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THE SYSTEMATIC STATUS OF TADARIDA BRASILIENSIS CYNOCEPHALA AND ANTILLEAN MEMBERS OF THE TADARIDA BRASILIENSIS GROUP, WITH COMMENTS ON THE GENERIC NAME RHIZOMOPS LEGENDRE.

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The close relationship of members of the *brasiliensis* group of the free-tailed bat genus *Tadarida* long has been recognized. H. Allen (1864) made neither specific nor subspecific distinctions between the named taxa of the group. Later, when he (1893) revised his monograph of North American bats, Allen included *Nyctinomus mexicanus*, *N. murinus*, and *Nycticea cynocephala* in the synonymy of *Nyctinomus brasiliensis*. Also included in *N. brasiliensis* were bats from St. Kitts Island, British West Indies, later referred to *N. antillularum* Miller. Allen noted that specimens of *N. brasiliensis* from California possibly deserved variety status.

Bangs (1898), in applying the name *Nyctinomus cynocephalus* to Austroriparian free-tails, contended that the chances of *N. brasiliensis* and *N. cynocephalus* being the same were too remote to consider. However, Miller and Rehn (1901) regarded populations in California and the southeastern United States as subspecies (*N. b. californicus* and *N. b. cynocephalus*) of *N. brasiliensis*. *Nyctinomus mohavensis* Merriam (= *T. mexicana*), which they must not have seen, was given specific rank. G. M. Allen (1908) did

not regard mainland populations of the group as warranting specific recognition, but he considered *N. antillularum* a distinct species. Later, however, Allen (1911) included in *N. brasiliensis* the subspecies *N. b. antillularum*, as well as *N. b. musculus* and *N. b. bahamensis*.

Lyon (1914) discussed the use of the name *Tadarida* in place of *Nyctinomus*, and subsequent authors have followed his opinion. Miller (1924) regarded the six named taxa of the group as separate species of *Tadarida*. Shamel (1931) recognized in the *brasiliensis* group the six species listed by Miller, included *T. murina* (omitted by Miller), and named two additional species, *T. intermedia* and *T. constanzae*. This arrangement was followed until Schwartz (1955) synonymized the nine species of Shamel on the basis that no structural differences distinguished one from any of the others, but he recognized each of the nine as subspecies of *T. brasiliensis*. Freeman (1981), in her morphometric comparison of 78 molossid species, followed Schwartz (1955) in taxonomic assignments within *T. brasiliensis*, considering *brasiliensis* to include the mainland races *mexicana* and *cynocephala*, as well as the Antillean populations.

A substantial body of evidence (Carter, 1962) led us to suspect that the taxonomic status of *T. b. cynocephala* deserved further evaluation. This study was undertaken, therefore, to examine the relationship of *T. b. cynocephala* to the species *T. brasiliensis*, with particular reference to two geographically adjacent subspecies, *T. b. mexicana* and *T. b. muscula*.

COMMENT ON *RHIZOMOPS* LEGENDRE

In his thorough odontological analysis of *Tadarida* and related genera, Legendre (1984) proposed the generic name *Rhizomops*, comprised only of *R. brasiliensis* and presumably including all currently recognized subspecies. Although his methods were in a general way phylogenetically oriented, his recognition of *Rhizomops* was based entirely on plesiomorphic characteristics (see his figure 15 for summary of pertinent character states). Therefore, we view his recognition of generic status for the *brasiliensis* group to be unsupported. It is possible, of course, that synapomorphies will be found eventually to resolve the basal fork in Legendre's figure 15, and we would point out that *Rhizomops* remains as an available name for the bats of the *brasiliensis* group should their generic status be supported appropriately. At the

present time, however, we retain the use of *Tadarida* as the generic name for the *brasiliensis* group.

METHODS

Protein Electrophoretic Analysis

Tissue homogenate of heart and kidney was prepared from individual bats following the methods of Svoboda *et al.* (1985). Specimens examined for electrophoretic variation were from the following groups: *T. b. mexicana*—Waco, Texas (14), western Texas (3), western Oklahoma (2); *T. b. cynocephala*—Florida (14), North Carolina (14), Louisiana (12); *T. b. muscula*—Cuba (20); *T. b. murina*—Jamaica (14); *T. b. antillarum*—Dominica (18). Preliminary analysis of protein electrophoretic patterns indicated a fixed allelic difference between eastern and western mainland populations based on the esterase-2 locus. Therefore, all available specimens of *T. b. cynocephala* and from Antillean populations were compared to representative specimens of *T. b. mexicana* based upon this locus. Alleles were coded numerically with the "100" allele denoting the common allele for western (*T. b. mexicana*) populations, and all other alleles designated as to their mobility relative to the "100" allele.

