Artibeus*; the blood in the stomachs may be explained as having come from the cleansing of wounds acquired during fighting among the bats as they were held together subsequent to their capture. Nevertheless, in support of his opinion on the alleged blood-feeding habits of this species, Ruschi mentioned (p. 7) having surprised an *A. lituratus* in the act of eating nestling robins (*Turdus rufiventris*) and noted that these bats accepted blood, in addition to fruit and insects, as food in captivity. Ruschi also observed *A. lituratus* pursue and capture sphingid moths.

Genus CENTURIO Gray

Centurio senex

Fruit.

Goodwin and Greenhall (1961) mentioned finding yellow fruit pulp in stomachs of *C. senex* from Trinidad. Walker *et al.* (1964) gave the diet as "soft mushy fruits." Felten (1956) may have meant to imply that *C. senex* feeds on figs (*Ficus* sp.) in El Salvador when he mentioned collecting a specimen when it was flying around a fig tree.

SUBFAMILY PHYLLONYCTERINAE

Genus BRACHYPHYLLA Gray

Brachyphylla cavernarum

Fruits and insects.

Bond and Seaman (1958:151), reporting on a roost of *B. cavernarum* in the Virgin Islands, noted, "an examination with a hand lens of the washed guano shows it to contain a high proportion of insect fragments, and some amorphous material which may or may not be fruit pulp. Seeds and partly eaten fruits are [present] in *Artibeus* guano. No such material was found in the guano of *Brachyphylla*, although a few small seeds of what appears to be a species of *Eugenia* were seen. These seeds could have passed through the bats or been brought in by mice. These observations could mean either that *Brachyphylla* is entirely insectivorous, or that it eats fruit but avoids small seeds, and cannot carry larger-seeded fruits back to the roost as does *Artibeus*." Nellis (1971) found *B. cavernarum* on St. Croix, Virgin Islands, feeding on the fruits of *Manilkara zapota*. Hall and Kelson (1959) and Tamsitt and Valdivieso (1970) referred to this species as the "St. Vincent Fruit-eating Bat."

Brachyphylla nana

Fruit, pollen, nectar, and insects.

Silva Taboada and Pine (1969) presented information on the contents of 43 stomachs of *B. nana* from Cuba. All stomachs contained masses of what appeared to be partially digested pollen grains. One stomach contained lepidopteran scales and another held fragments of a fly (Diptera). In Cuba, Silva Taboada frequently encountered individuals the head, chest, and shoulders of which were dusted with pollen. Silva Taboada and Pine (1969:15) considered *B. nana*, as well as Cuban *Phyllonycteris* and *Erophylla*, primarily to be "pollen eaters which probably also feed on soft fruit pulp and nectar."

Genus EROPHYLLA Miller

Erophylla bombifrons

Fruit, pollen, nectar, and insects.

Hall and Kelson (1959) referred to *E. bombifrons* as the "Brown Flower Bat"; however, Tamsitt and Valdivieso (1970) said it is frugivorous.

Erophylla sezekorni

A variety of fruits, pollen, nectar, and insects.

Osburn (1865) reported on finding breadnut kernels and munched berries of the clammy cherry (*Cordia collococca*) associated with cave roosts of bats he referred to as *Monophyllus* (= *Erophylla sezekorni*) in Jamaica. The stomach of one specimen he examined (p. 82) "was filled with a yellowish frothy pulp." Osburn described the feeding behavior of a captive: "The tongue was rapidly protruded and drawn in again, and the juice and softer pulp cleared away with great rapidity. I noticed he was very particular in cleaning out the bit of loose skin of the berry [*Cordia collococca*]." Osburn also noted (p. 84) the similarity of the berries eaten by this bat and those found beneath the cave roosts. Silva Taboada and Pine (1969) presented information on the stomach contents of 30 *E. sezekorni* from Cuba. They found masses of partially digested pollen grains in all stomachs. In addition, three contained seeds of bromeliaceous fruits (*Hohenbergia*) and four held insect remains identifiable as parts of an elaterid beetle (*Conoderus*), a roach (Orthoptera, Blattidae), Diptera, Lepidoptera, and Microlepidoptera. Silva Taboada and Pine (1969:15) expressed the opinion that *E. sezekorni* (along with Cuban *Brachyphylla* and *Phyllonycteris*) "are primarily pollen eaters which probably also feed on soft fruit pulp and nectar." Hall and Kelson (1959) referred to *E. sezekorni* as the "Buffy Fruit Bat."

