

REVIEW OF THE *TONATIA BIDENS* COMPLEX (MAMMALIA: CHIROPTERA), WITH DESCRIPTIONS OF TWO NEW SUBSPECIES

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Tonatia bidens has a broad distribution in Central and South America; the only extant form is monotypic. Our analysis reveals two species are involved: *T. bidens* (von Spix) from eastern Brazil, Paraguay, and Argentina; *T. saurophila* Koopman and Williams from Central America, northern and western South America, and Jamaica. These taxa are sympatric in northeastern Brazil. Both qualitative and quantitative assessments of morphological characters distinguish the species. Dental differences, previously noted between fossil material from Jamaica and mainland specimens representing *T. saurophila* as well as size differences between Central and South American *T. saurophila* warrant recognition of two subspecies representing extant mainland populations.

Key words: bats, *Tonatia bidens*, *Tonatia saurophila*, South America, Central America, México

Von Spix (1823) described *Vampyrus bidens* from Río São Francisco, Bahia, Brazil. This taxon became the type species (by monotypy) for *Tonatia* Gray, 1827. Within 15 years, Gray (1838) described a similar form, *Phyllostoma childreni*, from South America. Both species were recognized until Dobson (1878) synonymized them under the name of *Lophostoma bidens*. *Lophostoma* is a junior subjective synonym of *Tonatia*, and since the turn of the century, *Tonatia* has been used as the generic name for these bats (Cabrera, 1958; Goodwin, 1942; Hall, 1981; Miller, 1907; Palmer, 1898; Sanborn, 1936).

Tonatia bidens, a large-sized species of the genus, is differentiated from *Tonatia silvicola* and *Tonatia evotis* by its smaller ears, broader postorbital constriction, and absence of a low band connecting the ears across the forehead. Koopman and Williams (1951) described another large-sized species, *Tonatia saurophila*, based on fossil material from a cave in Jamaica. Koopman

(1976) subsequently recognized the taxon as *T. bidens saurophila*.

At present, *T. bidens* includes two subspecies (Koopman, 1976). *T. b. saurophila* is known only from fossil, cave material from Jamaica, whereas *T. b. bidens* has been reported from México, Belize, Honduras, Guatemala, Costa Rica, Panamá, Colombia, Venezuela, the Guianas, Brazil, Ecuador, Perú, Paraguay, and northern Argentina. With more specimens now available, a thorough systematic review of *T. bidens* can be completed.

Genoways and Williams (1980, 1984) compared species of *Tonatia* from Suriname. Criteria for differentiating species of *Tonatia* from Suriname were not useful for *Tonatia* from northeastern Brazil and resulted in misidentifications of Brazilian specimens (Mares et al., 1981; Willig, 1983; Willig and Mares, 1989). Closer examination of Brazilian specimens revealed three large-sized species of *Tonatia*: *T. silvicola*; two forms identified as *T. bidens*.

This prompted our assessment of the entire *Tonatia bidens* complex.

MATERIALS AND METHODS

Specimens ($n = 224$) were examined from the: American Museum of Natural History (AMNH); British Museum (Natural History; BM; now The Natural History Museum, London); Carnegie Museum of Natural History (CM); Field Museum of Natural History (FMNH); Museum of Zoology, Louisiana State University (LSUMZ); Museum of Zoology, University of Michigan (UMMZ); Royal Ontario Museum (ROM); Texas Cooperative Wildlife Collection, Texas A&M University (TCWC); Museum of Texas Tech University (TTU); National Museum of Natural History (USNM). Dial calipers, accurate to 0.1 mm, were used to measure length of forearm and nine cranial characters (Appendix I); measurements are given in millimeters. Statistical analyses were performed using SPSS programs (Norusis, 1990a, 1990b).

We used two-way multivariate analysis of variance (MANOVA) based upon the nine cranial characters to assess morphometric divergence between populations from Brazil and Suriname, while controlling for the effects of secondary sexual variation (Willig and Owen, 1987; Willig et al., 1986). The three commonly-used criteria (Wilks' Lambda, Lawley-Hotelling Trace, and Pillai's Trace statistics) for significance in MANOVA can differ in magnitude. Nonetheless, their statistical power is comparable, especially when departures from null hypotheses are small (Morrison, 1967; Pillai and Jayachandran, 1967). Our results (both F -values and significance levels) based upon these criteria were identical to three decimal places; hence, we drew identical conclusions from each.

We used a stepwise discriminant-function analysis to define the best linear combination of the original characters that distinguishes among the four groups (males and females from Brazil, males and females from Suriname) and to assess the morphometric affinities of specimens from Suriname and northeastern Brazil. In addition, morphometric affinities of all specimens of *T. bidens* from South America were quantified in the classificatory phase of discriminant-function analysis.

Once it became clear that two forms of the *T. bidens* complex in South America deserved specific recognition, we evaluated morphometric af-

finities of specimens of *T. bidens* from Central America and from western Venezuela. These individuals initially were treated as a distinct group based on geography and on qualitative assessments of morphology. A morphometric test of this hypothesis was conducted via two-way MANOVA, with sex and taxon as factors. A priori contrasts assessed dimorphism within species and interspecific variation regardless of sex. We subsequently performed discriminant-function analysis on the same six groups based upon combinations of taxon and sex. This analysis revealed mensural distinctiveness among taxa and clarified morphometric affinities of specimens heretofore considered as *T. bidens*.

Next, we conducted a pure model I two-way analysis of variance (ANOVA) on each character to evaluate the importance of each in distinguishing the six groups. These univariate tests were not used to determine if groups are morphometrically distinguishable, but were used to provide unbiased heuristic assessments of characteristics that are likely to contribute to group differences detected by MANOVA.

RESULTS

Qualitative analysis.—Extant members of the *T. bidens* complex have a broader postorbital constriction than do specimens of *T. silvicola*, with southern and eastern populations being even broader than northern and western populations (Fig. 1). These two forms also can be distinguished from other extant congeners by the presence of an antero-medial foramen, located between the upper incisors and incisive foramina. Characters useful in distinguishing the two mainland forms are: presence or absence of a secondary medial process on the mastoid (Figs. 2a and 2b); width of gap between lower canines (Figs. 2c and 2d); relative size of second lower premolar and degree of overlap of its crown by cingula of adjacent premolars (Figs. 2c and 2d); presence or absence of a stripe on top of head between ears.

