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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Protozoa, Acanthocephala, Pentastomida, Platyhelminthes, and Nematoda occurring in the Phyllostomatidae; an addition of unpublished parasite collection records; and a preliminary appraisal of various factors that have influenced the dispersal and speciation in the endoparasites of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, 1941*a*, 1941*b*, 1942). At about the same time, the nematodes of tropical American bats were studied ex-

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

TABLE 1.—Continued.

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

TABLE 1.—Continued.

	Trypanosoma vesperilionis	
<i>Carollia perspicillata</i> , "Lonchoglossa ecaudata"	Rio de Janeiro, Brazil	Dias, 1940
<i>Carollia perspicillata</i> , <i>Choeroniscus minor</i> , <i>Glossophaga soricina</i> , "Lonchoglossa ecaudata"	Brazil	Dias <i>et al.</i> , 1942 (see Deane, 1964 <i>a</i>)
<i>Carollia perspicillata</i> <i>Glossophaga soricina</i> , <i>Phyllostomus hastatus</i>	San José, Costa Rica	Zeledón and Vieto, 1957, 1958
<i>Macrotus waterhousii</i>	Coquimatlán, Colima, México	Mazzotti, 1946
<i>Phyllostomus hastatus</i>	Colombia	See Marinkelle, 1966 <i>b</i>
	Trypanosoma spp.	
<i>Carollia perspicillata</i>	Limón, Costa Rica	Zeledón and Rosabal, 1969 <i>b</i>
<i>Lonchophylla mordax</i>	Brazil	Romaña, 1940 (in Dias and Pifano, 1941)
" <i>Trachops elongatus</i> "	Brazil	Dias and Pifano, 1942
	OTHER SPECIES	
	Trypanosoma evansi	
<i>Artibeus jamaicensis</i> *, <i>Carollia perspicillata</i> *, <i>Glossophaga soricina</i> *, <i>Phyllostomus hastatus</i> *	Panamá	Clark and Dunn, 1933
<i>Desmodus rotundus</i> *	Panamá	Dunn, 1932; Clark and Dunn, 1933; Johnson, 1936 <i>a</i> , 1936 <i>b</i>
<i>Desmodus rotundus</i>	Arauca and Cali, Colombia	Ayala and Wells, 1974
<i>Desmodus rotundus</i>	Valle de Cauca, Colombia	Ayala, 1972 (in Ayala and Wells, 1974)
	Trypanosoma equinum	
<i>Desmodus rotundus</i> *	Argentina	Acosta and Romaña, 1938; Hoare, 1965
	Trypanosoma rangeli-like	
<i>Artibeus lituratus</i> , <i>Glossophaga soricina</i>	Central and western Colombia	Marinkelle, 1966 <i>b</i> ; Tamsitt and Valdivieso, 1970
	"not Trypanosoma cruzi-like"	
<i>Choeroniscus minor</i>	Pará, Brazil	Garnham <i>et al.</i> , 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, 1966a, 1968b). 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 (1968b), 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 (1964a); and the strains isolated from 11 species of phyllostomatids in Colombia (see Table 1) by Marinkelle (1966b, 1968b). 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), Esquivel *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; Esquivel *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 Marinkelle 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

Neonicola 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 (*Blattella 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*).

Phylum PENTASTOMIDA

Family Porocephalidae

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 mesenteries, 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 (1962*a*, 1962*b*, 1962*c*) did not employ bats. *Porocephalus crotali* is also recorded in man (Stiles and Nolan, 1931).

Phylum PLATYHELMINTHES

Class TREMATODA

Family Anenterotrematidae

Anenterotrema auritum Stunkard, 1938

Type host.—*Micronycteris megalotis*.

Site of infection.—Small intestine.

Type locality.—Cueva de Xmahit Tekax, Xconsacab, Tizimin, Yucatán, México.

Anenterotrema eduardocaballeri (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. ($\times 215$)

Other records.—Travossos *et al.* (1969) gave the following host records from Brazil: “*Molossidae* sp.,” *Molossus obscurus*, *M. major crassicaudatus*, and *Phyllostomus elongatus*. Teixeira 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. Teixeira 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 macleanii* 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) synonymy 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 Espírito 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 *Mollossus 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.