Morphometric Analyses

A total of 1000 specimens of *T. b. cynocephala* (375), *T. b. mexicana* (584), and *T. b. brasiliensis* (41) was examined, and a maximum of 20 different skin and skull measurements for each specimen was taken (Carter, 1962). Those measurements used in this paper are skull length (greatest length of skull from occiput to and including the incisors); zygomatic breadth (greatest transverse dimension from outside borders of zygomatic arches); forearm (greatest distance from back of elbow to anteriormost border of wrist with wing folded); and fifth metacarpal (greatest linear dimension of that bone).

Bats were aged according to four classes: 0, adult bats with no macroscopically obvious toothwear; I, with obvious toothwear but less than one-third of the upper canines worn away; II, one-third or more but less than two-thirds of the canines worn away; III, two-thirds or more of the canines worn away. Care was taken to avoid misclassifying a bat with broken canines by checking the cheekteeth for obvious toothwear. The age classes

are purely arbitrary and the time periods represented are not known. It is assumed, although without evidence other than that some bats seem relatively long-lived for small mammals (Cockrum, 1956; Hall *et al.*, 1957; Keen and Hitchcock, 1980), that each age class represents at least a three- to five-year period.

The effects of locality, sex, age class, and taxon on the observed variation of the variates were estimated with analysis of variance (ANOVA). The 0.01 level of probability (that the observations are due to randomness) was selected as the standard level of significance.

RESULTS

Protein Electrophoretic Analysis

Three alleles (100, 85, and 80) of the esterase-2 locus were observed over all *Tadarida* specimens examined. Genotypes for each specimen and allele frequencies for each population are presented in Table 1. All specimens of *T. b. mexicana* except one possessed the 100 allele in some combination. All *T. b. cynocephala* possessed the 80 allele, with two individuals from North Carolina and one from Louisiana being heterozygous with the 100 allele (100/80). All individuals from Cuba and Dominica were homozygous for the 80 allele. Another allele (85) was observed in the Jamaica and the Waco, Texas, populations. In Waco, a single specimen was homozygous for this allele (85/85) and three were heterozygotes (100/85). In contrast, half the Jamaican specimens were homozygous for the allele, with the remainder split about evenly between homozygous for 80 and heterozygotes of the two alleles.

Morphometric Analyses

Tadarida brasiliensis cynocephala can be distinguished from *T. b. mexicana* (and *T. b. brasiliensis*) based on skull length or zygomatic breadth (Tables 2 and 3). Carter (1962) discussed other aspects of morphology that serve to separate these two similar taxa, but all appear to be related to a general size factor. For additional information concerning morphometric relationships of *T. b. cynocephala* and *T. b. mexicana* populations, see Tables 4-12.

TABLE 1.—*Specimens examined, and electrophoretic mobility of the esterase-2 locus. Specimen numbers listed refer to the Texas Tech University frozen tissue (TK) catalog, except LJB numbers (donated by the Museum of Zoology, Louisiana State University). Waco specimens marked with an asterisk were taken on 3 April; all other Waco specimens were collected in winter (30 December-26 February). Specimens with only one allele listed were homozygous for that allele. Frequencies are presented as percentages for the 100, 85, and 80 alleles, respectively, for each population sample. Question mark indicates uncertainty in scoring that individual.*

<i>Tadarida brasiliensis mexicana</i>					
Waco, Texas		Western Texas		Western Oklahoma	
21826	100	26303	100	24870	100
21827	100	26304	100	24902	100
21828	100	26540	100		
21829	100/85			(100/0/0)	
21830	85(?)	(100/0/0)			
21831	100				
*26599	100/85				
*26600	100/85				
26601	100				
26602	100				
26603	100				
26604	100				
26605	100				
26606	100				
(86/14/0)					
<i>Tadarida brasiliensis cynocephala</i>					
Florida		North Carolina		Louisiana	
26635	80	21811	80	24825	80
26636	80	21812	80	24826	80
26637	80	21814	80	24827	80
26638	80	21815	100/80	24828	80
26639	80	21816	80	24829	80
26640	80	21817	80	24830	80
26641	80	21818	80	24831	80
26642	80	21819	100/80	24832	80
26643	80	21820	80	L JB 2100	80
26645	80	21821	80	L JB 2103	100/80
26646	80	21822	80	L JB 2105	80
26647	80	21823	80	L JB 2113	80
26648	80	21824	80		
26649	80	21825	80	(4/0/96)	
(0/0/100)		(7/0/93)			