Genus PHYLLONYCTERIS Gundlach

Phyllonycteris poeyi

Probably a variety of fruits, pollen, nectar, and insects.

Allen (1942:26-27) commented that *P. poeyi* have "long protrusible tongues, which are useful in licking up fruit pulp and juices on which they largely feed. Probably pollen and nectar are also eaten." Silva Taboada and Pine (1969) reported the stomachs of 42 *P. poeyi* they examined from Cuba as containing masses of what appeared to be partially digested pollen grains. One stomach also contained lepidopteran scales. They commented (p. 15) "that the Cuban representatives of *Brachyphylla*, *Phyllonycteris*, and *Erophylla* are primarily pollen eaters which probably also feed on soft fruit pulp and nectar."

Summary.—The diets of *Phyllonycteris major* and *P. aphylla* are not known; however, these "Flower Bats" (Hall and Kelson, 1959) likely have food habits similar to those of *P. poeyi* and include fruit, pollen, nectar, and insects in their diets.

SUBFAMILY DESMODONTINAE

Genus DESMODUS Wied-Neuwied

Desmodus rotundus

Blood of warm-blooded animals.

The folklore surrounding the sanguivorous habits of *D. rotundus*, enhanced by the imaginations of the early explorers and naturalists who visited the New World

tag, was killed while feeding on chickens." Villa-R. (1967) stated that *D. ecaudata* appears to prefer the blood of birds. The stomachs of 18 Brazilian *D. ecaudata* examined by Villa-R. *et al.* (1969) contained bird blood exclusively.

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This study appears to be the only instance in which the movements of phyllotso-matids between day roosts and feeding grounds have been documented.

Data obtained by banding (LaVal, 1970; Fleming *et al.*, 1972) indicate that some phyllostomatids have regular feeding grounds. Further evidence of this is provided by the observations of Baker (1973) concerning the visits of some glossophagines and one stenodermine to flowers. *Leptonycteris sanborni, Glossophaga* sp., *Glossophaga soricina*, and *Artibeus jamaicensis* have been observed to make fleeting visits to flowers (Baker, 1973). Baker (1973) and others (Vogel, 1968-69; Baker *et al.*, 1971) have remarked on the "trap lining" nature of these visits, which appears to indicate regular patterns of movements.

Phyllostomatids, including *Macrotus waterhousii* (Vaughan, 1959), *Lonchorina aurita* (Nelson, 1965), and *Leptonycteris sanborni* (Hayward and Cockrum, 1971), but especially the Phyllonycterinae and the Desmodontinae, are active later in the evening than are many other bats (see Silva Taboada and Pine, 1969; Leen and Novick, 1969; Wimsatt, 1969; Crespo *et al.*, 1972). In lowland rain-forest in Guyana, one of us (Fenton) made similar observations. Using mist nets and ultrasonic detectors (Fenton *et al.*, 1973), it was established that embal-lonurids, mormoopids, vespertilionids, and molossids were most active around dusk and dawn, whereas phyllostomatids (including *Phyllostomus elongatus, Glossophaga soricina, Carollia perspicillata, Rhinophylla pumilio, Sturnira lilium, Uroderma bilobatum, Vampyrops helleri, Vampyressa bidens, Chiroderma villosum, C. trinitatum, Ectophylla macconnelli, Artibeus cinereus, A. concolor, A. lituratus, Ametrida centurio,* and *Desmodus rotundus*), based on captures in mist nets, were active later in the evening and throughout the night until about one hour before dawn. Further observations on phyllostomatid activity have recently appeared (Heithaus *et al.*, 1974; Tuttle, 1974; Davis and Dixon, 1976).