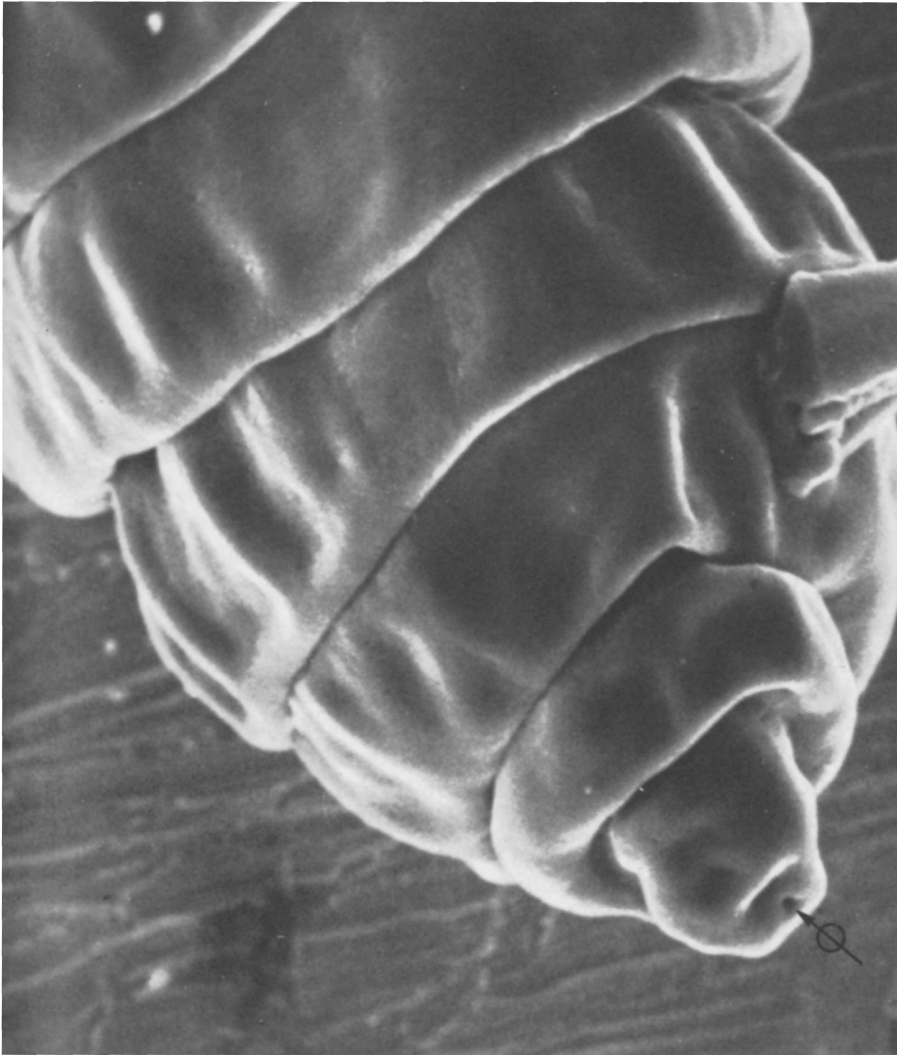


FIG. 2.—Scanning electron photomicrograph of posterior proglottids of the strobila of *Vampirolepis elongatus* from the small intestine of *Glossophaga soricina* collected in Nicaragua. Note the decreasing dimensions of the proglottids and the opening of the excretory system (at arrow). ($\times 700$)

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 artibeii 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, 1961a); *Glossophaga soricina* in Brazil (Arandas Rego, 1961a); *Phyllostomus* sp. in Venezuela (Diaz-Ungria, 1963); and an unidentified phyllostomatid bat in Brazil (Arandas Rego, 1961a).

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.