TABLE 1.—*Continued.*

<i>Tadarida brasiliensis muscula</i> , Cuba					
32012 80	32065 80	32083 80			
32059 80	32066 80	32092 80			
32060 80	32067 80	32093 80			
32061 80	32068 80	32094 80			
32062 80	32069 80	32095 80			
32063 80	32070 80	32096 80			
32064 80	32071 80				
			(0/0/100)		
<i>Tadarida brasiliensis murina</i> , Jamaica					
9232 85	9241 85	9247 80			
9234 80	9242 80	9248 85/80			
9235 85	9244 85/80	9250 85			
9236 85	9245 85	26745 80			
9239 85	9246 85/80				
			(0/61/39)		
<i>Tadarida brasiliensis antillarum</i> , Dominica					
15504 80	15557 80	15563 80			
15552 80	15558 80	15564 80			
15553 80	15559 80	15565 80			
15554 80	15560 80	15566 80			
15555 80	15561 80	15567 80			
15556 80	15562 80	15568 80			
			(0/0/100)		

DISCUSSION

Carter (1962) detailed a number of reasons for considering *cynocephala* to be a species separate from *brasiliensis* and from *mexicana*, which he also regarded as specifically distinct from *brasiliensis*. The morphometric data, some of which are compared in Tables 2 and 3, indicate that significant size differences exist between *T. b. cynocephala* and *T. b. mexicana*, with *cynocephala* being larger in the two crainal variates considered. In addition to morphometric data, Carter's (1962) evidence included physiological, distributional, ecological, and behavioral attributes of the two taxa. These will not be reiterated here, other than to point out that they comprised a rather compelling body of evidence for specific recognition of *cynocephala*.

Electrophoretic evidence presented herein indicates that there is an apparent allelic difference that effectively separates *T. b. mexicana* from *T. b. cynocephala* and the Antillean populations. The three occurrences of the *mexicana* (100) esterase-2 allele in

TABLE 2.—Comparison of measurement data for skull length of *T. b. cynocephala*, *T. b. mexicana*, and *T. b. brasiliensis*.

Subspecies	Sex	N	Min.	Max.	\bar{X}	s	CV
<i>T. b. cynocephala</i>	♂	128	16.7	18.4	17.48	.307	1.75
<i>T. b. mexicana</i>	♂	173	16.2	17.7	16.94	.308	1.81
<i>T. b. brasiliensis</i>	♀♂	41	16.1	17.8	17.28	.400	2.31
Main effect	d.f.		MS		F		P
Subspecies	2		10.68		104		<.001
<i>T. b. cynocephala</i>	♀	152	16.1	18.2	17.16	.306	1.78
<i>T. b. mexicana</i>	♀	164	16.1	17.4	16.72	.274	1.63
<i>T. b. brasiliensis</i>	♀♂	41	16.1	17.8	17.28	.400	2.31
Main Effect	d.f.		MS		F		P
Subspecies	2		9.99		107		<.001

TABLE 3.—Comparison of measurement data for zygomatic breadth of *T. b. cynocephala*, *T. b. mexicana*, and *T. b. brasiliensis*.

Subspecies	Sex	N	Min.	Max.	\bar{X}	s	CV
<i>T. b. cynocephala</i>	♂	123	9.6	10.8	10.27	.211	2.05
<i>T. b. mexicana</i>	♂	162	9.3	10.4	9.78	.186	1.90
<i>T. b. brasiliensis</i>	♀♂	32	9.1	10.5	9.95	.282	2.83
Main effect	d.f.		MS		F		P
Subspecies	2		8.36		192		<.001
<i>T. b. cynocephala</i>	♀	144	9.6	10.6	10.10	.189	1.87
<i>T. b. mexicana</i>	♀	104	9.3	10.2	9.70	.159	1.64
<i>T. b. brasiliensis</i>	♀♂	32	9.1	10.5	9.95	.282	2.83
Main effect	d.f.		MS		F		P
Subspecies	2		4.64		125		<.001

specimens of *cynocephala* sampled may or may not represent genetic introgression from populations of *mexicana*. It is important also to note that the *cynocephala* (80) allele was not found either in our *mexicana* samples (Table 1), or in those of Svoboda *et al.* (1985), which included 164 specimens of *T. b. mexicana* (our 80 allele is slower than any of the three esterase-2 alleles reported in their paper).