In part, these temporal differences can be accounted for by the sequence of departures from the day roosts. At Mount Plenty Cave in Jamaica, Leen and Novick (1969) observed that *Monophyllus redmani* was the first species to depart in the evening, followed by *Pteronotus psilotis, P. parnellii, Artibeus jamaicensis,* and *Phyllonycteris* sp. Whether or not these departures represent differential sensitivity to light, roost locations, or differences in circadian periodicity remains to be determined.

Captures of bats at different locations during the night have been used to in-dicate activity patterns (Brown, 1968; LaVal, 1970). However, comparison of activity patterns from different areas or seasons is difficult because the basic pat-terns of activity reflect, among other things, the proximity of the study site to day and night roosts.

For example, when the activity patterns of *Artibeus jamaicensis* in Costa Rica (Fig. 1a and 1b) are compared with those we obtained in Puerto Rico for this species (Fig. 1c), marked differences are evident. Given that the values provid-ed by Brown (1968) are absolute numbers and the other values are proportions, different levels of bat activity occur. Brown (1968) and LaVal (1970) obtained similar patterns of activity of *A. jamaicensis* in forests and banana groves, and we studied its activity at the entrance to a large cave system, parts of which were used
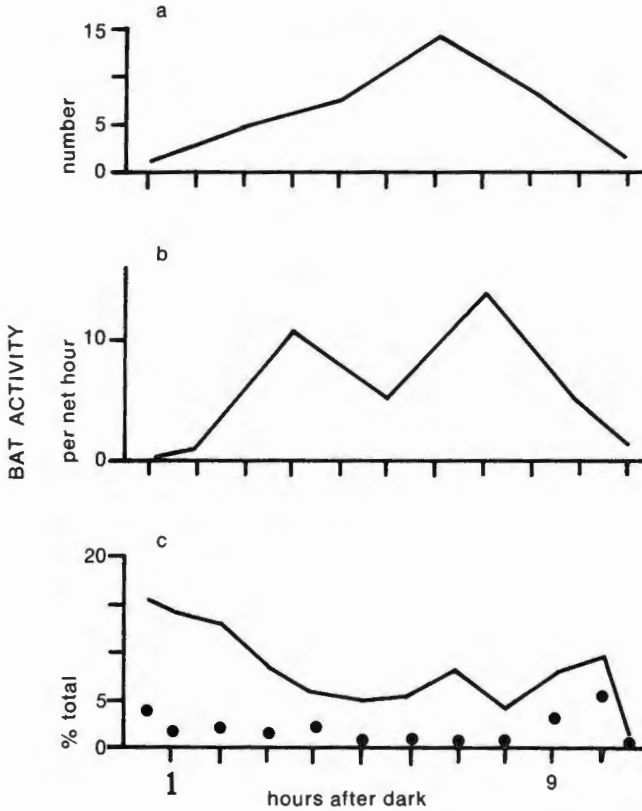
Fig. 1.—Nightly activity of *Artibeus jamaicensis*: A, Costa Rica, Banana Grove (after Brown, 1968; *N*=30); B, Costa Rica, Dry Forest (after LaVal, 1970; *N*=59); C, Puerto Rico, Cave entrance (This study, *N*=124; a solid circle indicates per cent adult males).

as day roosts by this species. The three patterns indicate that some individuals of this species are active throughout the night. Adult male *A. jamaicensis* in Puerto Rico were more active one hour after dark and one hour before dawn, but did show sporadic activity throughout the night (Fig. 1c).

Williams and Williams (1970) found that much of the activity of *Phyllostomus hastatus* in Trinidad occurred in the first few hours after sunset, considering the times when most individuals returned to their daytime refuges. They also noted an additional period of activity just before sunrise, although LaVal (1969) failed to observe comparable predawn activity for other phyllostomatids in Costa Rica. The disparity of these two reports may reflect differences in behavior of bats as a function of proximity to the day roost, since predawn feeding may be restricted to the immediate vicinity of the day roost.