Based on priority, cranial dimensions of holotypes (Carter and Dolan, 1978), and information on type localities, we assign specimens from Pernambuco, Brazil, to *T. bidens*. Because *Tonatia childreni* is a ju-

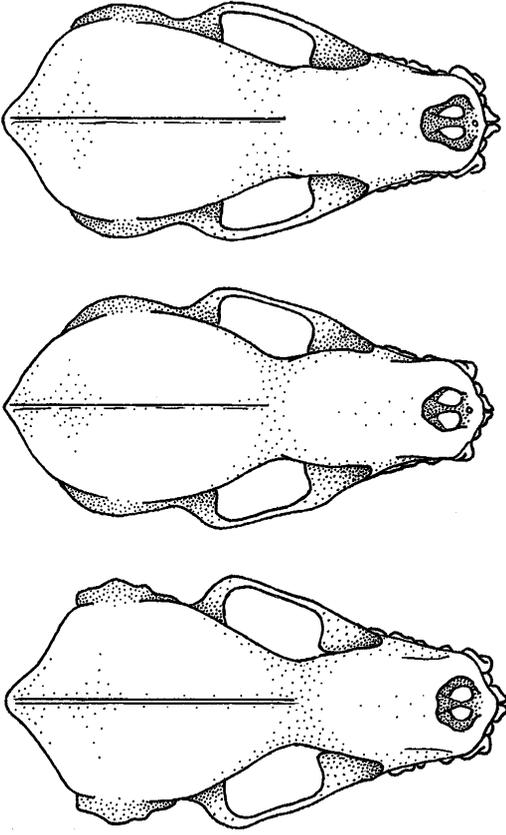


FIG. 1.—Illustration of the dorsal views of the cranium of *Tonatia bidens* (top; from Pernambuco, Brazil, CM 99127), *Tonatia saurophila* (center; from Suriname, CM 63663), and *Tonatia silvicola* (bottom; from Suriname, CM 63678). Note differences in breadth of postorbital constriction.

nior synonym of *T. bidens*, the next available name for the non-*bidens* members of the complex is *saurophila*. Consequently, we use the names *T. bidens* and *T. saurophila* to identify these species.

Quantitative analysis.—Qualitative information suggests recognition of two forms within the *T. bidens* complex; however, it was unclear if the same variation is reflected in mensural characters. Sixty specimens of *T. bidens* (Brazil) and *T. saurophila* (Suriname) were included in multivariate analyses. A significant two-way interaction in the MANOVA (taxon, $F =$

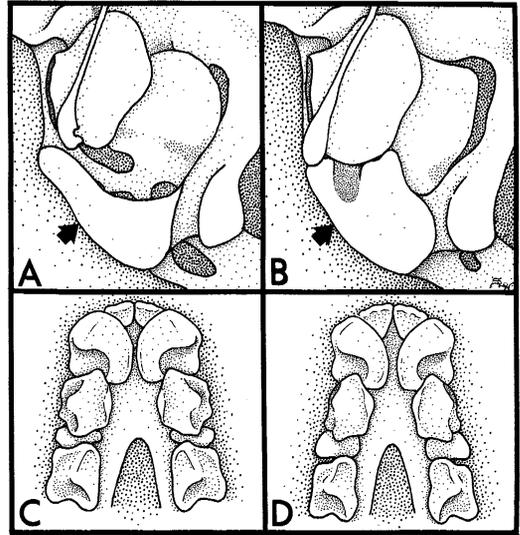


FIG. 2.—Illustrations showing the differences of the mastoid process below the auditory bullae between *Tonatia bidens* (a) and *Tonatia saurophila* (b). Lower illustrations show differences in the separation of the lower canines and the level of crowding of the lower second premolar between *T. bidens* (c) and *T. saurophila* (d). All illustrations are made to the same scale (distance between labial sides of canines is 3 mm).

95.655, $P < 0.001$; sex, $F = 2.924$, $P = 0.008$; interaction, $F = 2.247$, $P = 0.035$) revealed that the difference between populations depended on sex. The magnitude, but not direction, of variation between populations was sex-dependent with consistently larger means for specimens of *T. bidens* as compared with those of *T. saurophila* for nine cranial characters.

Discriminant-function analysis corroborated the MANOVA in that three functions significantly distinguished the four a priori groups: males from northeastern Brazil; females from northeastern Brazil; males from Suriname; females from Suriname. Nonetheless, axes differed greatly in importance; discriminant-functions I, II, and III accounted for 96.42, 2.05, and 1.53% of the variation among groups, respectively. Based on orientation of group centroids and associated clusters of specimens, discriminant-function I reflected interpopulational

differences, whereas discriminant-function II reflected intersexual differences. Characters highly correlated with discriminant-function I (breadth across upper canines, $r = 0.50$; breadth across postorbital constriction, $r = 0.40$; length of maxillary toothrow, $r = 0.39$; breadth of braincase, $r = 0.30$) contributed to interpopulational differences. Characters most highly correlated with discriminant-function II (zygomatic breadth, $r = 0.72$; greatest length of skull, $r = 0.69$; condylobasal length, $r = 0.58$; length of maxillary toothrow, $r = 0.46$) contributed to sexual dimorphism in populations from Suriname and northeastern Brazil.

During the classificatory phase of the discriminant-function analysis, all individuals were assigned correctly to their respective populations. Reflective of the lower level of significance obtained for sexual dimorphism in the MANOVA and ANOVAs and small amount of morphometric differentiation between sexes (discriminant-function II), all misclassifications were related to designation of sex. Nevertheless, errors related to sex were infrequent, with 90.0, 86.7, 80.0, and 90.0% of the specimens correctly identified as males or females from northeastern Brazil and males or females from Suriname, respectively.

As an independent test of species assignments based on geography and qualitative characters, we assigned the other 41 specimens from South America as unknowns during the classificatory phase of the discriminant-function analysis. With the exception of one specimen (a male *T. saurophila* from northern Venezuela, classified as a male *T. bidens*), identifications of all individuals to taxon agreed with qualitative characters used to differentiate *T. bidens* and *T. saurophila*.

We treated the Central American specimens as a distinct taxon and evaluated their morphometric affinities to *T. bidens* and *T. saurophila* with a two-way MANOVA, where taxon and sex were established as categorical variables. The MANOVA (tax-

on, $F = 52.233$, $P < 0.001$; sex, $F = 1.375$, $P = 0.204$; interaction, $F = 1.226$, $P = 0.238$) detected significant differences among the three taxa as reflected by significant differences ($P < 0.001$) associated with taxon in the two-way ANOVAs of each character. A priori contrasts from the MANOVA revealed that intersexual differences were significant for *T. bidens* ($F = 1.935$, $P = 0.050$), but not for *T. saurophila* ($F = 1.121$, $P = 0.352$) or for *Tonatia* from Central America ($F = 0.820$, $P = 0.599$). The main group of *T. saurophila* from South America also was significantly different from the Central American group ($F = 21.278$, $P < 0.001$), and the *T. bidens* group was significantly different from the other two groups combined, here identified as representing *T. saurophila* ($F = 128.962$, $P < 0.001$).

Discriminant-function analysis significantly distinguished six groups (males and females of each of three taxa) based on two axes (Table 1). Discriminant-function I accounted for 91.0% of the intergroup variation, whereas discriminant-function II accounted for 7.6% of that variation. Three characters were highly correlated with discriminant-function I (breadth across postorbital constriction, $r = 0.453$; breadth across upper canines, $r = 0.423$; breadth of braincase, $r = 0.432$), along which *T. bidens* is separated from other taxa (Fig. 3). All of the other characters were highly correlated with discriminant-function II ($r \geq 0.361$), which distinguished between *T. saurophila* and Central American populations and between sexes of *T. bidens*.

