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RESULTS OF THE ALCOA FOUNDATION-SURINAME EXPEDITIONS. IX. BATS OF THE GENUS *TONATIA* (MAMMALIA: CHIROPTERA) IN SURINAME

HUGH H. GENOWAYS
Curator, Section of Mammals

STEPHEN L. WILLIAMS
Collection Manager, Section of Mammals

ABSTRACT

Five species of *Tonatia* (*bidens, brasilense, carrikeri, schulzi,* and *silvicola*) are known to occur in Suriname. *Tonatia bidens* and *silvicola* are the largest in overall size (forearm length over 50 mm and greatest length of skull over 27.0 mm). However, *T. bidens* has a broader postorbital region (5.0 mm or more) and narrower mastoid region (less than 13.0 mm). The lower incisors of *T. bidens* are also noticeably broader than those of *T. silvicola.* These two species were found throughout most of the forested areas of Suriname. *T. bidens* displayed no secondary sexual variation in nine measurements tested, whereas female *T. silvicola* were significantly larger than the males in four of these measurements.

Tonatia brasilense can be distinguished from all other species in Suriname by its smaller size (forearm length less than 40 mm, greatest length of skull less than 21.0 mm). This species was often taken in association with secondary vegetation, or restricted forest, in savannah regions.

The two medium-sized species—*carrikeri* and *schulzi*—can be distinguished because the underparts of *carrikeri* are entirely white except on the chin and sides of the abdomen and in *schulzi* the dorsal surfaces of most membranes are covered with unique small wart-like granulations. Although the samples of these two species are small, it appears that specimens of *T. carrikeri* are slightly larger than specimens of *T. schulzi.* Both species were taken in dense lowland rainforest characterized by tall trees. The geographic distribution of *T. schulzi* is confined to the undisturbed forests of four nature preserves in central Suriname.

Submitted 21 October 1983.

INTRODUCTION

Six species (*T. bidens, T. brasiliense, T. carrickeri, T. evotis, T. schulzi,* and *T. silvicola*) presently are recognized in the bat genus *Tonatia* Gray (Davis and Carter, 1978; Koopman, 1982). Recently, there has been considerable controversy about the taxonomic status of four nominal, small-sized species of the genus—*brasiliense, nicarguae, minuta,* and *venezualae*—but most recent authors have treated these taxa as conspecific under the senior synonym *T. brasiliense* (Gardner, 1976; Handley, 1976; Koopman, 1978, 1982; Jones and Carter, 1979). Five of the six recognized species are known to occur in South America (Koopman, 1982); the sixth species, *T. evotis* (Davis and Carter, 1978), is confined to southern Mexico and northern Central America.

Suriname is the only geopolitical unit in which all five South American species of *Tonatia* are currently known to occur (Husson, 1978; Genoways and Williams, 1979, 1980). We have taken the opportunity to study material obtained during our field research to derive a better understanding of the morphological and ecological relationships of the species within this rather poorly known genus.

METHODS AND MATERIALS

Specimens were taken with nets and preserved as skin and skull or fluid preparation. Field weights were taken with Pisola scales, which are accurate to 0.1 g. Reproductive condition of the skin and skull specimens was determined by gross dissection in the field, whereas fluid preserved specimens were dissected in the laboratory.

Measurements of forearm and cranial dimensions were taken with dial calipers accurate to 0.1 mm. Only adult specimens (phalangeal epiphyses completely fused) were measured in this study. Our measurements were taken as follows:

Length of forearm.—Taken from the posteriormost projection of the elbow (olecranon process) to the anteriormost projection of the wrist joint with the wing in a flexed position.

Greatest length of skull.—Distance from the posteriormost projection of the cranium to the anterior edge of the upper incisors.

Condylobasal length.—Distance from the posteriormost projection of the exoccipal condyles to the anteriormost projection of the premaxillae.

Zygomatic breadth.—Greatest distance across the zygomatic arches at right angles to the longitudinal axis of cranium.

Postorbital breadth.—Least distance across the postorbital constriction at right angles to the longitudinal axis of cranium.

Mastoid breadth.—Greatest distance across the mastoid processes at right angles to the longitudinal axis of cranium.

Breadth of braincase.—Greatest distance across the braincase at right angles to the longitudinal axis of cranium.

Length of maxillary toothrow.—Distance from posterior lip of alveolus of M^3 to the anterior lip of alveolus of C^1.

Breadth across upper molars.—Greatest distance across upper molars at right angles to the longitudinal axis of cranium; measured at the lateralmost projections of the labial edges of the upper molars.

Univariate analyses of the foregoing measurements were undertaken with the UNIVAR program. This program yields standard statistics (mean, range, standard deviations,

standard error of the mean, variances, and coefficient of variation), and employs a single-classification analysis of variance (F-test, significance level 0.05) to test for significant differences between or among means (Sokal and Rohlf, 1969). When means were found to be significantly different, the Sum of Squares Simultaneous Test Procedure (SS-STP) developed by Gabriel (1964) was used to determine maximally nonsignificant subsets. The UNIVAR program was run on a DEC-10 computer at the University of Pittsburgh and used only with samples of three or more specimens.

The information available on the species of *Tonatia* in Suriname was summarized. This information includes variation within species, distribution in the country, differences among species, karyology, and natural history. A dichotomous key and a listing of collecting localities were constructed for purposes of future reference for work in Suriname and adjacent areas. Unless otherwise indicated, specimens listed for each account are maintained at the Section of Mammals, Carnegie Museum of Natural History.

ACKNOWLEDGMENTS

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GENERIC ACCOUNT

Tonatia Gray, 1827

1827. *Tonatia* Gray, *in* Griffith, The animal kingdom . . . by Baron Cuvier . . . 5:71.

Type species.—*Vampyrum bidens* Spix.

Diagnosis.—A genus of long-eared bats with well-developed noseleaf and short tail, most closely resembling some members of the genus *Micronycteris*. Lower incisors reduced to two giving a dental formula of i 2/1, c 1/1, p 2/3, m 3/3 = 32. Members of the genus *Mimon* have only two lower incisors as well, but have only two lower premolars. First upper premolar broader than long; middle lower premolar much reduced and crowded between the anterior and posterior teeth (see also Goodwin, 1942).

Key to Species of Tonatia *in Suriname*

1. Length of forearm over 50 mm; greatest length of skull 27.0 mm or more 2
1′. Length of forearm less than 50 mm; greatest length of skull less than 27.0 mm 3

2. Postorbital breadth 5.0 mm or more; mastoid breadth less than 13.0 mm (Fig. 2); lower incisors broad (Fig. 3); ears smaller (range 30–32); tragus small and simple (Fig. 4); ears not connected by a low band across the forehead; 2N = 16, FN = 20 ..... *T. bidens*
2′. Postorbital breadth less than 5.0 mm; mastoid breadth 13.0 mm or more (Fig. 2); lower incisors slender (Fig. 3); ears larger (range 33–40); tragus long, with three small tooth-like projections near base of outer border (Fig. 4); small connecting band present behind each ear, these two bands meeting near middle of forehead; 2N = 34, FN = 60 ..... *T. silvicola*
3. Forearm less than 40 mm; greatest length of skull less than 21 mm (Fig. 2); 2N = 30, FN = 56 ..... *T. brasiliense*
3′. Forearm more than 40 mm; greatest length of skull more than 21 mm 4
4. Forearm over 45 mm; greatest length of skull over 24 mm (Fig. 2); hair of underparts entirely white except on chin and sides of abdomen; lacking small wart-like granulations; 2N = 26, FN = 46 ..... *T. carrikeri*
4′. Forearm less than 45 mm; greatest length of skull less than 24.0 mm (Fig. 2); hair of underparts drab to grayish olive but with white bases; small wart-like granulations on dorsal surfaces of forearms, digits, and hind legs and on ears and noseleaf; 2N = 28, FN = 36 ..... *T. schulzi*