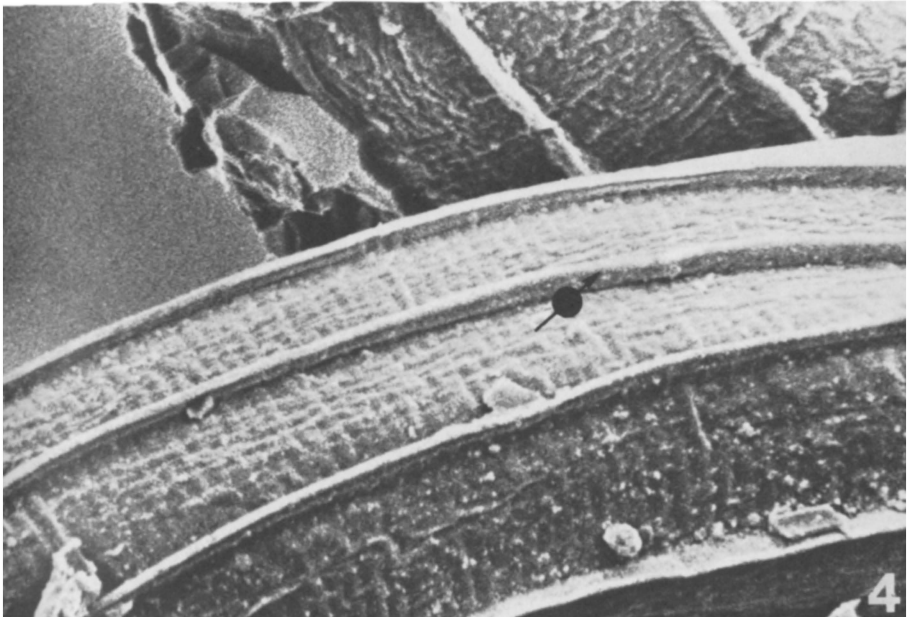
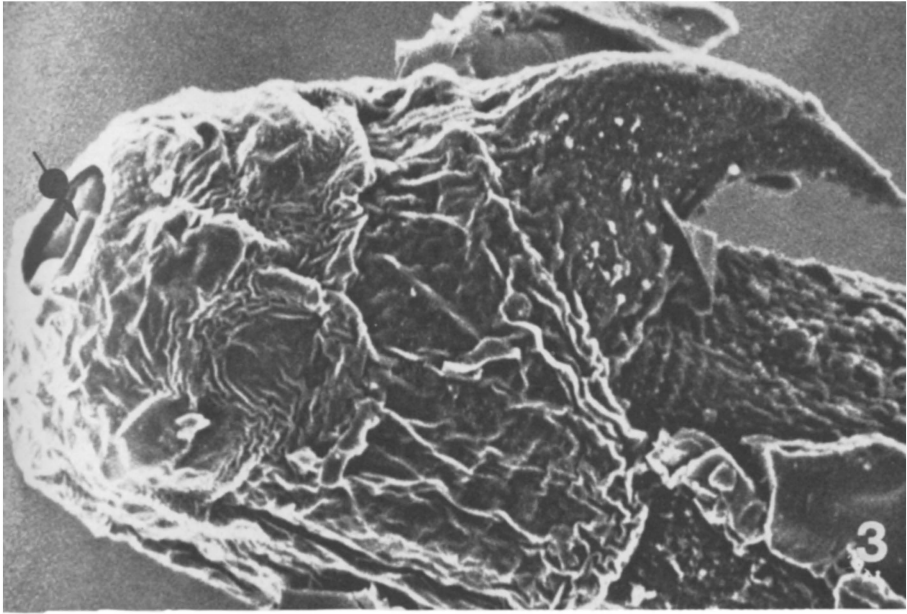


FIG. 3.—Scanning electron photomicrograph of anterior end of *Biacantha desmoda* from small intestine of *Desmodus rotundus* collected at La Pacifica, Costa Rica. The irregular surface is an artifact resulting from alcohol fixation. Note platelike teeth in vestibule (arrow). ($\times 765$)

FIG. 4.—Scanning electron photomicrograph of body surface of *Biacantha desmoda*. Ridges (arrow) are raised above the general body surface. ($\times 1175$)