The effect of roost proximity and, of course, season and weather on activity patterns of bats makes detailed comparisons from different areas tenuous. Inasmuch as we lack detailed analyses of activity patterns of bats from any area

(with the possible exception of Nyholm's, 1965, data from some species of *Myotis*), a comprehensive understanding of the situation is presently unrealistic.

Similarly, other than anecdotal observations, there are few data on the effects of weather on the activity of Phyllostomatidae. Tamsitt and Valdivieso (1961) reported a strong inhibiting effect of moonlight on bat activity in Costa Rica, but this was not observed by LaVal (1970), who noted that his mist nets had been set in closed forest, whereas Tamsitt and Valdivieso (1961) had been working in more open situations. Crespo *et al.* (1972) found a strong inhibiting effect of moonlight on the activity of *Desmodus rotundus*. Other studies have documented the effects of moonlight on bat activity (Erkert, 1974; Turner, 1975), which may be related in some areas to the threat of predation (Fenton and Fleming, 1976; Fenton *et al.*, n.d.). However, responses to possible predators is not a uniformly tenable explanation of the effects of moonlight on the activity of bats. Wimsatt (1969) suggested that heavy precipitation had a supressing effect on foraging activity of *D. rotundus*, and pointed out the need for detailed work on the effects of local environmental conditions on the activity of bats.

Interpretation of nightly activity patterns and comparisons of activity between sympatric taxa also must consider competitive strategies of resource use. Horizontal and vertical patchiness of habitat (including food and roost sites) probably are important parameters selecting for a reduction in interspecific competition. Vertical stratification of Neotropical bat faunas has been noted by Handley (1967), McNab (1971), and Fenton (1972). For example, among phyllostomatids, *Vampyressa bidens* and *Artibeus lituratus* were more commonly taken in canopy sampling than at ground level, whereas the reverse was true of *Carollia subrufa* and *C. perspicillata* (Handley, 1967). Before reliable temporal comparisons of different species can be made, vertical sampling must be undertaken in a variety of habitats.

The sensitivity of bats to disturbance is the main drawback to studies of bat activity that involve capture and marking of animals (either by banding or punch marking—Bonaccorso and Smythe, 1972). This is clearly reflected in the band recoveries reported by LaVal (1970) and Fleming *et al.* (1972), and further accentuated by our own experiences in Puerto Rico. Over four nights in May 1973, a total of 314 phyllostomatids was banded at Aguas Buenas Cave in Puerto Rico (168 *Artibeus jamaicensis*, 40 *Monophyllus redmani*, 80 *Brachyphylla cavernarum*, and 26 *Erophylla bombifrons*) and during this same period a total of 55 band recoveries was made (14.3 per cent of the total banded).

Remote sensing systems have been used to monitor the activity of some bats that use high intensity echolocating cries (Fenton *et al.*, 1973). This approach avoids disturbance to the bats, but is not particularly useful for most phyllostomatids, which are low-intensity echolocators. Photocells, photographic apparatuses, and thermister sensors may provide means of remote monitoring of phyllostomatid activity and thus permit analysis of the effects of various environmental parameters on the activity of these bats without introducing biases resulting from disturbance.

The tendency of some bats to use alternate roosts—as reported for *Desmodus rotundus* by Wimsatt (1969) and *Erophylla sezekorni* by Goodwin (1970)

—further complicates the problem of the impact of disturbance on roost-oriented studies (Turner, 1975). Knowledge of the location of alternate roosts has definite survival value for bats, because it permits them to vacate roosts that are temporarily or permanently rendered unsuitable in favor of roosts that have not been jeopardized.