SPECIES ACCOUNTS

Tonatia bidens bidens (Spix, 1823)

Specimens examined (31).—BROKOPONDO: Brownsberg, 1 (RMNH); Brownsberg Nature Park, 3 km S, 20 km W Afobakka, 1; Brownsberg Nature Park, 8 km S, 2 km W Brownsberg, 5; 1½ km W Rudi Kappelvliegveld, 2; 3 km SW Rudi Kappelvliegveld, 3. MAROWIJNE: Oelemarie, 2; Perica, 1. NICKERIE: Avanavero, 1; Grassalco, 4; Kabalebo, 1; Sipaliwini airstrip, 1. PARA: Zanderij, 1. SARAMACCA: Bigi Poika, 1; Bitagron (=Witagron), 1; Lower Geyskes Creek, Tafelberg, 1; SE side of Arrowhead Basin, Augustus Creek, Tafelberg, 1; Voltzberg, 4.

Remarks.—Although this species was not recorded from Suriname by Husson (1962, 1978), Spix's round-eared bat appears to be fairly common in Suriname (Genoways and Williams, 1979; Williams and Genoways, 1980). The species occurs throughout much of the country appearing to be excluded only from the coastal swamps and highly disturbed areas of human agriculture and occupation (Fig. 1). The report by Jentink (1887) of this species from Suriname was shown by Husson (1978) to be based upon a specimen of *Mimon bennettii*.

Generally *Tonatia bidens* is ubiquitous to any kind of forest situation—undisturbed or disturbed. It has been taken at localities such as Perica, Avanavero, Kabalebo, Zanderij, Bigi Poika, and Bitagron, where dominant coastal savannah-type vegetation is closely associated with forests. It has also been collected in undisturbed lowland rainforest at localities such as Brownsberg Nature Park, Rudi Kappelvliegveld, Oelemarie, and Voltzberg. Two specimens were collected in montane rainforest on Tafelberg, and a single specimen was obtained in forests bordering the Brazilian savannah at Sipalwini.

Spix's round-eared bat has been reported as being taken in associ-

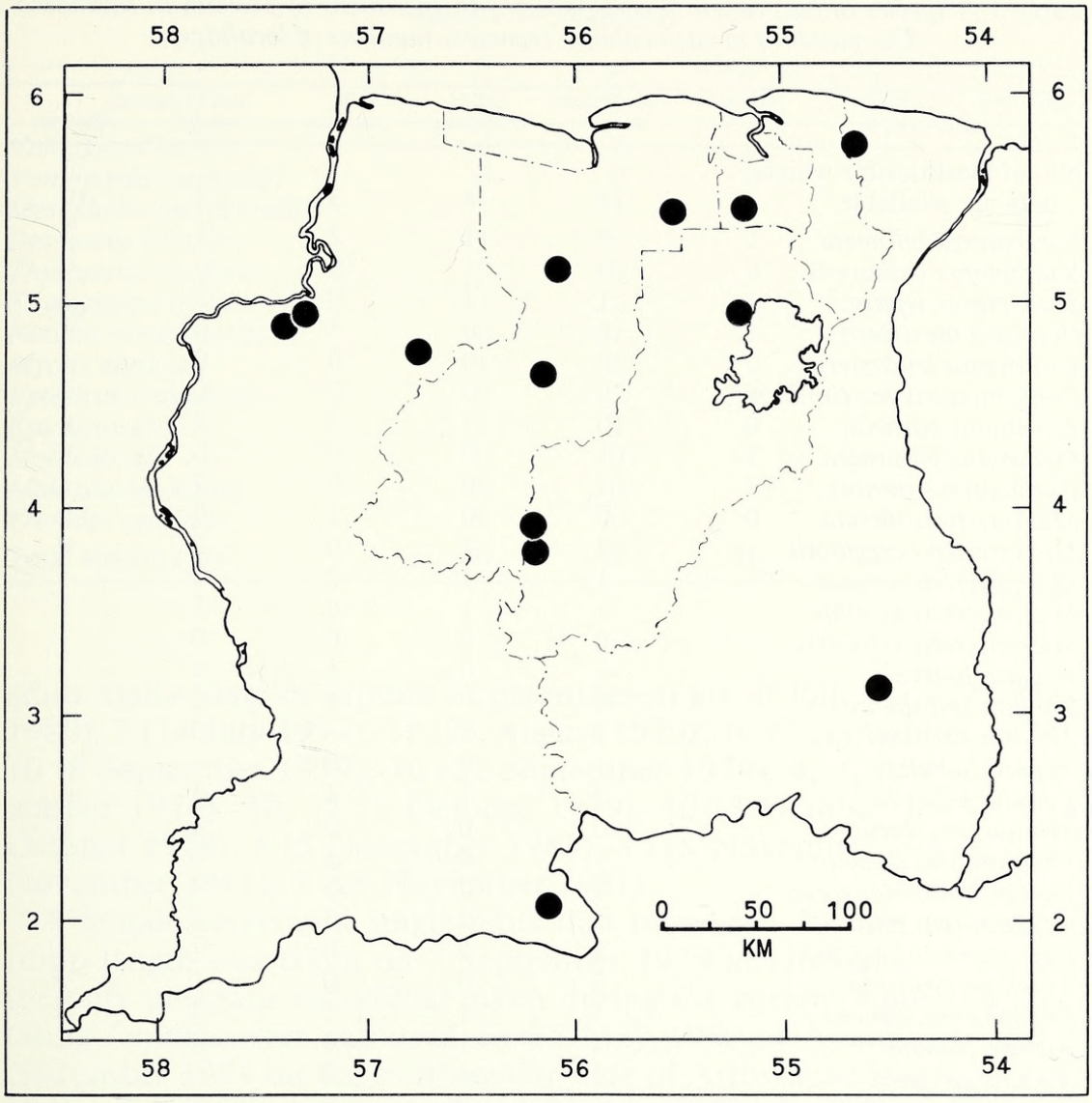

Fig. 1.—Geographic distribution of *Tonatia bidens* in Suriname.

ation with 40 other species of bats in Suriname (Table 1). Among these species are those with widespread distributions such as *Pteronotus parnellii, Lonchophylla thomasi, Carollia perspicillata,* and *Rhinophylla pumilio.* However, the more interesting associations are with the large number of phyllostomines, which undoubtedly reflects the forest dwelling habits of members of this subfamily. Other species having a relatively high association with *Tonatia bidens* are *Saccopteryx bilineata, Anoura caudifer, Sturnira lilium, Uroderma bilobatum, Vampyressa bidens,* and *Vampyrops helleri.*

One subadult male, as indicated by open phalangeal epiphyses, was taken in Brownsberg Nature Park on 7 July 1977. Testes lengths of