Several lines of evidence appear to point to the specific status of *cynocephala*, perhaps with the inclusion of the Antillean populations: 1) the evidence detailed by Carter (1962), including the

TABLE 4.—*Measurement data for skull length of T. b. cynocephala.*

Locality	N	Min.	Max.	\bar{X}	$CI_{\bar{x}}$	s	CV
<i>Males</i>							
Small samples,							
Georgia-Florida	15	17.0	17.8	17.32	.177	.231	1.33
Glennville, Georgia	14	17.0	18.1	17.46	.252	.313	1.79
Butler, Alabama	11	17.2	17.8	17.49	.216	.226	1.29
Brookhaven,							
Mississippi	14	17.1	18.0	17.61	.235	.292	1.65
Palestine, Texas	11	16.7	17.7	17.24	.301	.315	1.82
Pineland, Texas	77	16.7	18.4	17.51	.093	.309	1.76
Main effect	d.f.		MS		F		P
Localities	5		0.272		3.12		.02
<i>Females</i>							
Small samples,							
Georgia-Florida	22	16.7	17.8	17.22	.196	.325	1.88
Ocheesee, Florida	24	16.8	17.6	17.21	.142	.249	1.44
Colquitt, Georgia	30	16.5	17.7	17.12	.153	.303	1.76
Butler, Alabama	18	16.9	17.6	17.20	.120	.176	1.02
Pineland, Texas	58	16.1	18.2	17.14	.123	.352	2.05
Main effect	d.f.		MS		F		P
Localities	4		0.057		0.60		> .20
Sexes	1		6.900		73.17		< .01

TABLE 5.—*Measurement data for skull length of T. b. cynocephala collected at Pineland, Texas, 13 April 1961.*

Age class	N	Min.	Max.	\bar{X}	$CI_{\bar{x}}$	s	CV
<i>Males</i>							
0	37	16.7	18.1	17.38	.138	.310	1.78
I	26	17.1	18.4	17.63	.146	.268	1.52
Main effect	d.f.		MS		F		P
Age class	1		0.940		10.90		< .01
<i>Females</i>							
0	23	16.9	18.2	17.19	.167	.285	1.65
I	20	16.1	17.6	17.00	.219	.345	2.01
Main effect	d.f.		MS		F		P
Age class	1		0.390		3.88		.11

morphometric data presented herein, concerning the differences between *cynocephala* and the other mainland taxa (particularly

TABLE 6.—*Measurement data for zygomatic breadth of T. b. cynocephala.*

Locality	N	Min.	Max.	\bar{X}	CI $_{\bar{x}}$	s	CV
<i>Males</i>							
Small samples ,							
Georgia-Florida	12	9.6	10.5	10.11	.183	.204	2.01
Glennville, Georgia	14	10.0	10.5	10.25	.122	.152	1.48
Butler, Alabama	11	10.0	10.6	10.27	.181	.190	1.85
Palestine, Texas	9	9.9	10.4	10.13	.237	.224	2.21
Pineland, Texas	77	9.7	10.8	10.31	.065	.213	2.06
Main effect	d.f.		MS		F		P
Localities	4		0.152		3.69		.01
<i>Females</i>							
Small samples,							
Georgia-Florida	17	9.7	10.6	10.13	.165	.234	2.30
Ocheesee, Florida	24	9.9	10.4	10.09	.076	.135	1.31
Colquitt, Georgia	30	9.8	10.5	10.15	.079	.157	1.54
Butler, Alabama	15	9.9	10.4	10.13	.142	.185	1.82
Pineland, Texas	58	9.6	10.5	10.04	.071	.204	2.03
Main effect	d.f.		MS		F		P
Localities	4		0.072		2.08		.15
Sexes	1		2.060		51.50		<.01

TABLE 7.—*Measurement data for forearm of T. b. cynocephala.*

Locality	Sex	N	Min.	Max.	\bar{X}	CI $_{\bar{x}}$	s	CV
Merrits Island, Florida	♀♂	32	40.4	43.8	41.62	.401	.827	1.98
Panacea, Florida	♀♂	28	40.2	43.2	41.86	.526	1.005	2.40
Ocheesee, Florida	♀♂	48	40.2	43.8	42.22	.319	.826	1.95
Glennville, Georgia	♀♂	19	40.2	43.7	42.01	.627	.952	2.26
Colquitt, Georgia	♀♂	32	40.4	44.3	41.97	.469	.969	2.30
Butler, Alabama	♀♂	29	41.1	44.1	42.34	.453	.885	2.09
Brookhaven, Mississippi	♀♂	22	40.6	43.4	41.84	.484	.802	1.91
Palestine, Texas	♂	12	41.0	44.2	42.92	.919	1.025	2.38
Pineland, Texas	♂	76	40.0	44.8	42.30	.293	.956	2.26
Pineland, Texas	♀	64	39.5	43.9	42.17	.327	.982	2.32
Main effect	d.f.		MS		F		P	
Localities	9		2.800		3.25		<.01	
Sexes (Pineland)	1		0.610		0.650		>.20	

mexicana); 2) the wide geographic separation of the southernmost Antillean populations (St. Lucia—Jones and Phillips, 1970;