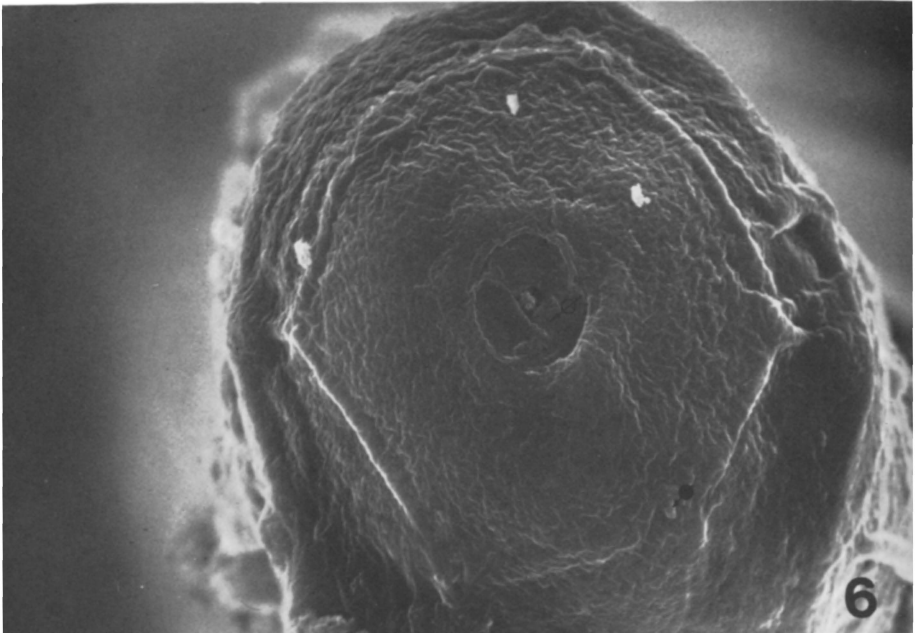
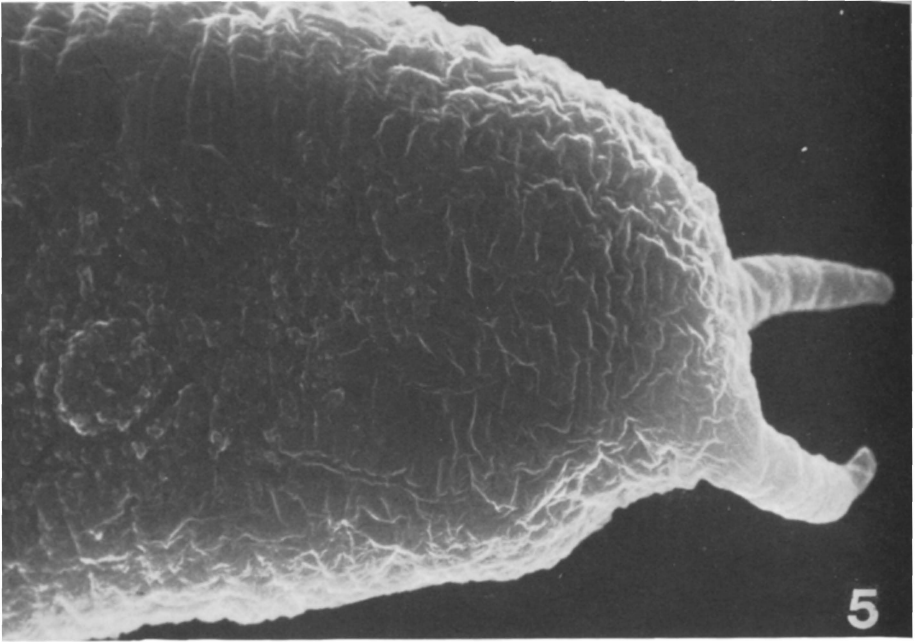


FIG. 5.—Scanning electron photomicrograph of posterior end of body of *Bidigiticauda vivipara*. ($\times 675$)

FIG. 6.—Scanning electron photomicrograph of head of *Bidigiticauda vivipara*. Papillae (arrow) and teeth in vestibule (clear arrow) are evident. ($\times 2840$)

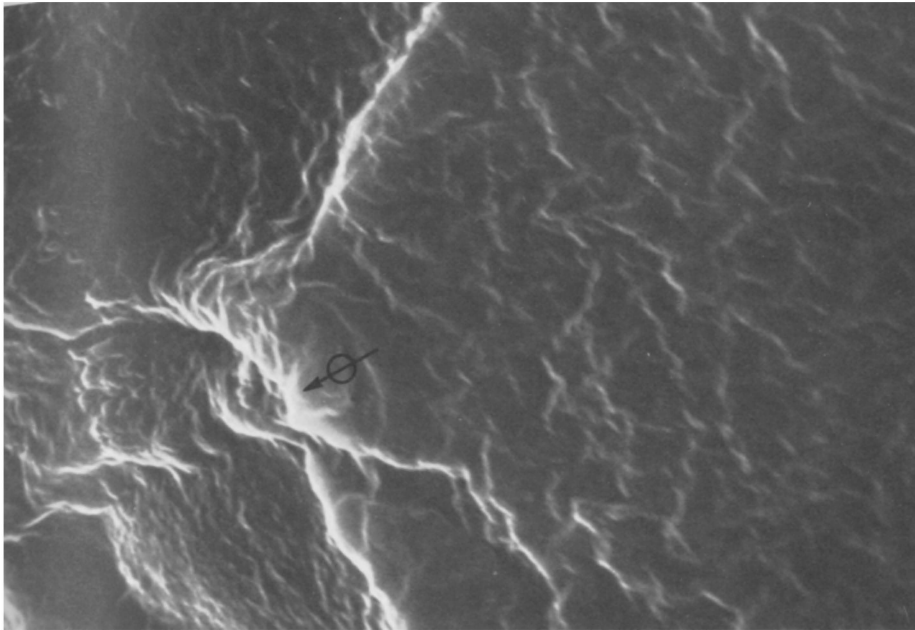


FIG. 7.—Scanning electron photomicrograph of cephalic papillae of *Bidigiticauda vivipara*. Papillae (at arrow) are raised above the cuticle. ($\times 3600$)