Table 1.—*Species of bats taken in association with specimens of* Tonatia *in Suriname. The numbers in each column represent numbers of localities.*

Species of bats	*T. bidens*	*T. brasiliense*	*T. carrikeri*	*T. schulzi*	*T. silvicola*
No. of localities for which data are available	14	4	3	4	10
Saccopteryx bilineata	4	1	2	1	2
Saccopteryx canescens	0	1	0	0	0
Saccopteryx leptura	1	1	0	3	3
Cormura brevirostris	0	0	1	0	1
Peronymus leucopterus	0	0	0	0	1
Centronycteris maximiliani	0	0	0	0	1
Pteronotus parnellii	10	1	2	3	6
Pteronotus personata	1	0	0	0	0
Chrotopterus auritus	1	0	0	2	1
Micronycteris hirsuta	0	0	1	0	0
Micronycteris megalotis	3	1	0	2	0
Micronycteris minuta	1	1	2	0	3
Micronycteris nicefori	1	1	0	1	1
Micronycteris sylvestris	0	0	0	0	1
Tonatia bidens	—	0	1	1	3
Tonatia brasiliense	0	—	1	0	1
Tonatia carrikeri	1	1	—	0	1
Tonatia schulzi	1	0	0	—	1
Tonatia silvicola	3	1	1	1	—
Mimon crenulatum	0	0	0	1	0
Phyllostomus discolor	1	0	1	0	2
Phyllostomus elongatus	5	2	3	4	7
Phyllostomus hastatus	3	2	3	2	2
Phyllostomus latifolius	2	0	0	1	1
Trachops cirrhosus	3	0	0	0	3
Phylloderma stenops	3	1	2	1	2
Anoura caudifer	4	1	0	1	1
Anoura geoffroyi	1	0	0	0	1
Lionycteris spurrelli	1	0	0	0	0
Lonchophylla thomasi	7	1	2	3	5
Glossophaga soricina	2	2	0	0	1
Carollia brevicauda	2	1	1	0	0
Carollia perspicillata	11	4	2	3	6
Rhinophylla pumilio	9	3	3	3	6
Sturnira lilium	4	4	2	0	2
Sturnira tildae	3	1	1	1	1
Ametrida centurio	1	0	0	0	0
Artibeus concolor	0	1	0	0	0
Artibeus (large species)	13	4	3	3	7
Artibeus (small species)	7	3	1	0	2
Uroderma bilobatum	3	2	1	1	2
Chiroderma trinitatum	1	0	1	0	2
Vampyressa bidens	3	0	0	0	1
Vampyressa brocki	0	1	0	0	0
Vampyrops brachycephalus	0	1	0	0	0

Table 1.—*Continued.*

Species of bats	*T. bidens*	*T. brasiliense*	*T. carrikeri*	*T. schulzi*	*T. silvicola*
Vampyrops helleri	4	2	2	1	3
Vampyrodes caraccioli	0	0	0	0	1
Mesophylla macconnelli	1	1	1	0	0
Desmodus rotundus	1	0	2	0	1
Thyroptera discifera	0	0	0	0	1
Thyroptera tricolor	1	2	1	0	0
Natalus tumidirostris	0	1	1	0	0
Myotis nigricans	1	1	2	1	1
Eptesicus brasiliensis	2	2	1	1	1
Eptesicus sp.	1	0	0	0	1
Molossus ater	0	0	1	0	0
Molossus molossus	0	0	1	0	0
Promops centralis	0	0	0	0	1
Total species (57)	40	32	31	23	41

adult males (date of capture in parentheses) are as follows: 8 (28 May 1980); 7 (14 July 1977); 11 (28 August 1979); 10 (7 September 1979); 10 (8 September 1979); 10 (21 September 1979); 4, 4, 8, 8 (23 September 1979); 10, 11 (1 October 1979); 10 (3 October 1979); 8 (4 October 1979); 8 (5 November 1981); 8 (18 November 1981); 7 (24 November 1981); 7 (29 November 1981).

A female carrying a single fetus that measured 30 mm in crown–rump length was taken on 7 September 1979 at Grassalco. This was the only pregnant individual taken during the current study, but lactating females were captured on 25 May 1980 at Avanavero and 2 November 1981 on the southeastern side of Arrowhead Basin on Tafelberg. Adult females that evinced no gross indication of reproduction were taken on the following dates: 28 August 1979 (2); 7 September 1979; 3 October 1979; 24 October 1981. Although these data are sketchy, they tend to support Wilson's (1979) hypothesis that *T. bidens* is a binodal, polyestrous species.

The mean weight of nine males was 24.3 (22–27) and of five females was 23.3 (22–25). The pregnant female weighed 30 g.

The sample of *T. bidens* was submitted to statistical analysis to determine the presence and amount of secondary sexual and individual variation present in this species (Table 2). No significant (0.05 level) secondary sexual variation was found in any of the nine measurements tested. In four measurements (length of forearm, greatest length of skull, condylobasal length, and breadth across upper molars), males averaged slightly larger than females, whereas, in three measurements (postorbital constriction, breadth of braincase, and mastoid breadth), the fe-

Table 2.—*Forearm and cranial measurements of two species of* Tonatia *from Suriname. Analyses of variance were performed to determine the presence of significant (.05 level) differences between sexes within each species and between the two species.*

Species	Sex	N	Mean (range) ± 2 SE	CV	Significant difference: Between sexes	Significant difference: Between species ♂♂/♀♀
			Length of forearm			
T. bidens	♂	8	55.5 (54.5–56.7) ± 0.47	1.2	ns	
	♀	8	55.3 (52.7–56.9) ± 1.04	2.7		*/ns
T. silvicola	♂	11	56.9 (54.9–59.3) ± 0.94	2.7	ns	
	♀	11	56.1 (52.1–58.1) ± 1.11	3.3		
			Greatest length of skull			
T. bidens	♂	8	27.8 (27.5–28.0) ± 0.15	0.8	ns	
	♀	8	27.5 (27.0–28.2) ± 0.26	1.3		*/*
T. silvicola	♂	11	28.9 (27.4–29.8) ± 0.45	2.6	*	
	♀	11	28.2 (27.3–29.5) ± 0.40	2.3		
			Condylobasal length			
T. bidens	♂	8	23.3 (23.1–23.6) ± 0.16	1.0	ns	
	♀	8	23.2 (22.5–23.8) ± 0.31	1.9		*/ns
T. silvicola	♂	11	23.8 (22.7–24.7) ± 0.34	2.3	*	
	♀	11	23.1 (22.2–23.9) ± 0.34	2.5		
			Zygomatic breadth			
T. bidens	♂	8	13.7 (13.3–14.0) ± 0.17	1.8	ns	
	♀	8	13.7 (13.3–14.2) ± 0.20	2.1		ns/ns
T. silvicola	♂	11	14.0 (13.3–14.7) ± 0.24	2.8	*	
	♀	11	13.5 (13.1–14.0) ± 0.18	2.2		
			Postorbital constriction			
T. bidens	♂	8	5.3 (5.1–5.6) ± 0.13	3.4	ns	
	♀	8	5.4 (5.2–5.5) ± 0.08	2.2		*/*
T. silvicola	♂	11	4.1 (3.8–4.4) ± 0.11	4.5	ns	
	♀	11	4.1 (3.9–4.4) ± 0.11	4.2		
			Breadth of braincase			
T. bidens	♂	8	10.3 (10.0–10.5) ± 0.12	1.6	ns	
	♀	8	10.4 (10.0–11.0) ± 0.21	2.9		*/*
T. silvicola	♂	11	10.7 (10.3–11.1) ± 0.16	2.4	ns	
	♀	11	10.6 (10.2–11.0) ± 0.13	2.1		
			Mastoid breadth			
T. bidens	♂	8	12.4 (11.8–12.7) ± 0.21	2.4	ns	
	♀	8	12.5 (12.4–12.9) ± 0.14	1.6		*/*
T. silvicola	♂	11	14.1 (13.2–14.8) ± 0.30	3.5	*	
	♀	11	13.7 (13.3–14.0) ± 0.17	2.0		
			Length of maxillary toothrow			
T. bidens	♂	8	9.3 (9.0–9.6) ± 0.13	2.0	ns	
	♀	8	9.3 (9.0–9.6) ± 0.18	2.8		*/*