All *T. bidens* were correctly assigned to species. In contrast, 5.6% of the South American *T. saurophila* were classified as Central American *Tonatia*, and 11.9% of the Central American *Tonatia* were classified as *T. saurophila*.

Significant differences among all groupings of *T. bidens*, *T. saurophila*, and Central American *Tonatia* suggest recognition of each as a distinct taxon. *T. bidens* exhibits sexual dimorphism and is more distant phe-

TABLE 1.—Structure matrix from discriminant-function analysis in which six groups of *Tonatia*, defined by combinations of taxon (*T. bidens*, *T. childreni*, and Central American specimens) and sex (males and females) were morphometrically distinguished based upon a suite of nine cranial characters. Pooled within-group correlations between characters and discriminant functions are ordered by the size of their correlations within discriminant functions and indicate the relative importance of variables in differentiating among groups. The break in the character list separates characters more highly associated with discriminant-function I from those more highly associated with discriminant-function II.

Character or statistical parameter	Discriminant function	
	I	II
Postorbital constriction	0.453	0.221
Breadth of braincase	0.432	0.323
Breadth across upper canines	0.423	-0.082
Condylobasal length	0.109	0.787
Length of maxillary toothrow	0.299	0.776
Greatest length of skull	0.126	0.715
Zygomatic breadth	-0.104	0.606
Mastoid breadth	0.385	0.584
Breadth across upper molars	0.267	0.361
Eigenvalue	9.493	0.791
Chi-square	479.895	113.186
Significance	<0.001	<0.001
Percent of variance explained	91.01	7.58

netically from the other two taxa than each is from the other. Further evidence of the close affinity between *T. saurophila* and the Central American *Tonatia* is the lack of secondary sexual variation, broadly overlapping 95% confidence ellipses (for specimens in space defined by discriminant-function analysis), and specimens misclassified during discriminant-function analysis. These patterns are not a consequence of distortion of morphometric space by discriminant-function analysis as a trade-off for distinguishing between sexes, because the same general systematic conclusions follow

from principal-components analysis (Fig. 4). Consequently, we recognize the *Tonatia* from Central America as being distinct from *T. bidens*, but phenetically allied with *T. saurophila*.

TAXONOMIC CONCLUSIONS

Among large-sized species (length of forearm >50 mm) of *Tonatia*, both *T. bidens* and *T. saurophila* can be differentiated from *T. silvicola* and *T. evotis* (Davis and Carter, 1978; Medellín and Arita, 1989) by having a postorbital constriction >5.0 mm and ears <32 mm. The first two taxa also can be distinguished from all other congeners by the presence of an anterio-medial foramen and well-haired rostrum, ears, forearms, legs, and feet. Overall, several qualitative cranial and pelage characters easily distinguish *T. bidens* from *T. saurophila*, as described in the following accounts.

SYSTEMATIC ACCOUNTS

Tonatia bidens (Von Spix, 1823)

Vampyrus bidens Von Spix, 1823:65. Type locality "Rio São Francisco, Bahia, Brasil." [*Tonatia*] *bidens* Gray, in Griffiths, 1827:71. *Phyllostoma childreni* Gray, 1838:488. Type locality "S. America."

Holotype.—Adult, sex undetermined; skin and skull; unnumbered specimen maintained at Zoologisches Staats-Sammlung, Munich, Germany.

Diagnosis.—Size large for *Tonatia*; secondary process on mastoid lacking (Fig. 2a); lower incisors narrow; lower canines either meet along their medial margin posteriorly or are separated by only a narrow gap (Fig. 2c); second lower premolar reduced, and crown of tooth obscured by cingula of adjacent lower premolars (Fig. 2c); average breadth across postorbital constriction, 5.9 mm; no stripe on top of head between ears.

Distribution.—Specimens are known from eastern and southern Brazil, Paraguay, and northern Argentina (Fig. 5). Locality records are listed in Appendix II.