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

Cheiropterinema 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 Quintín, 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).

Glyptostromylyus 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, Mayajigua, Las Villas Province, Cuba (Baruš and del Valle, 1967).

Histiostrongylus octacantha Lent and Freitas, 1940

Type host.—*Phyllostomus hastatus*.

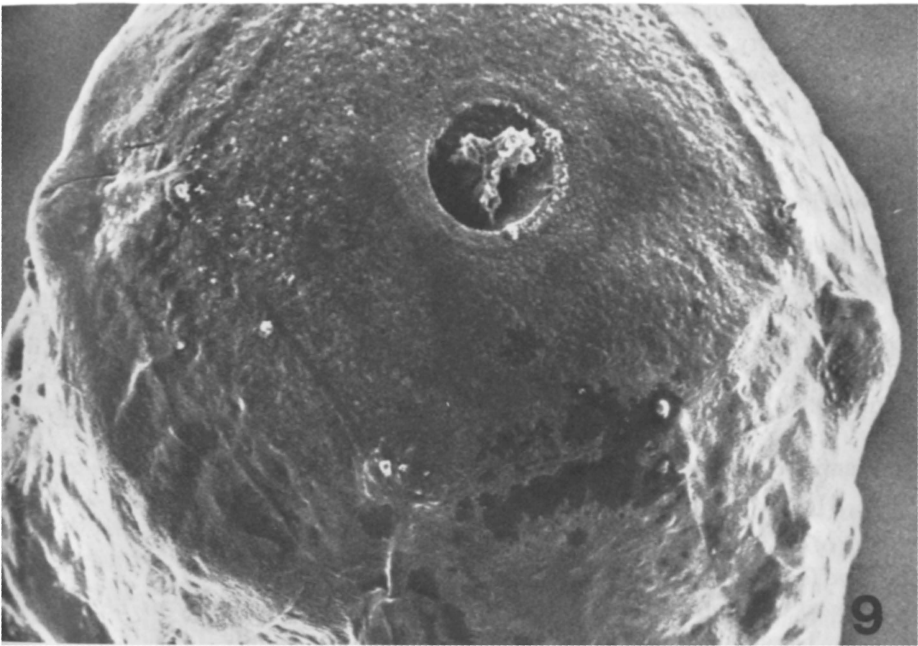
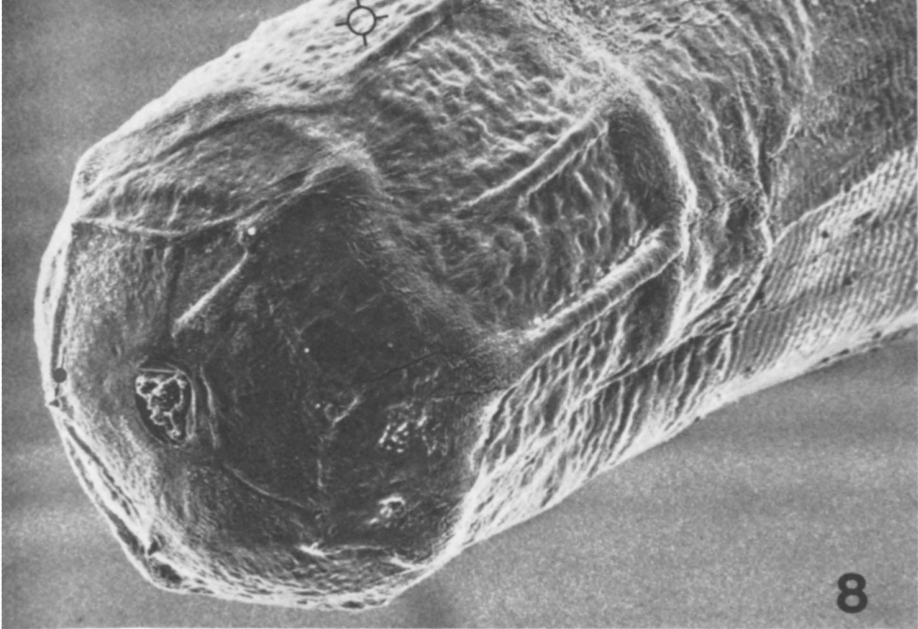