Table 2.—*Continued.*

Species	Sex	N	Mean (range) ± 2 SE	CV	Significant difference: Between sexes	Significant difference: Between species ♂♂/♀♀
T. silvicola	♂	11	9.7 (9.1–10.1) ± 0.16	2.7	ns	
	♀	11	9.5 (9.2–9.8) ± 0.13	2.2		
			Breadth across upper molars (M–M)			
T. bidens	♂	8	8.5 (8.1–8.8) ± 0.16	2.7	ns	
	♀	8	8.4 (8.0–8.7) ± 0.19	3.1		*/*
T. silvicola	♂	11	9.1 (8.3–9.6) ± 0.21	3.8	ns	
	♀	11	8.9 (8.4–9.4) ± 0.17	3.2		

males averaged slightly larger than males. The mean value was the same for males and females in zygomatic breadth and length of maxillary toothrow. The lack of secondary sexual variation in *T. bidens* is in contrast to the situation found in *T. silvicola* (see the account for this species), in which males were significantly larger than females in four measurements.

The amount of individual variation in the sample of *Tonatia bidens* was consistently lower than that in the sample of *T. silvicola.* Only in breadth of braincase and length of maxillary toothrow of females did the coefficient of variation of *T. bidens* exceed that of *T. silvicola.* The values of *T. bidens* were within the range values given by Taddei (1975) for other species of phyllostomines in Brazil. Only in postorbital breadth and mastoid breadth did individual variation of males exceed that of females. Postorbital constriction exhibited the largest amount of individual variation in males and breadth across upper molars exhibited the most in females.

Tonatia bidens is easily separated from other members of the genus living in Suriname, except *T. silvicola,* by its much larger size (Tables 2–3). On the average, *T. bidens* is smaller than *T. silvicola* for most measurements (Fig. 2). This is particularly true for mastoid breadth where there is no overlap in the range of measurements for the two species (11.8 to 12.9 for *T. bidens* as compared to 13.2 to 14.8 for *T. silvicola*). In contrast to the other measurements, *T. bidens* is much broader in postorbital constriction than is *T. silvicola*; in fact, in the Suriname material there is no overlap between the species in this measurement (5.1 to 5.6 for *T. bidens* as compared to 3.8 to 4.4 for *T. silvicola*). One of the best field characters for separating these two species is the noticeably broader lower incisors possessed by *T. bidens* (Fig. 3). Externally, the tragus is small and simple in *T. bidens,* but long

Table 3.—*Forearm and cranial measurements of three species of* Tonatia *from Suriname.*

Specimen	Sex	Forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital breadth	Breadth of braincase	Mastoid breadth	Length of maxillary toothrow	Breadth across molars
				Tonatia brasiliense						
CM 52777	Male	35.5	19.6	16.6	9.2	3.0	7.9	8.8	6.6	6.1
CM 76775	Male	35.5	20.2	16.6	9.1	3.2	8.0	9.0	7.0	6.3
CM 63667	Female	34.5	19.5	16.3	9.3	3.0	7.8	8.9	6.7	6.4
				Tonatia carrikeri						
CM 68400	Female	46.7	26.0	20.5	11.6	3.7	9.8	12.0	8.7	7.7
CM 63668	Female	45.8	25.0	20.3	11.2	3.8	9.7	12.2	8.1	7.6
				Tonatia schulzi						
CM 63686	Male	43.3	23.3	18.9	11.0	3.5	9.2	11.8	7.5	7.2
CM 63687	Male	42.0	23.0	19.0	11.1	3.5	9.3	11.6	7.4	7.3
CM 68409	Male	44.0	23.4	18.9	11.3	3.8	9.6	12.1	7.8	7.3
RMNH 26111	Male	—	23.8	19.8	11.0	3.7	9.5	12.0	7.7	7.0

with three small tooth-like projections near the outer border of the base in *T. silvicola* (Fig. 4). The ears are larger in *T. silvicola* and behind each ear small connecting bands meet near the middle of the forehead; these are absent in *T. bidens.*

Only one living mainland subspecies, *T. bidens bidens,* is currently recognized in this species (Jones and Carter, 1976). The only other recognized subspecies is known as a fossil from Jamaica. We have followed this arrangement, but believe that a thorough analysis of geographic variation is needed for this species.

The karyotype of *T. bidens* based upon material from Suriname is 2N = 16, FN = 20. The X-chromosome is metacentric and the Y-chromosome is acrocentric (Honeycutt et al., 1980).

Tonatia brasiliense (Peters, 1866)

Specimens examined (6).—BROKOPONDO: Brownsberg, 1 (RMNH); Brownsberg Nature Park, 7 km S, 18.5 km W Afobakka, 1. COMMEWIJNE: Nieuwe Grond Plantation, 1. MAROWIJNE: 3 km SW Albina, 1. NICKERIE: Sipaliwini airstrip, 1; Wageningen, 1 (RMNH).

This small species of *Tonatia* is known from four localities in northern Suriname and one in extreme southern Suriname (Genoways and Williams, 1979; Williams and Genoways, 1980; Fig. 4). This species was not recorded from Suriname by Husson (1978), although now there are specimens in the Rijksmuseum van Natuurlijke Historie. The species can probably be expected throughout the country in appropriate habitats, but nowhere have we found it to be abundant.