Seasonal

The seasonal movements (or migrations) of bats long have been of interest to biologists (see Allen, 1939), but most knowledge about them has been obtained in the temperate regions of the northern hemisphere and concerns rhinolophids, vespertilionids, and a few molossids. (Allen, 1939; Brosset, 1966; Leen and Novick, 1969; Griffin, 1970). Some Pteropodidae in various parts of their ranges, but particularly in eastern Africa and in Australia, have been shown to migrate, but the Phyllostomatidae are conspicuous by their absence from the roster of migratory bats.

Anderson (1969) suspected migration by *Macrotus waterhousii*, (= *M. californicus*, part), and their seasonal absence from the American Southwest led Barbour and Davis (1969) to suggest migration for *Leptonycteris nivalis*, *L. sanborni*, and *Choeronycteris mexicana*. There is now evidence that some nectarivorous species (for example, *L. sanborni*) return year after year to the same summer colony (Hayward and Cockrum, 1971) and that seasonal movements in these species are probably in response to the flowering seasons (Leen and Novick, 1969). Davis (1945) reported declines in numbers of *Carollia perspicillata*, *Anoura geoffroyi*, and *Desmodus rotundus* from October through December in Brazil. Greenhall (1956) suggested that similar declines reflect shifts of populations in response to exhaustion of local food supplies. Local migration in response to reduced flower availability is characteristic of nectar-feeding birds throughout the world (Wolf, 1970; Keast, 1968) and similar movements can be expected to occur in nectar-feeding phyllostomatids. Why such movements may be more characteristic of flower feeders than frugivorous kinds is in the ephemeral nature of flowers as compared to fruits (Leck, 1972).

The use of multiple roosts also may account for local shifts in the distribution of bats. Wimsatt (1969) pointed out that use of alternate roosts presented an adaptive advantage to *Desmodus rotundus* because of the restricted water budget of vampires. Local population shifts by this species to areas near food resources would concurrently lower evaporative water loss related to movements to and from the roosts, and, for the same reason, reduce levels of food consumption. We suspect that strategies employed by other phyllostomatids throughout their ranges will involve local, latitudinal, and altitudinal displacements.

The absence of marked migrations by phyllostomatids stands in sharp contrast to the situation as it is known for some pteropodids, which is obviously a function of at least size and habitats. The pteropodids for which migration is known are large and tend to form conspicuous "camps," which makes them easy to observe. The generally smaller and more secretive phyllostomatids are considerably less conspicuous.

Perhaps more significant, however, than size and roosting habits, are the differences in climate between South and Central America and Africa and Australia. Keast (1969) provided a convenient comparison of these three areas: whereas 32 percent of South and Central America is rainforest, this habitat accounts for 10 per cent and 5 per cent, respectively, of the area of Africa and Australia. Habitats in which marked seasonal fluctuations occur (with resultant seasonally available food sources) are more conducive to the evolution of migratory patterns than are habitats with less drastic fluctuations.

Climatic fluctuations also may account for the higher diversity of fruit and nectar-feeding bats in the Neotropics (relative to the Old World tropics). The larger size of the Pteropodidae (relative to the Phyllostomatidae) may reflect migratory habits because movement over long distances is proportionally less costly (energetically) for larger as opposed to smaller organisms (Schmidt-Nielson, 1972; Thomas and Suthers, 1972; Thomas, 1975).

Homing

Griffin's (1970) review of studies of homing by bats included one phyllostomatid. Williams *et al.* (1966) and Williams and Williams (1967, 1970) used radio tracking to examine homing by *Phyllostomus hastatus* and showed that bats displaced more than 30 kilometers from their homes were less effective at returning there than those displaced shorter distances. These studies also demonstrated the importance of visual cues to homing in *P. hastatus*. Banding studies have indicated homing by *Macrotus californicus* (Bradshaw, 1961; Davis, 1966) and *Leptonycteris sanborni* (Hayward and Cockrum, 1971).

The whole question of homing in bats was succinctly addressed by Wilson and Findley (1972) who, after examining the available evidence, including the aforementioned studies of Williams and colleagues, concluded that no one had demonstrated other than random movements by displaced bats. We concur with this opinion and with the importance of having information concerning the familiarity of bats with the area involved (for *P. hastatus*, up to 20 kilometers from home—Williams and Williams, 1970).