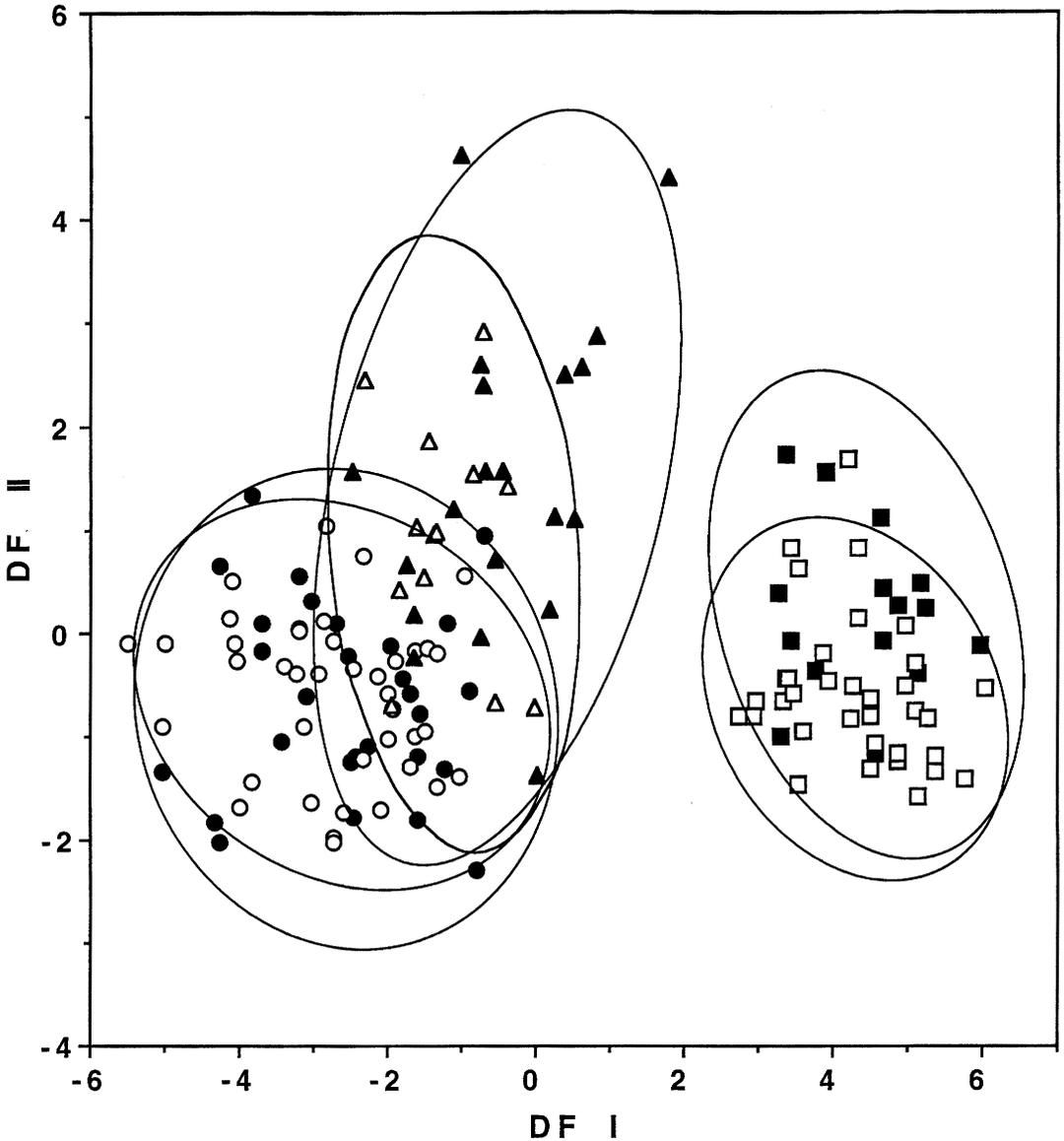


FIG. 3.—Two-dimensional portrayal of specimens of *Tonatia* based upon discriminant function analysis of nine cranial characters (squares = *T. bidens*; circles = *T. saurophila* from South America; triangles = *Tonatia* from Central America and northern Venezuela; closed figures = males; open figures = females). The 95%-confidence ellipses for each sex of each taxon are superimposed on the first two discriminant-function (DF) axes. Within a taxon, considerable overlap between the sexes occurred, whereas no overlap occurred between confidence ellipses of *T. bidens* and the other two groups of *Tonatia*.

Description.—“Brown, slightly grizzled, with grey tips to the hairs, beneath greyer; ears large with rather membranaceous rounded at the ends; nose-leaf ovate-lanceo-

late, rather longer than wide; wings brown; warts on lower lip in 3 or 4 arched series, crowded” (Gray, 1838:488); dorsal pelage darker than ventral; ears not joined by a

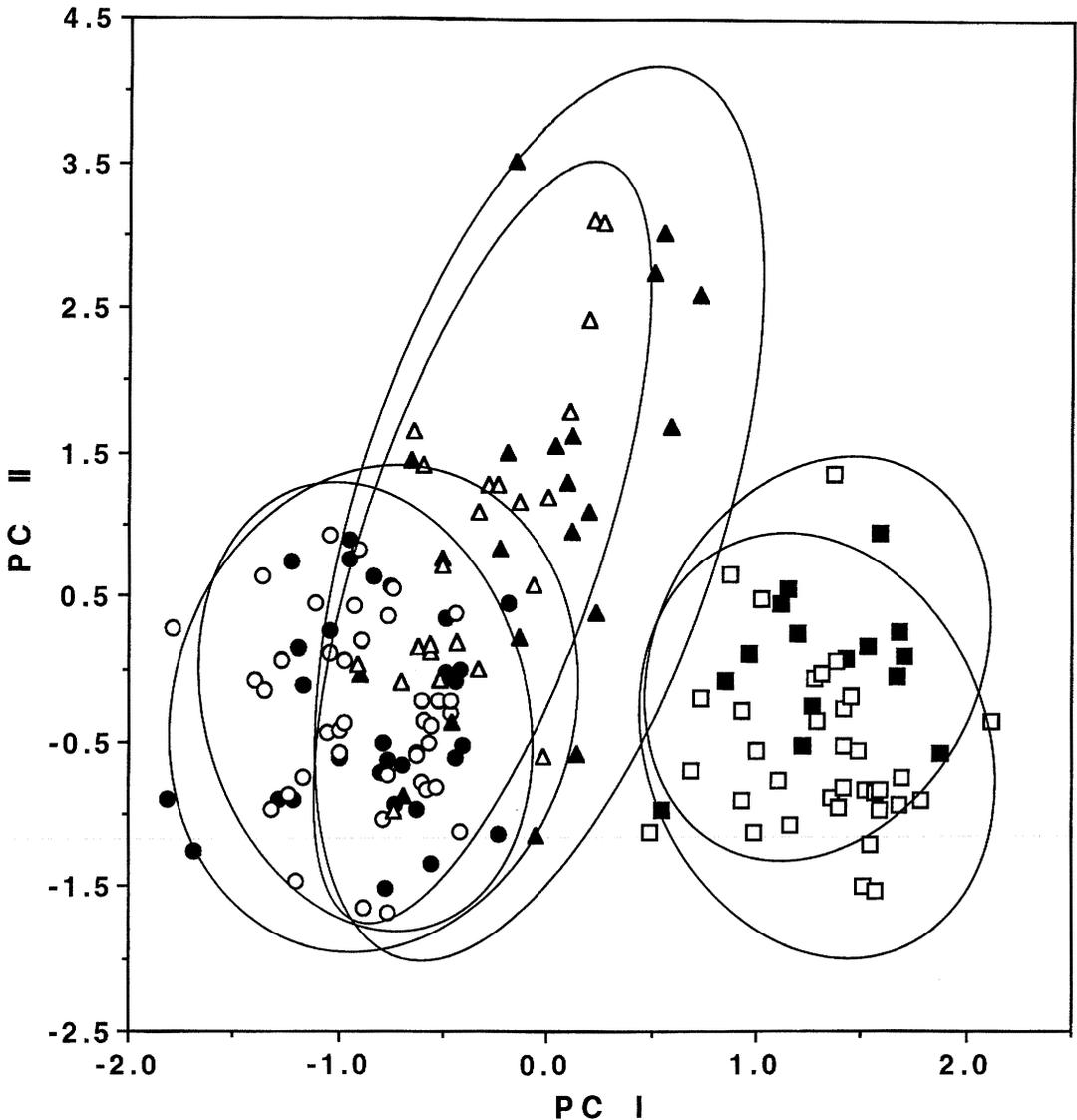


FIG. 4.—Two-dimensional portrayal of specimens of *Tonatia* based upon principal-components analysis of nine cranial characters (symbol designations are described in Fig. 3). The 95%-confidence ellipses for each sex of each taxon are superimposed on the first two principal-component (PC) axes. Within a taxon, considerable overlap between the sexes occurred, whereas little overlap occurred between confidence ellipses of *Tonatia bidens* and the other two groups of *Tonatia*.

band; forearm densely furred on proximal one-half; skull with continuous slope from frontal to rostral regions; lower first incisor weakly bilobed (Carter and Dolan, 1978). Species is sexually dimorphic as evidenced (mean followed by range) by length of forearm (males, 57.3, 55.6–59.3; females, 56.9,

55.1–58.4) and greatest length of skull (males, 28.5, 27.4–29.5; females, 28.4, 27.7–29.2). Breadth across postorbital constriction, mastoid breadth, and breadth across canines are 5.5–6.2, 12.8–13.7, and 5.5–6.4, respectively.