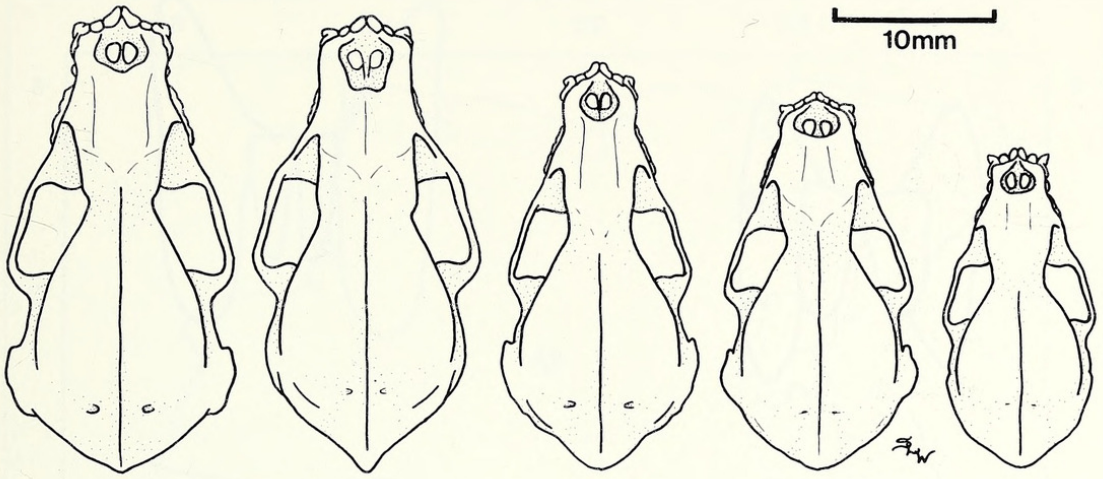

Fig. 2.—Dorsal view of the crania of five species of *Tonatia* from Suriname. From left to right, *T. silvicola* (CM 52779), *T. bidens* (CM 52776), *T. carrikeri* (CM 63668), *T. schulzi* (CM 63687), and *T. brasiliense* (CM 52777).

Unlike other species of *Tonatia,* the localities were *T. brasiliense* has been captured are often associated with secondary vegetation, or restricted forest, in savannah regions. Many of these areas, such as Afobakka, Nieuwe Grond Plantation, Albina, and Wageningen, lie along the coastal savannah and have been subjected to a variety of local ecological disturbances by man (for example, road construction, gardening, mining, and deforestation). The habitat at Brownsberg may be considered atypical for the species; however, this area does border the coastal savannah. Sipaliwini is the only locality not associated with the coastal savannah; instead it has affinities with the Brazilian savannah to the south.

In the relatively few places where this species was taken, it was captured in association with a high number of other species of bats in Suriname (Table 1). Looking beyond the widespread species, a significant association is found for this species with others preferring more open habitats, such as *Glossophaga soricina, Artibeus concolor, Uroderma bilobatum, Vampyrops helleri, Thyroptera tricolor,* and *Eptesicus brasiliensis.* This was predictable based upon the habitat preferences of *T. brasiliense.*

The only adult female obtained during our studies carried a single fetus that measured 18 mm in crown–rump length when taken on 13 September 1979 at Nieuwe Grond Plantation. The pregnant female weighed 10 g. Three adult males had testes measurements as follows: 4 (9 July 1977); 4 (20 October 1981); 5 (16 November 1981).

As mentioned in the Introduction, there has been disagreement about the taxonomy of the small-sized members of the genus *Tonatia.*

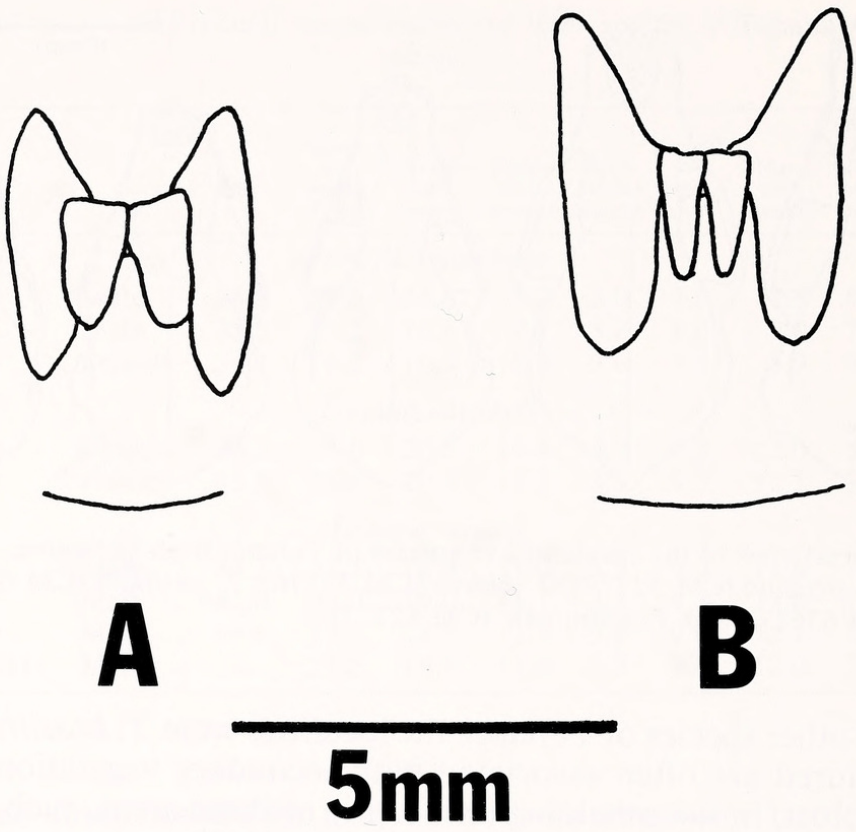

Fig. 3.—Lower incisors of *Tonatia bidens* (A) and *T. silvicola* (B).

The names *brasiliense* (Peters, 1866; type locality: Baia, Brazil), *venezuelae* (Robinson and Lyon, 1901; type locality: Macuto, Venezuela), *minuta* Goodwin, 1942 (type locality: Boca del Curaray, Peru), and *nicaraguae* Goodwin, 1942 (type locality: Kanawa Creek, near Cukra, Nicaragua) are available for bats in this group. Many recent authors (Gardner, 1976; Handley, 1976; Koopman, 1978, 1982; Jones and Carter, 1979) have treated these taxa as a single species under the name *Tonatia brasiliense,* which is the senior synonym. Our examination of material in the National Museum of Natural History and American Museum of Natural History and comparison of this material with our Suriname specimens revealed no consistent morphological character separates these taxa. However, it must be pointed out that Baker (1979) has retained the names *brasiliense, minuta,* and *venezuelae* in reporting karyological information. Possibly, future chromosomal or genic studies will lead to a better understanding of the relationships of these taxa. However, for the present, we are following other authors in recognizing a single small-sized species of *Tonatia.* We have not used a subspecific designation because there is not sufficient material available at this time to do an adequate analysis of geographic variation.