The size of the familiar area is greatly influenced by the roosting habits of the bats involved and, as indicated by Fleming *et al.* (1972), by the size of the bat. Future studies involving displacements of bats from their home roosts probably will demonstrate that larger bats and bats that form large colonies will have proportionally larger spatial areas of familiarity than small or solitary bats. Migratory species such as *Leptonycteris nivalis*, *L. sanborni*, *Choeronycteris mexicana*, and *Macrotus californicus* will have a greater degree of spatial familiarity than sedentary species of the same size.

Using rates of recovery of marked individuals, LaVal (1970) suggested that *Phyllostomus discolor*, *Carollia brevicauda*, and *C. castanea* (for which he obtained high recovery rates) may have smaller home ranges than species for which he had low recovery rates, such as *Artibius jamaicensis*, *Glossophaga commissarisi*, and *Uroderma bilobatum*. Because body size or colony size (or both) generally reflect resource requirements and distribution of resources, it is clear that

the local and geographic differences in areas of familiarity will in part be a function of resource distribution and density. Present agricultural practices and high cattle densities in some areas of the Neotropics may select against a large familiar area for bats using such artificial concentrations of food resources (for example, *Desmodus rotundus*).

<div align="center">BEHAVIOR</div>

<div align="center">*Sensory*</div>

The eyes of phyllostomatids probably serve regular complex visual functions (Chase and Suthers, 1969), such as surveillance for predators (Suthers, 1970), distance orientation (Williams *et al.*, 1966), and the location of feeding areas (Williams and Williams, 1970). Suthers (1970) postulated that passive visual surveillance by a resting bat may function to permit it to select visually important events before making a more detailed acoustical investigation. The relative impotance of visual as opposed to acoustical information in the responses of phyllostomatids is not well understood, but probably depends upon light conditions (as it does for *Rousettus* sp.) and the general circumstances (Manske and Schmidt, 1976). The importance of vision in surveillance for predators also is suggested by some anatomical features such as the transparent dactylopatagium minus of some phyllostomatids (Vaughan, 1970).

The hypothesis that vision is important in orientation and feeding is supported from experiments conducted by Williams and colleagues (Williams *et al.*, 1966; Williams and Williams, 1967, 1970) and from theoretical constraints relating to the relatively short effective range of echolocation (Griffin, 1958, 1971; Suthers, 1970; Fenton, 1974).

Well-developed vomeronasal organs and associated olfactory bulbs as reported by Schneider (1957), Mann (1961), and Suthers (1970) and anecdotal observations indicate well-developed olfactory senses in the Phyllostomatidae. *Phyllostomus hastatus* can locate fruit hidden from view (Mann, 1961) and the sniffing behavior of *Desmodus rotundus* before licking and biting prey (Greenhall, 1972; Schmidt, 1973) points to the importance of olfaction. The acute odor discrimination shown by *D. rotundus* probably permits it to detect differences between breeds of cattle (Schmidt, 1973). Olfaction may be equally important for nectar and pollen-feeding bats; Baker (1973) noted that one of the characteristics of flowers visited by bats is a sour smell. Recent comparisons of the olfactory systems of some phyllostomatids with those of other bats (Bhatnagar, 1975; Bhatnagar and Kallen, 1974, 1975) further emphasizes the importance of odor in the lives of bats.