FIG. 8.—Scanning electron photomicrograph of *Cheiropteranema globocephala* from *Artibeus lituratus* from Nicaragua. Cephalic collar (clear circle) is collapsed. Lateral papillae (arrow) are prominent. ($\times 2890$)

FIG. 9.—Scanning electron photomicrograph of *Cheiropteranema globocephala*. Higher magnification of head showing mouth opening. ($\times 2940$)

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 (1941a) 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, Mayajign, Las Villas Province, 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 Teixeira 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 pinto Teixeira 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 Teixeira de Freitas (1934) redescribed the species based on the type specimens from the Institute of Oswaldo Cruz, Brazil.

Capillaria viguerasi Teixeira 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 *Neonicicola* 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 (1965a, 1965b, 1965c, 1965d) 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 *Cheiropterinema*. This complex (excluding *Cheiropterinema*) 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: *Cheiropterinema* 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; *Cheiropteroneuma 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; *Histiostromylus 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 *Vampirolepis elongatus*, *Cheiropteroneuma 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 hymenolepid 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 Teixeira 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	<i>Artibeus jamaicensis</i>
“piroplasma” (see Renjifo <i>et al.</i> , 1952)	<i>Carollia perspicillata</i>
<i>Phyllostomus hastatus</i>	<i>Choeroniscus minor</i>
Plasmodiidae	<i>Desmodus rotundus</i>
<i>Polychromophilus deanei</i>	<i>Trypanosoma phyllostomae</i>
<i>Glossophaga soricina</i>	<i>Carollia perspicillata</i>
Toxoplasmatidae	<i>Trypanosoma pifanoi</i>
<i>Toxoplasma gondii</i>	<i>Artibeus lituratus</i>
<i>Artibeus lituratus</i>	<i>Phyllostomus hastatus</i>
Trypanosomatidae	<i>Trypanosoma rangeli-like</i>
<i>Trypanosoma cruzi</i>	<i>Artibeus lituratus</i>
<i>Artibeus jamaicensis</i>	<i>Glossophaga soricina</i>
<i>Artibeus lituratus</i>	<i>Trypanosoma vespertilionis</i>
<i>Carollia perspicillata</i>	<i>Anoura caudifer</i>
<i>Desmodus rotundus</i>	<i>Carollia perspicillata</i>
<i>Glossophaga soricina</i>	<i>Choeroniscus minor</i>
<i>Phyllostomus discolor</i>	<i>Glossophaga soricina</i>
<i>Phyllostomus hastatus</i>	<i>Macrotus waterhousii</i>
<i>Uroderma bilobatum</i>	<i>Phyllostomus hastatus</i>
<i>Trypanosoma cruzi-like</i>	<i>Trypanosoma sp. (megadermae-type)</i>
<i>Artibeus cinereus</i>	<i>Anoura caudifer</i>
<i>Artibeus jamaicensis</i>	<i>Carollia perspicillata</i>
<i>Artibeus lituratus</i>	<i>Choeroniscus minor</i>
<i>Carollia perspicillata</i>	<i>Desmodus rotundus</i>
<i>Choeroniscus minor</i>	<i>Glossophaga soricina</i>
<i>Desmodus rotundus</i>	<i>Trypanosoma sp. (verpertilionis-type)</i>
<i>Glossophaga soricina</i>	<i>Carollia perspicillata</i>
<i>Lonchophylla mordax</i>	<i>Lonchophylla mordax</i>
<i>Lonchophylla thomasi</i>	<i>Trypanosoma sp. (not T. cruzi-like)</i>
<i>Micronycteris megalotis</i>	<i>Choeroniscus minor</i>
<i>Mimon bennettii</i>	
<i>Phyllostomus discolor</i>	
<i>Phyllostomus elongatus</i>	
<i>Phyllostomus hastatus</i>	
<i>Uroderma bilobatum</i>	
<i>Vampyrum spectrum</i>	
<i>Trypanosoma equinum</i>	
<i>Desmodus rotundus*</i>	
<i>Trypanosoma evansi</i>	
<i>Artibeus jamaicensis*</i>	
<i>Carollia perspicillata*</i>	
<i>Desmodus rotundus</i>	
<i>Desmodus rotundus*</i>	
<i>Glossophaga soricina*</i>	
<i>Phyllostomus hastatus*</i>	
<i>Trypanosoma lineatus</i>	
<i>Vampyrops lineatus</i>	
<i>Trypanosoma pessaoui</i>	
<i>Artibeus cinereus</i>	
	ACANTHOCEPHALA
	Oligacanthorhynchidae
	<i>Neonicicula novellae</i>
	<i>Artibeus jamaicensis</i>
	PENTASTOMIDA
	Porocephalidae
	<i>Porocephalus crotali</i>
	<i>Phyllostomus discolor</i>
	TREMATODA
	Anenterotrematidae
	<i>Anenterotrema auritum</i>
	<i>Micronycteris megalotis</i>
	<i>Anenterotrema eduradocaballeri</i>
	<i>Phyllostomus elongatus</i>
	<i>Anenterotrema freitasi</i>
	<i>Micronycteris hirsuta</i>