Measurements.—Measurements (in mil-

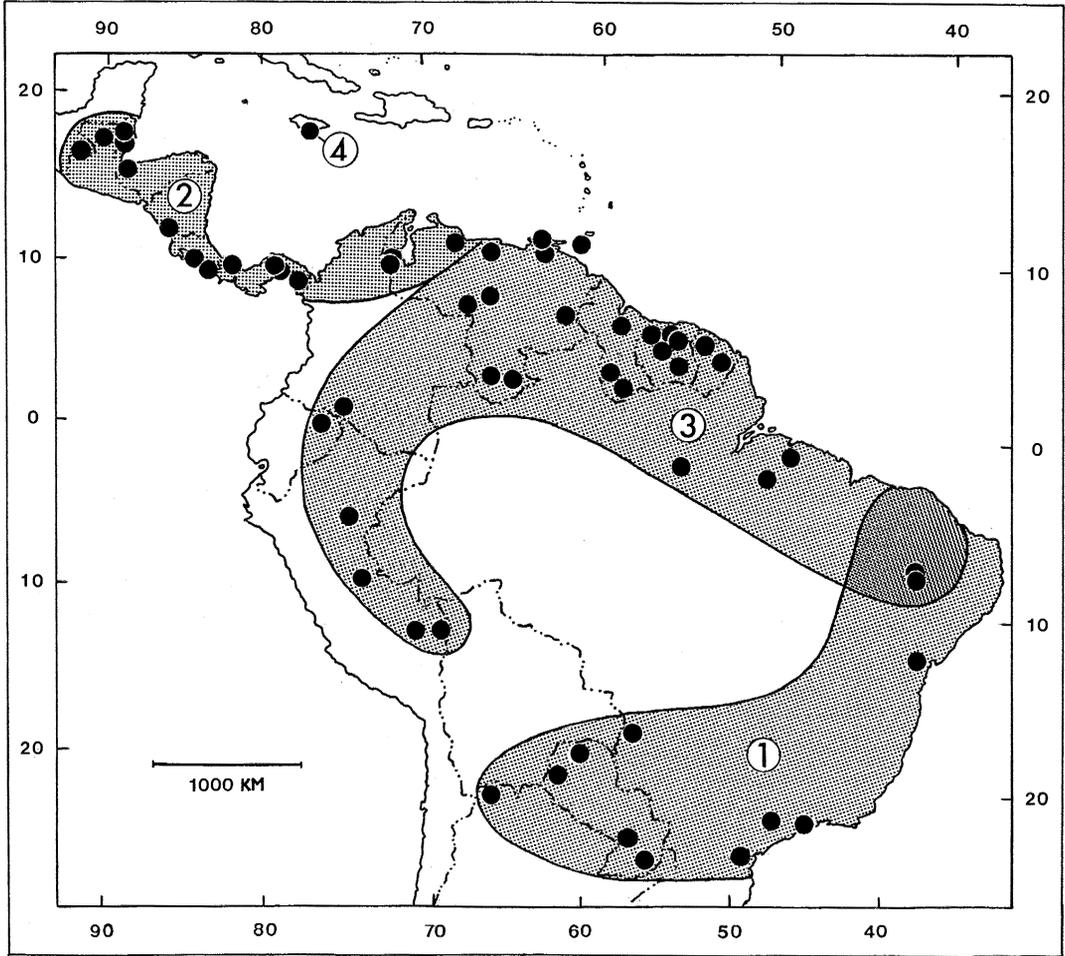


FIG. 5.—Map of South America and southern Central America showing collecting localities and geographic distributions of *Tonatia bidens* (1) and *Tonatia saurophila* (2, *T. s. bakeri*; 3, *T. s. maresi*; 4, *T. s. saurophila*).

limeters) of the holotype (from Carter and Dolan, 1978) are: length of forearm, 57.0; length of ear, 20.0; greatest length of skull, 28.6; condylobasal length, 24.8; palatal length, 12.9; zygomatic breadth, 13.8; mastoid breadth, 13.3; breadth of braincase, 11.4; least postorbital breadth, 6.0; length of maxillary toothrow, 10.0; greatest breadth across upper molars, 8.8; greatest breadth across upper canines, 6.2; length of mandibular toothrow, 11.2. Cranial measurements for other specimens are presented in Table 2.

Comparisons.—*Tonatia bidens* is among

the larger-sized species of the genus, and is distinguishable from the medium-sized *Tonatia carrikeri* and *Tonatia schulzi*, and the smaller species in the *Tonatia brasiliensis* complex (*Tonatia minuta*, *Tonatia nicaraguae*, and *Tonatia venezuelae*). *T. bidens* can be distinguished from *T. evotis* and *T. silvicola* (Davis and Carter, 1978; Medellín and Arita, 1989) by its broader postorbital constriction (>5.4 mm), shorter ear (<30.0 mm), and lower, less-developed sagittal crest. *T. bidens* is most similar to *T. saurophila* from which it can be distinguished by cranial differences (Fig. 2) and

TABLE 2.—Descriptive statistics (sample size, mean, range, standard error, and coefficient of variation) for *Tonatia bidens* and two subspecies of *T. saurophila*.

Measurement	Males				Females			
	<i>n</i>	\bar{X} (range)	SE	CV	<i>n</i>	\bar{X} (range)	SE	CV
<i>Tonatia bidens</i>								
Length of forearm	19	57.3 (55.6–59.3)	0.25	1.88	38	56.9 (55.1–58.4)	0.15	1.68
Greatest length of skull	19	28.5 (27.4–29.5)	0.12	1.83	38	28.4 (27.7–29.2)	0.06	1.23
Condylobasal length	20	24.3 (22.9–25.6)	0.13	2.30	38	24.0 (23.1–25.6)	0.08	2.15
Zygomatic breadth	19	13.7 (13.1–14.1)	0.06	1.90	37	13.5 (12.9–14.1)	0.05	2.04
Postorbital constriction breadth	20	5.9 (5.6–6.1)	0.03	2.35	38	5.9 (5.5–6.2)	0.03	3.29
Breadth of braincase	20	11.1 (10.8–11.4)	0.04	1.67	38	11.1 (10.7–11.8)	0.03	1.78
Mastoid breadth	20	13.4 (13.0–13.7)	0.04	1.29	36	13.2 (12.8–13.6)	0.04	1.78
Length of maxillary toothrow	18	9.9 (9.5–10.2)	0.05	1.97	38	9.8 (9.4–10.2)	0.03	1.61
Breadth across upper molars	19	8.9 (8.1–9.8)	0.08	4.04	38	8.8 (8.5–9.2)	0.03	1.81
Breadth across upper canines	19	6.1 (5.5–6.3)	0.05	3.52	37	6.1 (5.8–6.4)	0.03	2.46
<i>Tonatia saurophila bakeri</i>								
Length of forearm	19	58.0 (52.5–61.2)	0.54	4.05	21	58.2 (55.6–61.0)	0.33	2.59
Greatest length of skull	20	28.9 (27.2–30.7)	0.22	3.39	22	28.9 (27.6–30.5)	0.17	2.82
Condylobasal length	20	24.6 (23.3–26.3)	0.18	3.21	22	24.7 (23.3–26.2)	0.15	2.93
Zygomatic breadth	20	14.2 (13.4–15.0)	0.11	3.49	22	14.1 (13.3–15.1)	0.11	3.77
Postorbital constriction breadth	20	5.6 (5.2–5.9)	0.04	3.36	21	5.5 (5.3–5.8)	0.03	2.45
Breadth of braincase	19	10.8 (10.3–11.7)	0.09	3.56	21	10.7 (10.4–11.3)	0.05	2.11
Mastoid breadth	20	13.1 (12.6–13.7)	0.01	2.53	22	13.1 (12.4–13.7)	0.07	2.43
Length of maxillary toothrow	20	9.8 (9.2–10.3)	0.07	3.14	22	9.8 (9.4–10.2)	0.05	2.61
Breadth across upper molars	20	8.9 (8.4–9.3)	0.06	3.04	22	8.8 (8.3–9.3)	0.06	3.05
Breadth across upper canines	20	5.7 (5.2–6.1)	0.05	4.13	22	5.6 (5.2–6.1)	0.06	4.73
<i>Tonatia saurophila maresi</i>								
Length of forearm	25	54.9 (51.8–57.1)	0.26	2.42	35	55.6 (52.4–58.0)	0.26	2.78
Greatest length of skull	34	27.9 (26.9–28.9)	0.09	1.93	43	27.8 (26.6–29.1)	0.07	1.68
Condylobasal length	31	23.7 (23.0–24.9)	0.08	1.86	44	23.5 (22.6–24.6)	0.07	1.97
Zygomatic breadth	35	13.8 (13.0–14.5)	0.06	2.57	46	13.8 (13.0–14.4)	0.05	2.24
Postorbital constriction breadth	35	5.4 (5.0–5.6)	0.03	3.20	44	5.4 (5.1–5.6)	0.02	2.57
Breadth of braincase	34	10.4 (10.1–10.8)	0.04	2.10	44	10.4 (10.0–11.0)	0.03	2.09
Mastoid breadth	34	12.6 (11.9–13.3)	0.05	2.13	44	12.6 (12.2–13.1)	0.03	1.51
Length of maxillary toothrow	34	9.3 (8.9–9.8)	0.03	2.04	46	9.3 (9.0–9.7)	0.03	2.05
Breadth across upper molars	34	8.5 (7.7–9.0)	0.04	2.99	46	8.5 (8.0–9.0)	0.03	2.48
Breadth across upper canines	35	5.5 (5.1–6.0)	0.04	3.91	46	5.5 (5.0–5.9)	0.03	3.33