<div align="center">*Intraspecific*</div>

Phyllostomatids show a variety of roosting habits with respect to numbers of individuals occupying a roost. Estimates of colony size vary considerably and have usually been based on visual counts during emergence or directly in roosts under low light levels (usually after the bats have been disturbed). Some phyllosto-

matids appear to roost alone or in small groups (for example, *Micronycteris mega-lotis*, *M. minuta*, *M. hirsuta*, *M. brachyotis*, *Lonchorina aurita*, *Tonatia sylvicola*, *Tonatia bidens*, *Phyllostomus elongatus*, and *Artibeus phaeotis*—Goodwin and Greenhall, 1961; Leen and Novick, 1969; Tuttle, 1970; Goodwin, 1970). Others are sometimes found in small aggregations or on other occasions in large colonies (for example, *Carollia perspicillata*—Pine, 1972; *Phyllostomus hastatus*—Williams and Williams, 1970; *Artibeus jamaicensis*—Leen and Novick, 1969), whereas still others appear to occur only in large aggregations (such as *Brachyphylla cavernarum* in Puerto Rico). The size of the roost may exert an important limiting factor on the size of the colony, as is indicated by the occurrence of larger aggregations of individuals of some species in artificial structures than are known from natural roosts (*Desmodus rotundus*, for example). Species that regularly roost in large rooms in caves probably are more commonly encountered in large aggregations than are those that roost in cavities of trees.

Aside from observations on colony or cluster size, little has been published on intraspecific behavior of bats in colonies. Some evidence is available indicating that there are social units of groups within colonies and that these may play important roles in reproduction, food gathering, and orientation. It seems logical to expect more elaborate social interactions in gregarious than in solitary species (as in some Canidae—Kleiman, 1972).

Williams and Williams (1970) reported "coherent social groups" for *Phyllostomus hastatus* ranging from five to 20 individuals and consisting of groups of both sexes with one or more dominant males. Bradbury (n.d.) has provided more information on the social groups of *Phyllostomus hastatus* and *P. discolor*.

Phyllostomus hastatus forms large colonies in caves and the population in any roost site consists of harems (25 to 30 females per male) and nonharem juveniles and males. Harem males protect their females and perform elaborate displays when another male approaches. To feed, females leave the harem singly and in twos, whereas the male departs when the number of remaining females is at its lowest, and remains away for only a short time. Removal of a harem male results in his replacement by another male with little or no turnover among the harem females.

Phyllostomus discolor establishes colonies in hollow trees and again the populations include harem (one to 12 females per male) and nonharem bats. However, harem composition in this species is more variable than in *P. hastatus*, with some females being regularly present in the harem and others somewhat nomadic. Female *P. discolor* are more aggressive than female *P. hastatus* and are actively involved in maintaining the integrity of the harem. A bat returning to a harem group performs elaborate displays, which include tactile, olfactory, and vocal cues, to gain admission to the group. Allogrooming by members of harems is common.

In both species, the nonharem groups may be quite stable in their composition and tend to be more nomadic than the harems. F. Potter (personal communication) has observed harem structures in *Carollia perspicillata* and it seems likely that this situation may be common in phyllostomatids that aggregate in large numbers.

Departures of groups of bats from roosts (for example, *Leptonycteris san-borni*—Hayward and Cockrum, 1971; *Desmodus rotundus*—Wimsatt, 1969, and Greenhall *et al.*, 1971) also suggest the presence of social groupings. Similar observations have been reported for other bats (Rhinolophidae—Möhres, 1967; Vespertilionidae—Hall and Brenner, 1968, and Dwyer, 1970) and indicate that this behavior may be widespread in the Chiroptera.

Segregation of females into discrete groups prior to parturition and until the young are weaned has been reported for *Artibeus jamaicensis* (Leen and Novick, 1969) and implied by the observations of Jones *et al.* (1973) for *Desmodus rotundus*. The observations of Leen and Novick (1969) for *A. jamaicensis* and those of Schmidt (1973) for *D. rotundus* indicate that olfactory cues may be important in social organization and mother-young relationships. However, other information, some of it from phyllostomatids, suggests that vocalizations are important in interactions between females and their young (Brown, 1976; Gould, 1975*a*, 1975*b*; Gould *et al.*, 1973; Schmidt and Manske, 1973) and in a variety of other intraspecific contexts (for example, Bradbury and Emmons, 1974; Wickler and Siebt, 1976).