APPENDIX 1.—Continued.

<i>Anenterotrema lilipatianum</i>	<i>Litomosoides colombiensis</i>
<i>Phyllostomus elongatus</i>	<i>Artibeus jamaicensis</i>
<i>Anenterotrema stunkardi</i>	<i>Vampyrops dorsalis</i>
<i>Phyllostomus hastatus</i>	<i>Litomosoides fosteri</i>
Dicrocoeliidae	<i>Glossophaga soricina</i>
<i>Athesmia parkeri</i>	<i>Litomosoides guiterasi</i>
<i>Artibeus jamaicensis</i>	<i>Artibeus jamaicensis</i>
<i>Parametadelphis compactus</i>	<i>Glossophaga</i> sp.
<i>Micronycteris behni</i>	<i>Glossophaga soricina</i>
Lecithodendriidae	<i>Litomosoides leonilavazquezae</i>
<i>Lecithodendrium pricei</i>	<i>Macrotus waterhousii</i>
<i>Artibeus jamaicensis</i>	<i>Litomosoides teshi</i>
<i>Limatulum aberrans</i>	<i>Carollia perspicillata</i>
<i>Macrotus waterhousii</i>	Filaridae
<i>Phyllostomus discolor</i>	<i>Filaria serpiculum</i>
<i>Limatulum isthmicus</i>	<i>Carollia perspicillata</i>
<i>Micronycteris hirsuta</i>	<i>Phyllostomus</i> sp.
<i>Limatulum oklahomensis</i>	<i>Sturnira lilium</i>
<i>Macrotus waterhousii</i>	Trichostrongylidae
Urotrematidae	<i>Biacantha desmoda</i>
<i>Urotrema scabridum</i>	<i>Desmodus rotundus</i>
<i>Phyllostomus</i> sp.	<i>Bidigiticauda vivipara</i>
<i>Phyllostomus hastatus</i>	<i>Artibeus jamaicensis</i>
	<i>Artibeus lituratus</i>
	<i>Cheiropteronema globocephala</i>
	<i>Artibeus jamaicensis</i>
	<i>Artibeus lituratus</i>
	<i>Artibeus phaeotis</i>
	<i>Artibeus toltecus</i>
	<i>Carollia perspicillata</i>
	<i>Glyptostromgylus collaris</i>
	<i>Macrotus californicus</i>
	<i>Histiostrongylus</i> sp.
	<i>Phyllostomus hastatus</i>
	<i>Histiostrongylus cornatus</i>
	<i>Phyllonycteris poeyi</i>
	<i>Phyllostomus discolor</i>
	<i>Phyllostomus hastatus</i>
	<i>Histiostrongylus octacantha</i>
	<i>Artibeus jamaicensis</i>
	<i>Phyllostomus hastatus</i>
	<i>Torrestrongylus torrei</i>
	<i>Macrotus waterhousii</i>
	<i>Tricholeiperia leiperi</i>
	<i>Trachops cirrhosus</i>
	Unidentified strongylid nematodes
	<i>Glossophaga soricina</i>
	Trichuridae
	<i>Capillaria</i> sp.
	<i>Micronycteris megalotis</i>
	<i>Capillaria cubana</i>
	<i>Artibeus jamaicensis</i>

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

APPENDIX 1.—Continued.