the lack of a stripe on top of head between ears.

Remarks.—Measurements provided by Carter and Dolan (1978), and observations by one of the authors (F. A. Reid) and P. Jenkins (The Natural History Museum, London) help clarify identities of type specimens of *Tonatia*. Information about the holotype of *T. bidens* provides specific dimensions and collecting locality. However, we have less information on the holotype of *T. childreni*, which is a subadult, has a badly damaged skull, and has a type locality sim-

ply described as South America. Available measurements (in millimeters) for the holotype of *T. childreni* (length of forearm, 51.8; zygomatic breadth, 13.0; postorbital constriction breadth, 5.6; breadth across upper canines, 5.6; mastoid breadth, 12.0) are at the lower end of the range for *T. bidens* (Table 2), possibly because of the maturity of the specimen. Observations provided by P. Jenkins (in litt.) support previous assessments (Dobson, 1878) about the status of *T. childreni*. She states, "Observations on the holotype of *Tonatia childreni* (Gray, 1866)

[sic] are as follows: 1. The skin is too faded to be certain, but there is no sign of a stripe. 2. The rear of the cranium is missing, including the mastoids and bullae. 3. The second lower premolar is significantly obscured by the first and third, as in Fig. 2c. 4. The lower canines are practically in contact as in Fig. 2c. Therefore, on the observable characters, the holotype agrees with *T. bidens*. . . .” These observations indicate that *T. childreni* is a synonym of *T. bidens*; thus, the name *T. saurophila* is the name available for northwestern and central populations of the complex.

Tonatia saurophila Koopman and Williams, 1951

Tonatia saurophila Koopman and Williams, 1951:11. Type locality “Wallingford Roadside Cave, Balaclava, St. Elizabeth Parish, Jamaica, British West Indies.”

Holotype.—Adult, sex undetermined; partial mandible from cave deposits; number 147206 at the American Museum of Natural History (AMNH).

Diagnosis.—Size large for *Tonatia*; secondary process of mastoid present and partially obscures base of auditory bulla (Fig. 2); lower canines separated postero-medially by a relatively wide gap (Fig. 2d); second lower premolar larger with crown less than one-half occluded by cingula of adjacent premolars (Fig. 2d); breadth across postorbital constriction averaging from 5.4 (in South America) to 5.5 mm (in Central America); stripe present on top of head between ears.

Distribution.—The species occurs in Central America and South America, southward from southern México to Perú, and eastward to Northeast Brazil (Fig. 5). The only records of the nominate subspecies are based on fossil cave material from Jamaica (Koopman and Williams, 1951).

Description.—The species has a breadth across postorbital constriction, mastoid breadth, and breadth across canines that measure 5.0–5.9, 11.9–13.7, and 5.1–6.1

mm, respectively. Goodwin’s (1942:205) description is as follows: “Size large, ears short and broad, proximal half of forearm well haired; base of thumb and uppersides of feet hairy. Color of upper parts varying from ochraceous tawny to blackish Mummy brown, base of hairs behind ears and on neck more or less white; underparts paler and grayer than back and washed with pale buff. Skull large and massive, rostrum broad, flat and not constricted in orbital region; braincase low and broad; superior outline evenly elevated from front of nasals and without depression in orbital region; palate narrow; toothrow only slightly converging anteriorly; sagittal crest low and fine.”

Measurements.—Measurements (in millimeters) of the holotype taken from Koopman and Williams (1951): length of mandibular toothrow, 9.8; depth of ramus behind last molar, 3.1. Cranial measurements of other specimens are presented in Table 2.

Comparisons.—*Tonatia saurophila* differs from *T. bidens* by size, cranial and dental characters (Fig. 2), and the presence of a short, pale stripe on top of head between ears. The secondary process on the mastoid that partially obscures the base of the bulla is unique within the subfamily; its shape may be autapomorphic in this species (Fig. 2b).

Remarks.—The species was described by Koopman and Williams (1951:11) from fossil, cave material, which they distinguished from Central American and northern South American specimens (identified as *T. bidens*) “in having the axis of the talonid of m3 running not obliquely in a lingual-labial direction but straight anteroposteriorly, in having a slightly lower coronoid, a slightly more bulbous forehead, and the labial posterior lobe of the last upper premolar better developed.” They regarded the species as slightly smaller than mainland populations. A reassessment by K. Koopman (pers. comm.) indicated that characters previously used to distinguish populations

were variable. For this reason, he later considered the Jamaican material to be only subspecifically distinct from mainland populations (Koopman, 1976). It should be noted that all mainland "*bidens*" studied by Koopman and Williams (1951) now are referred to as *T. saurophila*. We recognize the Jamaican taxon as subspecifically distinct from mainland *T. saurophila*, which we describe hereafter.

Tonatia saurophila bakeri, new subspecies

Holotype.—Adult male; skin and skull, number 39120 at the Museum of Texas Tech University (TTU); from 6 km SW Cana, ca. 1,200 m, Darién, Panamá; collected 31 January 1983 by R. J. Baker; prepared by M. S. Hafner, original number 1195; karyotype reference number TK22573.