Tonatia brasiliense is easily separated from all other species of the

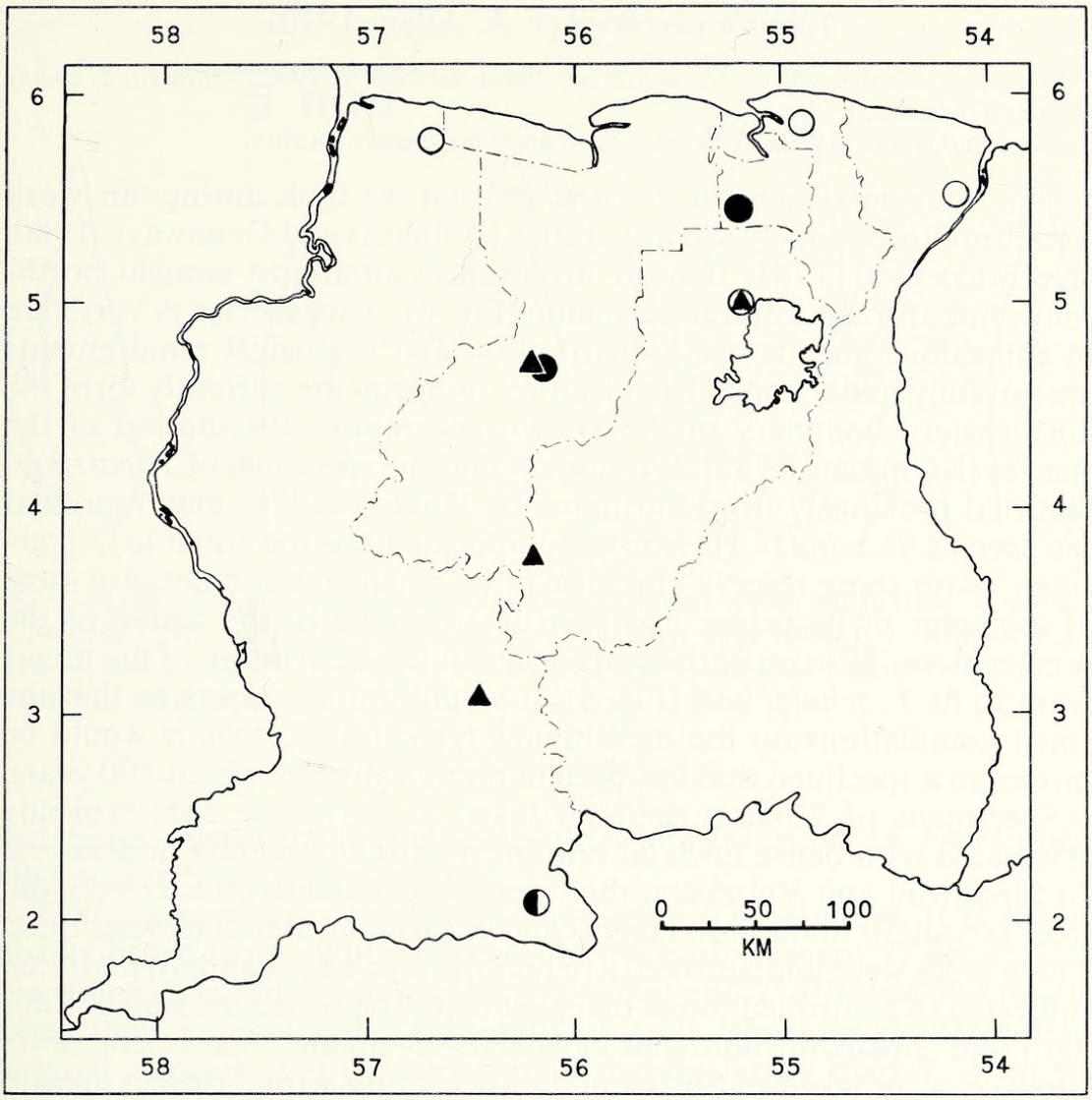

Fig. 4.—Geographic distribution in Suriname of *Tonatia brasiliense* (open circles), *T. carrikeri* (closed circles), and *T. schulzi* (closed triangles). Combined symbols indicate that two species were taken at the same locality.

genus in Suriname by its much smaller size (forearm less than 40.0 and greatest length of skull less than 21.0) in all external and cranial measurements (Tables 2–3; Fig. 2). This species is much more likely to be confused with some members of the genus *Micronycteris*. However, generic characters such as two lower incisors as opposed to four and the size and shape of the first upper and middle lower premolars, will set this species apart from any member of the genus *Micronycteris*.

The karyotype of *T. brasiliense* based upon a female specimen from Suriname is 2N = 30 and the FN is probably 56. The sex chromosomes were not determined (Honeycutt et al., 1980).

Tonatia carrikeri (J. A. Allen, 1910)

Specimens examined (3).—NICKERIE: Sipaliwini airstrip, 1. PARA: Zanderij, 1. SARAMACCA: Voltzberg, 1.

Additional record (Husson, 1978).—Suriname: no specific locality.

The three specimens of *T. carrikeri* that we took during our work were from three widely separated sites (Williams and Genoways, 1980; Genoways et al. 1981) that are arranged in an almost straight north-south line through central Suriname (Fig. 4). This species is very rare in collections and its exact distribution and ecological requirements are not fully understood. The localities in Suriname currently form the northeastern boundary of the known geographic distribution of the species (Koopman, 1982). We suspect that the specimen of *T. carrikeri* reported previously from Suriname by Husson (1978) may represent the species *T. schulzi.* Husson even allocated the specimen to *T. carrikeri* "with some reserve" because of its small size and because most of the color of its pelage had been lost because of the action of the preservative. The size of the specimen and the description of the tragus seem to fit *T. schulzi* best (Fig. 5). It would not be surprising that the small granulations on the membranes typical of *T. schulzi* would be missed in a specimen that has been in preservative for about 100 years.

Specimens of *Tonatia carrikeri* taken in Suriname were typically associated with dense lowland rainforest with a moderate understory. At Sipaliwini and Voltzberg, the forest was characterized by very tall trees (about 50 to 60 m in height) and occasional, standing dead trees. These areas were undisturbed, whereas the area near Zanderij had been subjected to controlled forest management. The collecting sites at Zanderij and Sipaliwini bordered extensive savannahs. Specimens of *T. carrikeri* were taken in Suriname in association with 31 other species of bats (Table 1). In addition to association with common, widespread species, *T. carrikeri* also was associated frequently with several other species of phyllostomines, such as *Micronycteris minuta, M. hirsuta* (both taken near Zaderij), *Phyllostomus elongatus, P. hastatus,* and *Phylloderma stenops.* Of the stenodermines, it was taken most often with *Sturnira lilium* and *Vampyrops helleri.* Perhaps the most interesting association is with *Desmodus rotundus,* a rare species in Suriname, which also was taken at two of the three localities where we obtained *T. carrikeri.*

Among the three specimens from Suriname that we examined, two are adult females and one is an adult male. One of the females was lactating when captured on 18 May 1980 (Zanderij); the other female revealed no gross evidence of reproductive activity when netted on 28 August 1979 (Voltzberg). This latter specimen weighed 18 g. The male