Evidence from other mammals strongly suggests that bats will be shown to exhibit various patterns of social dominance within groups. Places where these interactions may be expected are roosts and common feeding sites. Laboratory observations of Schmidt and Greenhall (1972) on the interactions of feeding vampires support this suggestion; they suggested that certain "dominant" animals in a group feed first and that, while they are feeding, they chase off other individuals as in some carnivores (Ewer, 1973). Similar interactions will certainly be reported from situations where food resources are localized (for example, concentrations of ripe fruit). However, species that are nectarivorus or carnivorous (including insectivorous) where food resources are diffuse are more apt to demonstrate territorial interactions than dominance hierarchies at feeding sites (see, for example, Baker's, 1973, observations of trap-lining in some nectar-feeding bats).

The whole subject of sexual behavior and the details of mother-young interactions are poorly known, and we were unable to find any published information on this subject for phyllostomatids.

Interspecific

Various species of bats are known to share the same roosts, but in some cases, use of a roost by one species will result in its being abandoned by another species (for example, *Artibeus jamaicensis* and *Molossus* sp.—Leen and Novick, 1969). Often several species of bats may roost in one structure (tree, cave, building, and so forth) and not come into physical contact with one another except possibly at times of arrival or departure. There is little information on interspecific behavior of bats, although biting is presumed to occur and possibly be involved with the epidemiology of rabies virus (Constantine, 1970). As with intraspecific interactions, it is likely that interspecific altercations will occur where food resources or roosts are localized or limited. The work of Colwell (1973) on the interactions of some hummingbirds suggests that similar interspecific behavior patterns may

be described for nectar-feeding bats, especially in the light of the trap-lining nature of the visits of some of these bats to flowers.

Miscellaneous

Several species of bats are known to carry their young with them away from their roosts. Tamsitt and Valdivieso (1965) observed this for *Artibeus lituratus* in Colombia, but Fenton (1969) found no evidence of it for *A. jamaicensis* in Puerto Rico. In a review of the literature on this subject, Davis (1970) reported that some phyllostomatids had been found to transport their young after disturbances in their roosts (*Macrotus californicus, Choeronycteris mexicana, Leptonycteris sanborni*), whereas others would do this even in the absence of disturbance (*Glossophaga soricina* and *Leptonycteris sanborni*). It is likely that species that use alternate roosts will be found to transport their young more regularly than those that do not, but certainly the presence of disturbance is an important consideration in this regard.

Tuttle (1970) reported that the vocalizations of a captured *Mimon crenulatum* attracted other individuals of the same species to the site of capture, and similar effects were elicited by the "distress calls" of several species of bats. At present we have no definite information as to which frequencies of bat cries are important in "distress" or other calls that evoke responses from other individuals. Recent work has indicated that some bats respond preferentially to "distress" calls of conspecifics (Fenton *et al.*, 1976).

FURTHER RESEARCH

From the preceeding discussion, it should be obvious that almost any aspect of the movements and behavior of phyllostomatids will provide productive topics for research. Documentation of the daily and seasonal patterns of the activity of these bats with respect to various environmental parameters such as meteorological conditions, lunar cycles, and seasonal changes in the abundances of food (from insects to fruit) should be a primary goal. At the same time, the whole spectrum of intra and interspecific behavior patterns (territoriality, partitioning of food and roost resources, reproductive, and mother-young behavior) requires close attention.

As we have pointed out, many of these subjects may now be addressed with the aid of electronic equipment (notably for telemetry and observation at low light levels) and a reasonable knowledge of the phyllostomatids that occur in different areas. This situation is reflected by a variety of recent studies ranging from roosting behavior (Timm and Mortimer, 1976), through feeding and orientation behavior (Howell 1974*a*, 1974*b*; Fleming *et al.*, n.d.), to detailed studies of specific bats (Turner, 1975).

The programs of recent North American Symposia on Bat Research indicate that work on some of these subjects is in progress for some species. We expect that the next few years will see the publication of results that will greatly advance our knowledge of the movements and behavior of bats in general and the Phyllostomatidae in particular.

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