TABLE 8.—*Measurement data for fifth metacarpal of T. b. cynocephala. Males and females present in all samples.*

Locality	N	Min.	Max.	\bar{X}	CI $_{\bar{x}}$	s	CV
Merrits Island, Florida	45	23.0	25.4	24.38	.250	.624	2.55
Panacea, Florida	28	23.8	26.0	24.86	.296	.566	2.27
Ocheegee, Florida	48	23.1	27.2	25.05	.314	.814	3.24
Glennville, Georgia	19	23.6	26.4	24.94	.515	.781	3.13
Colquitt, Georgia	32	22.4	26.8	24.52	.500	1.034	4.21
Butler, Alabama	29	23.2	26.6	24.79	.470	.916	3.69
Brookhaven, Mississippi	22	23.0	26.4	24.57	.481	.800	3.25
Palestine, Texas	12	23.6	27.5	25.11	.913	1.019	4.05
Pineland, Texas	140	22.4	26.5	24.82	.163	.748	3.01
Main effect	d.f.	MS		F		P	
Localities	8	2.000		3.22		< .01	
Sexes (Pineland)	1	0.560		1.00		> .20	

TABLE 9.—*Geographic distribution of the sample means for the forearm and fifth metacarpal of T. b. cynocephala. Grand mean for forearm is 42.12; for fifth metacarpal, 24.77.*

Forearm		Fifth Metacarpal	
\bar{X}	Locality (Year)	\bar{X}	Locality (Year)
41.62	Merrits Island, Florida (1923)	24.38	Merrits Island, Florida (1923)
41.84	Brookhaven, Mississippi (1937)	24.32	Colquitt, Georgia (1959)
41.86	Panacea, Florida (1958)	24.57	Brookhaven, Mississippi (1937)
41.97	Colquitt, Georgia (1959)	24.79	Butler, Alabama (1959)
42.01	Glennville, Georgia (1959)	24.82	Pineland, Texas (♂♂ + ♀♀) (1958-61)
42.17	Pineland, Texas (♀♀) (1958-61)	24.86	Panacea, Florida (1958)
42.22	Ocheegee, Florida (1959)	24.94	Glennville, Georgia (1959)
42.30	Pineland, Texas (♂♂) (1958-61)	25.05	Ocheegee, Florida (1959)
42.34	Butler, Alabama (1959)	25.11	Palestine, Texas (1959)
42.92	Palestine, Texas (1959)		

Varona, 1974; Baker and Genoways, 1978; Jones, 1990) from those nearest on the South American mainland (western Venezuela—Koopman, 1982); and 3) the populational differences in the esterase-2 protein locus, presented herein. Based on this evidence, we think it likely that *T. b. cynocephala* and the Antillean populations are isolated reproductively from

TABLE 10.—*Measurement data for skull length of T. b. mexicana.*

Locality	N	Min.	Max.	\bar{X}	$CI_{\bar{x}}$	s	CV
<i>Males</i>							
Nogales, Arizona	14	16.5	17.4	16.96	.247	.307	1.81
Arizona	31	16.5	17.4	16.94	.132	.268	1.58
Grimes Co., Texas	9	16.4	17.7	17.23	.419	.375	2.18
Durango, México	21	16.4	17.6	17.06	.196	.317	1.86
Sinaloa, México	26	16.2	17.5	16.86	.160	.294	1.74
Michoacán, México	19	16.5	17.4	16.97	.177	.268	1.58
Chiapas, México	42	16.3	17.5	16.89	.135	.327	1.94
Chimaltínago, Guatemala	11	16.5	17.2	16.81	.202	.212	1.26
Main effect	d.f.		MS		F		P
Localities	7		0.224		2.49		.035
<i>Females</i>							
Cochise Co., Arizona	9	16.5	17.2	16.85	.265	.237	1.41
Pima Co., Arizona	23	16.2	17.0	16.62	.130	.222	1.34
Arizona	33	16.2	17.2	16.69	.122	.254	1.52
Grimes Co., Texas	9	16.3	17.4	16.87	.479	.430	2.55
Durango, México	26	16.2	17.4	16.75	.166	.304	1.81
Sinaloa, México	22	16.1	17.1	16.59	.157	.261	1.57
Michoacán, México	23	16.2	17.2	16.76	.161	.275	1.64
Chiapas, México	19	16.4	17.2	16.77	.133	.202	1.20
Main effect	d.f.		MS		F		P
Localities	7		0.160		2.23		.06
Sexes	1		4.260		49.71		<.01