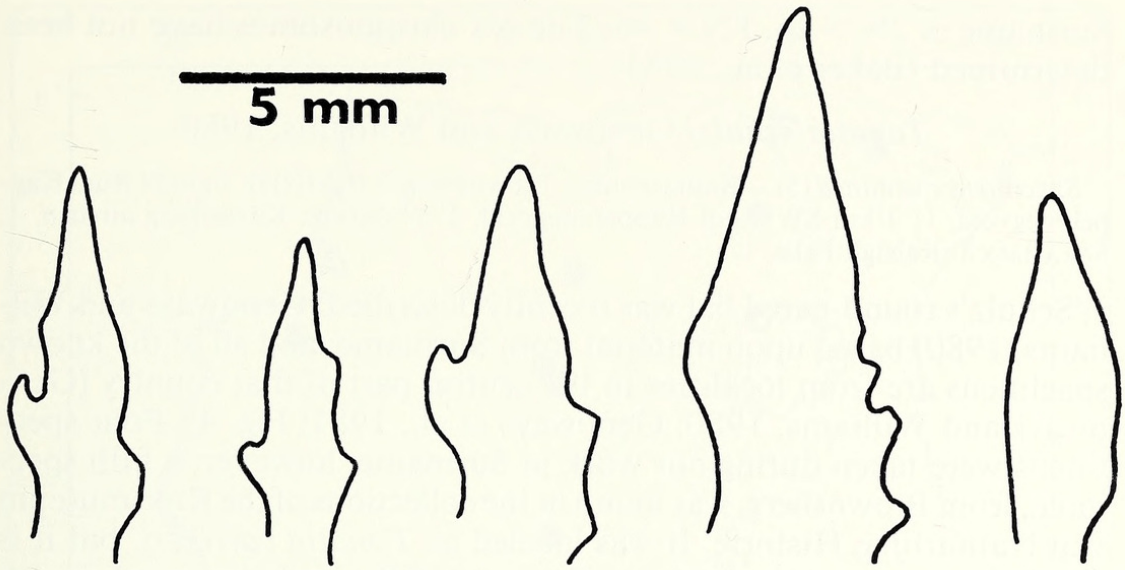

Fig. 5—Tragus of five species of *Tonatia* from Suriname. From left to right, *T. schulzi* (CM 63687), *T. brasiliense* (CM 63667), *T. carrikeri* (CM 63668), *T. silvicola* (CM 63674), and *T. bidens* (CM 63659). The left side of each illustration represents the inner margin of the tragus.

had testes measuring 7 mm in length when taken on 16 November 1981 at the Sipaliwini airstrip.

Tonatia carrikeri is a medium-sized species of *Tonatia.* It is easily distinguished from all other species in the genus, except *T. schulzi,* by size alone. It is much smaller than *T. bidens* and *T. silvicola* and much larger than *T. brasiliense* (Tables 2–3; Fig. 2). Based on available material it appears that *T. carrikeri* is slightly larger than *T. schulzi*; however, more material of both species will be necessary to confirm this observation. Externally the two species are easily separated as pointed out by Genoways and Williams (1980). In *carrikeri,* the underparts are pure white except on the chin and sides of the abdomen, whereas in *schulzi* the underparts are uniformly drab gray, although the bases of the hairs are white. The small wart-like granulations found on the dorsal surfaces of the membranes in *schulzi* are lacking in *carrikeri.*

Currently, *Tonatia carrikeri* is regarded as monotypic. The measurements of two females taken during our survey are listed in Table 3. These measurements match closely with those of specimens of *T. carrikeri* from Venezuela, Bolivia, and Peru (Gardner, 1976; Goodwin, 1953; Swanepoel and Genoways, 1979).

The karyotype of *T. carrikeri* based upon a female specimen from

Suriname is 2N = 26, FN = 46. The sex chromosomes have not been determined (Baker et al., 1981).

Tonatia schulzi Genoways and Williams, 1980

Specimens examined (5).—BROKOPONDO: Brownsberg, 1 (RMNH); 1 km N Rudi Kappelvliegveld, 1; 3 km SW Rudi Kappelvliegveld, 1. NICKERIE: Kayserberg airstrip, 1. SARAMACCA: Raleigh Falls, 1.

Schulz's round-eared bat was recently described (Genoways and Williams, 1980) based upon material from Suriname, and all of the known specimens are from localities in the central part of that country (Genoways and Williams, 1980; Genoways et al., 1981; Fig. 4). Four specimens were taken during our work in Suriname; however, a fifth specimen, from Brownsberg, was found in the collections of the Rijksmuseum van Natuurlijke Historie. It was labeled as *Tonatia carrikeri,* but it is not the specimen reported by Husson (1978) and discussed in the account of *carrikeri* herein. To our knowledge, the specimen from Brownsberg (RMNH 26111) has not appeared previously anywhere in the literature.

The habitats where *Tonatia schulzi* has been obtained are characterized by dense, undisturbed, lowland rainforest where the understory often provided moderate groundcover. In such areas the local influence of man on the habitat either has been limited or nonexistent (all known localities for this species are within designated nature preserves of Suriname). Secondary vegetation was not observed at any collecting site. At 3 km SW Rudi Kappelvliegveld and at Kayserberg the species was taken in mist nets set on hillsides where tall dakama forest dominated. Specimens of *T. schulzi* were taken in association with only 23 other species of bats during our work in Suriname. The list of associated species is far less than for any other species of *Tonatia* (Table 1). Excluding the obviously widespread species, interesting associations are found with *Phyllostomus elongatus* (which was taken at all four localities), *Saccopteryx leptura* (taken from three of the four localities), and *Chrotopterus auritus, Micronycteris megalotis,* and *Phyllostomus hastatus* (taken at two of the four localities).

All known specimens of Schulz's round-eared bat are males. All specimens have the phalangeal epiphyses closed, but the pelage of the specimen from 1 km N Rudi Kappelvleigveld is darker and finer, which may indicate that it is a young animal just completing closure of the epiphyses. This specimen weighed 15 g (30 September 1979), and the other specimen from nearby weighed 16 g (1 October 1979). The testes of the specimen from Kayserberg measured 5 mm in length on 6 May 1980, and those of the specimen from Raleigh Falls measured 7 on 10 May 1980.