<i>Capillaria phyllonycteris</i>	<i>Capillaria pusilla</i>
<i>Phyllonycteris poeyi</i>	<i>Sturnira lilium</i>
<i>Capillaria pintoii</i>	<i>Capillaria viguerasi</i>
Unidentified bat	<i>Macrotus waterhousii</i>

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.

<i>Anoura caudifer</i>	<i>Litomosoides teshi</i>
Protozoa	Protozoa
<i>Trypanosoma vespertilionis</i>	<i>Trypanosoma cruzi</i>
<i>Trypanosoma</i> sp. (megadermae-type)	<i>Trypanosoma cruzi</i> *
<i>Artibeus cinereus</i>	<i>Trypanosoma cruzi</i> -like
Nematoda	<i>Trypanosoma evansi</i>
<i>Litomosoides artibeii</i>	<i>Trypanosoma pessoai</i>
Protozoa	<i>Trypanosoma phyllostomae</i>
<i>Trypanosoma cruzi</i> -like	<i>Trypanosoma vespertilionis</i>
<i>Trypanosoma pessoai</i>	<i>Trypanosoma</i> sp. (megadermae-type)
<i>Artibeus jamaicensis</i>	<i>Trypanosoma</i> sp. (vespertilionis-type)
Acanthocephala	"Carollia subflavus" ¹
<i>Neonicicula novellae</i>	Nematoda
Nematoda	<i>Litomosoides brasiliensis</i>
<i>Bidigiticauda vivipara</i>	<i>Choeroniscus minor</i>
<i>Capillaria cubana</i>	Protozoa
<i>Cheiropteranema globocephala</i>	<i>Trypanosoma cruzi</i> -like
<i>Histiostromylus octacantha</i>	<i>Trypanosoma pessoai</i>
<i>Litomosoides</i> sp.	<i>Trypanosoma vespertilionis</i>
<i>Litomosoides chandleri</i>	<i>Trypanosoma</i> sp. (megadermae-type)
<i>Litomosoides colombiensis</i>	<i>Trypanosoma</i> sp. (not <i>T. cruzi</i> -like)
<i>Litomosoides guiterasi</i>	<i>Desmodus rotundus</i>
Protozoa	Nematoda
<i>Trypanosoma cruzi</i>	<i>Biacantha desmoda</i>
<i>Trypanosoma cruzi</i> -like	Protozoa
<i>Trypanosoma pessoai</i>	<i>Trypanosoma cruzi</i>
<i>Trypanosoma evansi</i>	<i>Trypanosoma cruzi</i> -like
Trematoda	<i>Trypanosoma evansi</i>
<i>Athesmia parkeri</i>	<i>Trypanosoma evansi</i> *
<i>Lecithodendrium pricei</i>	<i>Trypanosoma equinum</i> *
<i>Artibeus lituratus</i>	<i>Trypanosoma pessoai</i>
Cestoda	<i>Trypanosoma</i> sp. (megadermae-type)
<i>Vampirolepis elongatus</i>	<i>Glossophaga</i> sp.
Nematoda	Nematoda
<i>Bidigiticauda vivipara</i>	<i>Litomosoides brasiliensis</i>
Protozoa	<i>Litomosoides guiterasi</i>
<i>Toxoplasma gondii</i>	<i>Glossophaga soricina</i>
<i>Trypanosoma cruzi</i>	Cestoda
<i>Trypanosoma cruzi</i> -like	<i>Oochoristica immatura</i>
<i>Trypanosoma pifanoi</i>	<i>Vampirolepis elongatus</i>
<i>Trypanosoma rangeli</i> -like	Nematoda
<i>Artibeus phaeotis</i>	<i>Litomosoides</i> sp.
Nematoda	<i>Litomosoides brasiliensis</i>
<i>Cheiropteranema globocephala</i>	<i>Litomosoides fosteri</i>
<i>Artibeus toltecus</i>	<i>Litomosoides guiterasi</i>
Nematoda	Protozoa
<i>Cheiropteranema globocephala</i>	<i>Polychromophilus deanei</i>
<i>Carollia perspicillata</i>	<i>Trypanosoma cruzi</i>
Nematoda	<i>Trypanosoma cruzi</i> -like
<i>Cheiropteranema globocephala</i>	<i>Trypanosoma evansi</i>
<i>Filaria serpiculum</i>	<i>Trypanosoma rangeli</i> -like
<i>Litomosoides brasiliensis</i>	<i>Trypanosoma</i> 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
 Glyptostongylus 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
 Trypanoxoma 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.]