other taxa of *T. brasiliensis*. Additionally, we note the work of previous authors (particularly Shamel, 1931) who pointed out that considerable external and morphometric differences serve to distinguish *T. b. cynocephala* from Antillean populations.

Notwithstanding these conclusions, we do not believe that sufficient evidence is yet available concerning the species limits of *cynocephala* with respect to either the adjacent mainland or insular populations. Resolution of this issue is critical not only to our understanding of the evolution and biogeography of the *T. brasiliensis* group, but also to the nomenclature. Assuming that *cynocephala* is specifically distinct from *mexicana*, then the name *brasiliensis* probably would not be applicable to the *cynocephala* bats. If these prove also to be specifically distinct from Antillean bats, then the name *cynocephala* Le Conte, 1831, is certainly applicable at the specific level. If, on the other hand, *cynocephala*

TABLE 11.—*Measurement data for zygomatic breadth of T. b. mexicana.*

Locality	N	Min.	Max.	\bar{X}	CI _{\bar{x}}	s	CV
<i>Males</i>							
Sta. Cruz Co., Arizona	13	9.5	10.1	9.71	.152	.180	1.85
Arizona	31	9.4	10.1	9.75	.094	.190	1.95
Grimes Co., Texas	8	9.6	10.4	9.92	.317	.256	2.58
Durango, México	21	9.5	10.3	9.87	.131	.211	2.14
Sinaloa, México	24	9.3	10.0	9.75	.102	.179	1.84
Michoacán, México	17	9.6	10.1	9.80	.093	.132	1.35
Chiapas, México	37	9.5	10.2	9.78	.072	.161	1.65
Guatemala	11	9.5	10.0	9.74	.183	.192	1.97
Main effect	d.f.		MS		F		P
Localities	7		0.067		2.00		.10
<i>Females</i>							
Pima Co., Arizona	17	9.3	9.9	9.68	.108	.152	1.57
Grimes Co., Texas	7	9.4	10.1	9.75	.352	.251	2.57
Durango, México	25	9.3	10.2	9.69	.093	.167	1.72
Sinaloa, México	17	9.4	9.9	9.65	.088	.125	1.30
Michoacán, México	21	9.3	10.0	9.74	.094	.151	1.55
Chiapas, México	17	9.4	10.0	9.71	.109	.155	1.60
Main effect	d.f.		MS		F		P
Localities	5		0.020		0.775		> .20
Sexes	1		0.400		12.78		< .01

populations are conspecific with those of the Greater Antilles, the name *murina* Gray, 1827, would have priority.

An alternate possibility to consider is that bats referred to *cynocephala* are specifically distinct from adjacent *mexicana* populations but not from those west coast populations of *mexicana* that are nonmigratory. These, and all nonmigratory populations in western North America, Central America, and South America might be conspecific, in which case the specific name *brasiliensis* would apply to the *cynocephala* bats but not to migratory populations of *mexicana*. Because of these diverse and unresolved issues concerning the affinities of *cynocephala*, in the interest of nomenclatorial stability we follow current taxonomic opinion (Wilkins, 1989) until clearer evidence is available. The relevant synonymy and other taxonomic and biological information concerning *Tadarida brasiliensis cynocephala* are presented here.

TABLE 12.—*Measurement data for forearm of T. b. mexicana.*

Locality	Sex	N	Min.	Max.	\bar{X}	$CI_{\bar{x}}$	s	CV
Frio Cave, Texas	♀♂	42	40.7	45.8	42.81	.465	1.114	2.60
La Boca Cave, Nuevo León, México	♀♂	55	40.8	45.4	42.95	.342	.949	2.21
España Cave, Durango, México	♀♂	98	41.0	45.9	43.03	.259	.975	2.26
España Cave, Durango, México	♀♂	35	41.0	44.5	42.56	.426	.926	2.18
Chinacaterra Cave, Sinaloa, México	♀♂	82	40.4	44.6	42.71	.314	1.077	2.52
Calaya, Guanajuato, México	♂	15	40.8	44.8	42.87	.789	1.025	2.39
Janitzio, Michoacán, México	♀♂	48	40.6	45.6	43.07	.389	1.000	2.32
Jalisco, México	♀♂	30	40.2	44.2	42.41	.546	1.086	2.56
Zapaluta Cave, Chiapas, México	♂	51	40.7	45.5	42.94	.129	.346	0.80
Zapaluta Cave, Chiapas, México	♀	128	38.7	45.2	42.84	.187	.812	1.90
Main effect	d.f.		MS		F		P	
Localities	9		1.852		2.118		.04	