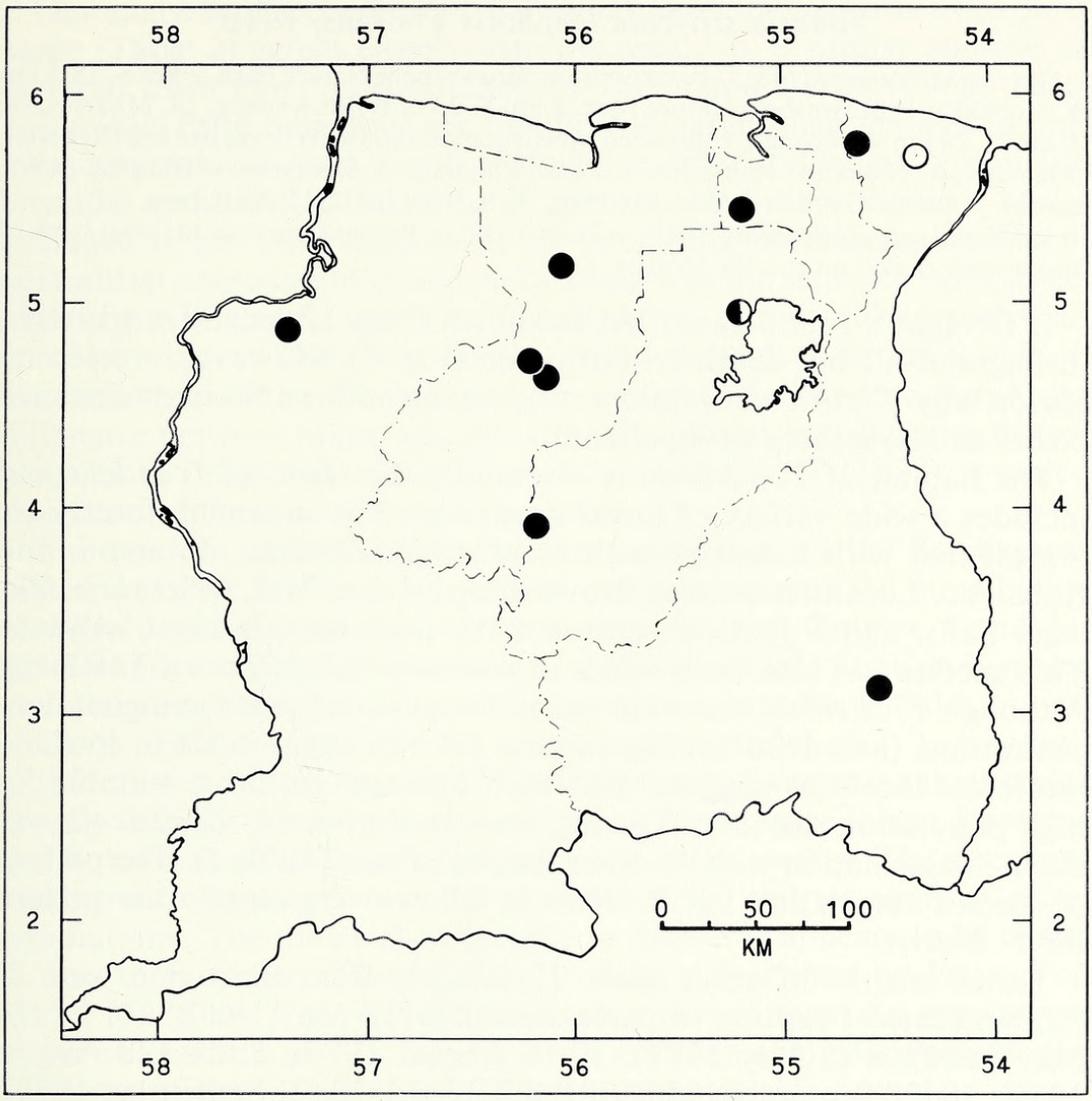

Fig. 6.—Geographic distribution of *Tonatia silvicola* in Suriname. Closed circles indicate specimens examined; open circles indicate localities based upon the literature.

Tonatia schulzi is a medium-sized member of the genus, which may be confused only with *T. carrikeri* based on size alone (Tables 2–3; Fig. 2). Characters for separating these species are discussed in the account of *carrikeri* and by Genoways and Williams (1980). The unique character exhibited by this species is the presence of small wart-like granulations on the dorsal surfaces of the forearms, digits, and hind legs and on the ears and noseleaf. This character is found in no other member of the genus or any other phyllostomid bat.

The karyotype of *T. schulzi* based upon material from Suriname is 2N = 28, FN = 36. The X-chromosome and Y-chromosome are acrocentric (Honeycutt et al., 1980; Baker et al., 1981).

Tonatia silvicola laephotis Thomas, 1910

Specimens examined (48).—BROKOPONDO: Brownsberg Nature Park, 7 km S, 18.5 km W Afobakka, 1; Brownsberg Nature Park, 8 km S, 2 km W Brownsweg, 14. MAROWIJNE: 10 km N, 24 km W Moengo, 1; between Moengotapoe and the Wiawia Bank, 2 (RMNH); Oelemarie, 4. NICKERIE: Kabalebo, 1. PARA: Zanderij, 2. SARAMACCA: Bitagron (=Witagron), 1; Lower Geyskes Creek, Tafelberg, 1; Raleigh Falls, 15; Voltzberg, 6.

Additional records (Husson, 1978).—BROKOPONDO: Brownsberg near the west bank of Brokopondo Lake; no specific locality.

D'Orbigny's round-eared bat is known from 12 localities scattered throughout all but southern Suriname (Fig. 6). However, we see no reason why *T. silvicola* should not occur in southern Suriname at such places as Kayserberg or Sipaliwini.

The habitat of *T. silvicola* is essentially the same as *T. bidens* and includes a wide variety of forest situations. The savannah forests are represented with localities such as Moengo, Zanderij, Bitagron, and Kabalebo. Localities such as Brownsberg Nature Park, Oelemarie, Raleigh Falls, and Voltzberg represent the lowland rainforest habitats. This species has also been taken in montane rainforest on Tafelberg. Although *T. silvicola* occurs in many forest situations, the higher concentrations (based on netting-success rate) of individuals in lowland rainforest localities suggests that such habitats are most suitable for high population densities. During work in Suriname, *T. silvicola* was taken in association with 41 other species of bats (Table 1). The pattern of species association for *T. silvicola* follows very closely the pattern for *T. bidens.*

Testes lengths of adult male *T. silvicola* from Suriname were as follows (date of capture in parentheses): 9 (12 May 1980); 10, 12 (14 May 1980); 8 (8 July 1977); 10 (6 August 1977); 8, 10 (28 August 1979); 10 (20 September 1979); 10, 12, 13, 13, 13 (21 September 1979); 13 (23 September 1979); 12 (24 September 1979); 8 (26 September 1979); 11 (29 November 1981). Two males taken at Raleigh Falls on 14 May 1980 were subadults based on unfused phalangeal epiphyses (length of forearm, 49.7, 51.4). A female carrying a single fetus that measured 25 mm in crown–rump length was taken on 28 August 1979 at Voltzberg. Lactating individuals were captured on 14 May 1970 at Raleigh Falls and 21 and 22 September 1979 in the Brownsberg Nature Park. Females that exhibited no gross reproductive activity were netted on the following dates: 14 May 1980; 19 May 1980; 28 May 1980; 4 September 1979; 21 September 1979 (2); 24 September 1979. Although these data certainly are not definitive, they do suggest a reproductive pattern similar to that of *T. bidens.* However, Wilson (1979) found no evidence of more than one young being produced per year with births occurring during the early half of the rainy season.

The mean weight of 13 adult males was 33.4 (27–38); of eight females, 28.4 (24–36). The pregnant female weighed 32 g.

Our analysis of secondary sexual variation in the material from Suriname (Table 2) agrees closely with the results of a similar analysis of material from Panama conducted by Davis and Carter (1978). Male *T. silvicola* from Suriname are significantly larger than females in four measurements (greatest length of skull, condylobasal length, zygomatic breadth, and mastoid breadth) of the nine that were studied. Males averaged larger than females in all remaining measurements except postorbital constriction in which the mean was the same for both sexes. Males from Suriname were significantly larger in mastoid breadth than females, whereas there was no significant secondary sexual variation in cranial breadth in the Panamanian sample. We found no significant difference between males and females in length of maxillary toothrow, whereas the material studied by Davis and Carter (1978) revealed significant differences between the sexes.

The amount of individual variation exhibited by the Surinamese material (Table 2) is low. Postorbital constriction was the most highly variable measurement studied for both males and females. Condylobasal length showed the lowest amount of individual variation in males and mastoid breadth displayed the lowest amount for females.

Davis and Carter (1978) did not include material of *T. s. laephotis* in their review of the *Tonatia silvicola* complex. Examining their tables reveals that the Suriname material has on the average longer forearms and broader skulls than other populations of the species. The maxillary toothrow in *laephotis* may be proportionally shorter than in other populations. The material assignable to *laephotis* appears to be closer in size to specimens from Central America described by Davis and Carter (1978) as *T. s. centralis* than other named taxa. An assessment of the exact status of *T. s. laephotis* will await an analysis of geographic variation of the species that includes this material.

A comparison of *T. silvicola* and *T. bidens* in Suriname is given in the account of the latter species. Davis and Carter (1978) gave reasons for the spellings of *silvicola* and *laephotis* used in our paper.

The karyotype of *T. silvicola* based upon material from Suriname is 2N = 34, FN = 60. The X-chromosome is submetacentric and the Y-chromosome is acrocentric (Honeycutt et al., 1980).

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