Diagnosis.—*Tonatia s. bakeri* is a large bat distinguished from other recognized forms of the species by larger average forearm and cranial measurements (Table 2); breadth across lower incisors comparatively narrow with respect to height of crown; axis of m3 talonid tends to be oblique in a lingual-labial direction; posterolabial lobe of P4 less developed than that of *T. s. saurophila*, but usually larger than that of other South American populations (A. L. Gardner, in litt.).

Distribution.—This taxon occurs in Central America and northwestern South America, with records from México, Belize, Guatemala, Honduras, Nicaragua, Costa Rica, Panamá, and Venezuela (north of Cordillera de Mérida). The Cordillera de Mérida of Venezuela appears to be a physiographic boundary separating South American subspecies of *T. saurophila* (Fig. 5). Locality records are listed in Appendix II.

Description.—Holotype has gray-brown dorsal pelage expressed primarily on hair tips. Basally, the hair color is paler. Dorsal pelage has white-based hairs in shoulder and neck regions and behind base of ears. White-tipped hairs form a pale stripe on top of head between ears. Ventral pelage is

much paler, with individual hairs being darker below buffy-colored hair tips; throat region has more uniformly colored hair.

The body is densely furred dorsally and ventrally, with mid-dorsal hair (12.0) longer than mid-ventral hair (5.0 mm). Shorter hairs occur on forearm for about one-third its length; ventral surface is more densely furred than dorsum. The inner (proximal) margins of ventral uropatagium and wing membranes contain short, sparse hair. Short hair also occurs on thumbs and feet.

Skull of holotype is massive with a well-defined sagittal crest. Except for a few notches along sagittal crest, skull is complete and in perfect condition. An atlas also is present.

Measurements.—External measurements of holotype are: total length, 105.0 mm; length of tail, 36.0 mm; length of hind foot, 15.0 mm; length of ear from notch, 14.0 mm; length of calcar (dry), 20.0 mm; mass, 33.0 g; length of forearm, 60.6 mm. Cranial measurements (in millimeters) of holotype are: greatest length of skull, 30.2; condylo-basal length, 25.3; zygomatic breadth, 15.0; breadth across postorbital constriction, 5.6; breadth of braincase, 11.7; mastoid breadth, 13.5; length of maxillary toothrow, 10.1; breadth across upper molars, 9.1; breadth across canines, 5.9; breadth across lower incisors, 1.6; height of crown of lower incisor, 1.5. Measurements for other specimens are presented in Table 2.

Comparisons.—Subspecific recognition of Central American *T. saurophila* is based on larger size, as exemplified by populations from Panamá and Costa Rica. For example, the largest measurement for greatest length of skull from the South American populations ($n = 75$) was 29.1 mm compared with 30.7 mm for Central American populations ($n = 42$). Comparable trends are apparent in other measurements (Table 2).

Remarks.—The name, *T. s. bakeri*, is given in recognition of contributions of Robert J. Baker to genetics and systematics

of New World leaf-nosed bats, family Phyllostomidae.

Tonatia saurophila maresi, new subspecies

Holotype.—Adult female; skin, skull, and partial postcranial skeleton; number 9774 at the Museum of Texas Tech University (TTU); from Blanchisseuse, Trinidad, Trinidad and Tobago; collected 12 July 1969 by R. J. Baker; prepared by S. L. Williams, original number 318.

Diagnosis.—*Tonatia s. maresi* is distinguished by shorter average forearm and smaller average cranial measurements (Table 2) than those of *T. s. bakeri*; breadth across lower incisors comparatively wider with respect to height of crown; axis of m3 talonid tends to be oblique in a lingual-labial direction; posterolabial lobe of P4 usually smaller than that of *T. s. bakeri* (A. L. Gardner, in litt.).

Distribution.—This taxon is known from Venezuela eastward through the Guianas, northern Brazil, and south along eastern slopes of the Andes in Colombia, Ecuador, and Perú. In Venezuela, this subspecies is separated from Central American populations in the vicinity of Cordillera de Mérida (Fig. 5). Localities are listed in Appendix II.

Description.—Holotype has dark gray dorsal pelage with white-based hairs in shoulder and neck region and behind base of ears. White-tipped hairs form a pale stripe on top of head between ears. Ventral pelage is somewhat paler and includes hairs that are white-tipped; throat region has more uniform-colored hair.

The body is densely furred with mid-dorsal hair (12.0 mm) longer than mid-ventral hair (5.5 mm). Shorter hairs grow on forearms for about one-half their length, with ventral surface being more furred than dorsal surface. Short, sparse hair occurs on inner margins of ventral uropatagium and wing membranes; short hair also occurs on thumbs and feet.

Skull of holotype is complete and in perfect condition. Specimen includes a com-

plete and articulated axial skeleton. Articulated appendicular components include clavicles, scapulae, and part of left humerus.

Measurements.—External measurements (in millimeters) of holotype are: total length, 94.0; length of tail, 19.0; length of hind foot, 13.5; length of ear from notch, 30.0; length of calcar (dry), 16.0; length of forearm, 55.0. Cranial measurements (in millimeters) of holotype are: greatest length of skull, 28.2; condylobasal length, 24.0; zygomatic breadth, 14.3; breadth across postorbital constriction, 5.3; breadth of braincase, 10.5; mastoid breadth, 12.9; length of maxillary toothrow, 9.2; breadth across upper molars, 8.3; breadth across canines, 5.6; breadth across lower incisors, 1.8; height of crown of lower incisor, 1.6. Measurements for other specimens are presented in Table 2.

Comparisons.—Members of this subspecies are smaller than those of *T. s. bakeri* (see previous account) with broader lower incisors (Genoways and Williams, 1984). Differences in color of dorsal pelage of holotypes of *T. s. maresi* and *T. s. bakeri* represent individual variation.

Remarks.—Based on habitat associations of the species and records around the delta of the Amazon River, new records throughout the Amazon Basin are expected. Bolivia separates the southwestern distributions of *T. saurophila* and *T. bidens* (Fig. 5). Anderson (1991) reported one Bolivian specimen of "*T. bidens*" that currently is maintained in Japan. The geographic proximity of the collection locality of this specimen (Chive, 12°23'S, 68°35'W) would suggest that it is *T. saurophila*. Examination of its morphological features would clarify its identity.

The name *T. s. maresi* is given in recognition of the contributions of Michael A. Mares to the systematics, ecology, and zoogeography of South American mammals.

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APPENDIX I

Description of measurements from dry specimens.—Length of forearm—distance, with the wing in a flexed position, from the anteriormost projection of the wrist joint to the posteriormost projection of the elbow; greatest length of skull—distance from the anterior face of the upper incisors to the posteriormost projection of the cranium; condylobasal length—distance from the anteriormost projection of the premaxillae to a line connecting posterior margins of the occipital condyles; zygomatic breadth—greatest distance between outer margins of zygomatic arches at right angles to the longitudinal axis of the cranium; breadth across postorbital constriction—shortest distance between the orbits at right angles to the longitudinal axis of the cranium; breadth of braincase—greatest distance of the braincase at right angles to the longitudinal axis of the cranium; mastoid breadth—greatest distance across the mastoid processes at right angles to the longitudinal axis of the cranium; length of maxillary toothrow—greatest distance from the anterior lip of the alveolus of C1 to the posterior lip of the alveolus of M3; breadth across upper molars—greatest distance between the lateral-most projections of the labial margins of the upper molars, at right angles to the longitudinal axis of the cranium; breadth across upper canines—greatest distance between the lateral-most projections of the labial margins of the upper canines, at right angles to the longitudinal axis of the cranium.