Tadarida brasiliensis cynocephala (Le Conte)

Nyct[icea] cynocephala Le Conte, in McMurtrie's Cuvier, 1831, Animal kingdom, 1:432 (type locality—probably near Riceboro, Liberty Co., Georgia; type not designated).

Molossus cynocephalus, Cooper, 1837, Ann. Lyceum Nat. Hist. New York, 4:65, pl. 3, figs. 1 and 2.

Molossus fuliginosus Cooper, 1837, Ann. Lyceum Nat. Hist. New York, 4:67, pl. 3, figs. 3 and 4 (type locality—Milledgeville, Georgia; type not known to be in existence). One specimen was sent to the Lyceum of Natural History; it differed from *M. cynocephalus* in having four rather than six lower incisors and in having smooth rather than crimped ears.

Rhinopoma carolinense, Le Conte (not Geoffroy St.-Hilaire), 1855, Proc. Acad. Nat. Sci. Philadelphia, 7:437-438. Le Conte's citation of Geoffroy (1829, Dict. de Sciences Naturelles, p. 45) was an error, but Le Conte believed that this bat was from North America and had priority—his source of reference may have been Gundlach (1840, Arch. Naturgeschichte, p. 358). Tomes (1861, Proc. Zool. Soc. London, pp. 68-69) examined the type in the Paris Museum and discovered that an accidental exchange of labels had occurred between a small African molossid and a *Lasiurus borealis* from North America.

Nyctinomus nasutus, Tomes, 1861, Proc. Zool. Soc. London, pp. 68-69 (part). Tomes (not H. Allen, 1864, Smiths. Misc. Coll., 165:7) was the first to use this name combination; it was based on the belief that *N. cynocephala* Le Conte was a synonym of *Molossus nasutus* Spix.

Nyctinomus brasiliensis, H. Allen, 1893 (not True, 1884), Bull. U. S. Nat. Mus., 43:163-171 (part). True (1884, Proc. U. S. Nat. Mus., 7:603) stated that the distribution of *N. brasiliensis* is Kansas and California to Chile and thereby excluded *T. cynocephala*.

Nyctinomus cynocephalus, Bangs, 1898, Proc. Boston Soc. Nat. Hist., 28:218.

Tadarida cynocephala, Miller, 1924, Bull. U. S. Nat. Mus., 128:85.

Tadarida brasiliensis cynocephala, Schwartz, 1955, J. Mamm., 36:106-109.

Type Locality.—Probably the Le Conte plantation, near Riceboro, Liberty Co., Georgia. No type was designated but what appears to be an original specimen (USNM 4742) collected by J. E. Le Conte is deposited in the United States National Museum of Natural History (Poole and Schantz, 1942).

Geographic Distribution.—From Harnett County, North Carolina (Lee and Marsh, 1978), south along the Atlantic coast through Florida at least as far south as Miami, west through Georgia, Alabama, Mississippi, and Louisiana to eastern Texas (Spenrath and LaVal, 1974), and north and west as far as Conway and Hot Springs, Arkansas (Saugey *et al.*, 1988). Additional isolated records have been reported from Ohio (Smith and Goodpaster, 1960; Mills, 1971) and Kentucky (Barbour and Davis, 1974).

Diagnosis.—*T. b. cynocephala* is similar in size and perhaps in habits to *T. b. brasiliensis* (perhaps only in part), but it averages larger than *T. b. mexicana* and *T. b. muscula* in many variates (Shamel, 1931). Series of specimens can be determined on the basis of skull length and zygomatic breadth (Tables 2 and 3; see also Tables 4, 6, 10, and 11). It is a sedentary, colonial species that utilizes buildings and hollow trees as diurnal roosts, and may be inactive at times, or even hibernate, during the winter.

Variation.—Sexual dimorphism occurs with respect to the cranial variates analyzed. The skulls of males average larger than those of females and the differences between the means are significant (Tables 4 and 6). The forearm and fifth metacarpal evidently are not sexually dimorphic elements (Tables 7 and 8).