APPENDIX II

Specimens examined.—*Tonatia bidens* (63)—ARGENTINA: Jujuy: Palma Sola (3 ROM, TCWC); Palma Sola, Mina de Azucro (3 ROM); Santa Bárbara: Laguna la Brea (3 ROM, TCWC). BRAZIL: Mato Grosso: Urucum de Corumba (2 FMNH); Pernambuco: Exu, Fazenda Colonha (CM); Exu, Fazenda Gambá (6 CM); Exu, Fazenda Gritadeira (4 CM); Exu, Fazenda Manicoba (3 CM); Exu, Fazenda Pomonha (5 CM); Exu, Serrote das Lajes (28 CM). Santa Catarina: Joinville (BM); São Paulo: Iporanga, Barro da Serra, Caverna Curo Grosso (AMNH). PARAGUAY: Chaco: Orloff (FMNH). Itapúa: 2 km NNW San Rafael, Arroyo San Rafael (UMMZ). Nueva Asunción: 19 km (by road) WSW Km 588 Trans-Chaco Road (UMMZ). Paraguari: Sapacuy (BM; = Sapucaí). SOUTH AMERICA: specific locality unknown (BMNH, holotype). Other records—BRAZIL: Bahia: bank of Río São Francisco (von Spix, 1823; holotype). São Paulo: Ilha de São Sebastiao (Vieira, 1942).

Tonatia saurophila saurophila (5)—JAMAICA: St. Ann Parish: Dry Harbor (Discovery Bay), Dairy Cave (3 AMNH). St. Elizabeth Parish: Balaclava, Wallingford Cave (2 AMNH, includes holotype).

Tonatia saurophila bakeri (55)—BELIZE: Cayo: 1.6 km NW Augustine, along Río Frio River, near Big Río Frio Cave (CM); Toledo: Nimli Punit, 12.4 km NE Big Falls, Río Grande Bridge (CM); Columbia Forest Reserve, 2.2 km NNE Forestry Camp, Salamanca (CM); Columbia Forest Reserve, 2.1 km NNE Forestry Camp, Salamanca (CM). COSTA RICA: Puntarenas: Osa Peninsula, Llorona (Piedra el Arco) (USNM); Herédia, Parque Nacional Braulio Carrillo, 11 km S, 4.6 km W Puerto Lieto, 300 m (2 USNM); Palmar (Pacific) (8 AMNH); 14.5 miles N Quepos (LSUMZ). GUATEMALA: Izaabal: 25 km SSW Puerto Barrios (TCWC); El Petén: Tikal National Park (4 FMNH). HONDURAS: Atlantida: Lancetilla, 40 m (7 TCWC); 2 km SE Lancetilla, 150 m (TCWC). NICARAGUA: Rivas: 6.9 miles E San Juan del Sur (2 TTU). PANAMA: Bocas del Toro: Almirante (USNM). Canal Zone: Barro Colorado Island (4 LSUMZ; 5 TCWC; USNM); Barro Colorado Island, Barbour Creek (USNM); Barro Colorado Island, 6 miles N Gamboa (USNM); Barro Colorado Island, Gatun Lake, Lutz-Donato (USNM); Darién (USNM). Darién: 6 km SW

Cana, 1,200 m (TTU, holotype). Panamá: Cerro Azul (USNM). VENEZUELA: Falcon: 19 km NW Urama, Km 40 (5 USNM); Zulia: El Rosario, 48 km WNW Encontrados, 54 m (USNM); Río Tocuyo (AMNH). Other records—MEXICO: Chiapas: confluence of Río Chajul and Río Lacantun, 16°06'N, 90°57'W (Medellín, 1983).

Tonatia saurophila maresi (100)—BRAZIL: Pará: Belém, Mocamb (FMNH); Belém Station A, IAN (2 USNM); Belém, Utinga (USNM); Ilha do Taiuna, Río Tocantins (5 AMNH); Santarem, Río Tapajós (AMNH); Pernambuco: Exu, Fazenda Cantareno (CM); Exu, Fazenda Manicoba (2 CM). COLOMBIA: Putumayo: Estación de Bombeo Guamez, 3,000 feet (FMNH). EC-UADOR: Napo: Yasuní (USNM). FRENCH GUIANA: Cayenne: River Arataye, 30 m, 4°00'N, 52°40'W (USNM). GUYANA: Mazaruni-Potaro: 24 miles along Potaro Road from Bartica, Forest Reserve (BM); Dadanawa, Aroquoi (10 ROM); Kuitaro River area, 50 m E Dadanawa (3 ROM); head of Kamam River, Kanuku Mountains (ROM); Kartabo (2 AMNH); Nere River, Amuku Creek, Upper Essequibo (ROM). PERU: Ucayali: Río Curanja, Balta, ca. 300 m (6 LSUMZ); Lagarto, Upper Ucayali River (4 AMNH); Madre de Dios: Cerro de Pantia Colla, E slope NR Summit, ca. 4 km NNE Shintuya (FMNH); mouth of Río de Torre, S bank

of Río Tambopata (LSUMZ). SURINAME: Brokopondo: Brownsberg Nature Park, 3 km S, 20 km W Afobakka (CM); Brownsberg Nature Park, 8 km S, 2 km W Brownsberg (3 CM); 1½ km W Rudi Kappelvliegveld (CM); 3 km SW Rudi Kappelvliegveld (2 CM); Marowijne: Oelearie (CM); Nickerie: Avanavero (CM); Grassalco (4 CM); Kabalebo (CM); Saramacca: Bigi Poika (2 CM); Bitagron (= Witagron) (CM); SE side of Arrowhead Basin, Augustus Creek, Tafelberg (CM); Voltzberg (4 CM). TRINIDAD AND TOBAGO: Trinidad: Blanchisseuse (3 TTU); Caura Valley (TTU); Arena Reserve, 3 miles S, 3 miles W Cumuto (CM); La Brea (AMNH); Las Cuevas (3 TTU); Siparia (4 AMNH); specific locality unknown (AMNH). VENEZUELA: Territorio Federal Amazonas: Casiquiari Canal, Capibara, 130 m (USNM); Río Mavaca, 108 km SE Esmeralda, 140 m (2 USNM); Apure: Hato Cariben, Río Cinaruco, 60 km NE Puerto Paez, 76 m (USNM); Bolívar: Hato la Florida, 14 km S, 45 km E Calcara, 50 m (USNM); 59 km SE El Dorado, Km 74 (USNM); S El Dorado, Km 85 (2 CM); Monagas: 17 km NW Caripito (TCWC); Miranda: Birongo, 60 km E Caracas, 60 m (USNM); Sucre: 40 km NW Caripito (CM; 2 TCWC). Other records—FRENCH GUIANA: St. Laurent-du-Maroni: St. Elie (Brosset and Charles-Dominique, 1990).