Individual variation is low for all variates tested. The length of the fifth metacarpal is the most variable, but it is still less variable than is normal for linear dimensions of anatomical elements of mammals (Simpson *et al.*, 1961:91).

A large sample of males taken at Pineland, Texas, in April 1961 contains two age classes of adults. The younger males (class 0) average smaller in skull length than the older individuals (class I), and the means are significantly different (Table 5). Such a difference between age classes of females from Pineland is not

demonstrated. Because most samples (representing localities) were not large enough to allow a segregation of age classes, the effect of locality may be confounded with an effect of age class.

Locality has no significant effect on differences between sample means of skull length and zygomatic breadth (Tables 4 and 6), although for both characters males show a nearly significant effect. For length of the forearm and the fifth metacarpal, locality has a significant effect (Tables 7 and 8). Neither the array for mean lengths of the forearm nor that for means of the fifth metacarpal is correlated with the geographic position of localities. Further, the two arrays do not correspond closely to each other with regard to locality. The locality effect does not seem to constitute a geographic cline; rather, the observed geographic variation seems to be only of a random nature.

Biogeography and Evolutionary History.—*T. b. cynocephala* occasionally is found roosting in hollow trees (Carter, 1962), and it is likely that this species was strictly tree-dwelling before buildings became available. The shift from trees to man-made structures as roosting sites obviously was not a difficult transition, because the bats now are found most commonly in buildings. The northern distribution of the species probably is limited by unfavorable winter conditions. Inasmuch as *T. b. cynocephala* overwinters in unheated buildings or in hollow trees, neither of which would be well protected against severely cold weather over a prolonged period of time, the subspecies probably is restricted to the southeastern United States where winters are relatively mild and where subfreezing conditions seldom last for more than a few days. The occurrence of populations as far north as North Carolina and Arkansas and as far west as eastern Texas may represent a post-Pleistocene expansion of the late Pleistocene distribution.

The western limit of this bat's geographic distribution generally conforms with the western limit of the pine-hardwood forest region of the southeastern United States. It is in this region that a seasonal overlap may occur between *T. b. cynocephala* and *T. b. mexicana* (Carter, 1962; Spenrath and LaVal, 1974; Glass, 1982). Although we cannot completely exclude the possibility of gene flow between *cynocephala* and *mexicana*, we emphasize that at most it appears to be minimal and unidirectional. Of the 40 specimens of *cynocephala* that we examined electrophoretically, the 100 allele was found three times, each time as a heterozygote.

Of the 19 *mexicana* that we examined and the 164 specimens examined by Svoboda *et al.* (1985), none possessed the 80 allele. Carter (1962) and Spenrath and LaVal (1974) pointed out that the populations most critical to evaluating the possibility of gene flow between these two taxa are those found in, and southeast of, Brazos County, Texas. Certainly, intensive collecting and analysis of specimens from eastern Texas and western Louisiana will be needed to resolve this question.

Regardless of that outcome, the problem remains concerning the relationship of *cynocephala* to the various populations in the Greater and Lesser Antilles. Each of the three island populations we sampled (from Cuba, Jamaica, and Dominica) shared the 80 allele with *cynocephala*, and in fact those from Cuba and Dominica appear to be monomorphic for that allele. Whether these populations are conspecific with *cynocephala* must be ascertained based on other evidence, but the important point is that the 80 allele appears to be a synapomorphy uniting *cynocephala* and the Antillean bats. The question of the origin of these bats is probably quite germane to the more general questions of Antillean zoogeography. Generally it is assumed that three possible invasion routes have been available for volant animals to colonize the Antilles: 1) from North America, through Florida; 2) from Central America, through the Yucatán Peninsula; and 3) from South America, through Trinidad. Although *T. brasiliensis* does not currently occupy the Yucatán Peninsula or Venezuela except in the far west, it is possible that it did occur in those areas at times when colonization took place. Clearly, the presence of the 80 allele in populations from México south of the Isthmus of Tehuantepec, from Central America, or from northern South America, would provide insight into the zoogeographic history of these bats.

If in fact *cynocephala* is found to have originated from Antillean populations, the area of contact in eastern Texas would be a zone of secondary contact, and, therefore, would be especially important to evaluate. If genetic introgression is occurring there, and is in fact unidirectional, this provides an excellent natural situation in which to evaluate genetic mechanisms involved in speciation events (Baker *et al.*, 1989). If no gene flow is found to occur in the area of sympatry or parapatry, pre- and postmating isolating mechanisms may be evaluated in these populations.

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