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ELECTROPHORETIC STUDIES OF RELATIONSHIPS OF SIX SPECIES OF ARTIBEUS (CHIROPTERA: PHYLLOSTOMIDAE)

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The present work was initiated to investigate further the preliminary electrophoretic findings of Straney *et al.* (1979) and Straney (1981) who suggested that the genus *Artibeus* is an artificial assemblage of species representing several evolutionary lineages within the subfamily Stenodermatinae. Specifically, we examined the phenetic and cladistic relationships among four species of small *Artibeus* (*A. cinereus*, *A. toltecus*, *A. phaeotis*, and *A. watsoni*) as compared to single individuals of the large species (*A. jamaicensis* and *A. concolor*) as indicated by protein electrophoresis. Specific questions addressed were as follows: What are the inter- and intraspecific relationships of these four small species? Did the smaller species share a common ancestry after divergence from the lineages of the larger *Artibeus jamaicensis* and *A. concolor*? Is the genus *Artibeus* a composite taxon resulting from combining species that have retained the exophenotypically primitive condition, as suggested by the studies of Straney *et al.* (1979) and Straney (1981)? The relationship between the small *Artibeus* and other congeneric species (*A. jamaicensis* and *A. concolor*) relative to representatives of *Chiroderma*, *Uroderma* and *Vampyrops* will be examined in an effort to determine the primitive condition.

METHODS AND MATERIALS

Bats were collected with mistnets from natural populations. Immediately after sacrifice, liver, kidney, and heart samples were

removed and frozen in liquid nitrogen. Methods for tissue preparation, starch gel electrophoresis, and enzyme designations were similar to those of Selander *et al.* (1971) as modified by Greenbaum and Baker (1976). Twenty-two isozymes (presumptive loci) consisting of enzymatic and nonenzymatic proteins were assayed. Lactate dehydrogenase -1 and -2 (Ldh-1, 2), Malate dehydrogenase -1,2 (Mdh-1,2), Isocitrate dehydrogenase -1,2 (Idh-1,2), Lactate dehydrogenase -1,2 (Ldh-1,2), Phosphoglucomutase -1,2 (Pgm-1,2), Hemoglobin (Hb), Indophenol oxidase -1,2 (Ipo-1,2), Glutamate oxalate transaminase -1,2 (Got-1,2), and Mannose-6-phosphate isomerase (Mpi) were resolved using a triscitrate pH 6.7 continuous buffer system. Albumin (Alb), Alcohol dehydrogenase (Adh), 6-Phosphogluconate dehydrogenase (6-Pgd), Phosphoglucose isomerase -1,2 (Pgi-1,2), and Peptidase -1,2,3 (Pep-1,2,3) were resolved using a triscitrate pH 8.0 continuous buffer system. The substrate used for resolving Pep-2 was the dipeptide Glycyl-L-leucine and for Pep-1 and -3, tripeptide Leucyl Glycyl glycine. Esterases were examined, but we were unable to score them confidently because of the high degree of variability among species and populations. To verify results, all individuals were electrophoresised at least twice for each system, and subsequent scoring was blind relative to previous scoring. This type of testing of results revealed consistent scoring.

To assess primitive and derived character states of the isozymes, *Artibeus jamaicensis*, *A. concolor*, *Uroderma bilobatum*, *Chiroderma villosum*, and *Vampyrops brachycephalus* were used as outgroups for *Artibeus cinereus*, *A. phaeotis*, *A. toltecus*, and *A. watsoni*. Plesiomorphic states were assigned on the basis of shared allozymes between one or more outgroups and one or more species within the group examined. After determining the primitive condition, we resolved autapomorphic and synapomorphic character states. A cladogram was then drawn from a locus by locus analysis (Patton *et al.*, 1981). Presumed synonomous isozymes and allozymes were determined using side-by-side comparisons.

Further analysis of the electrophoretic data was done using the Fitch and Margoliash (1967) method to construct phylogenetic trees from Rogers' distance values, and a phenogram based on the UPGMA option (Rohlf and Kishpaugh, 1974) was generated using Rogers' similarity values (Rogers, 1972).

Presumed loci are listed numerically with "1" indicating the most anodally migrating isozyme; more cathodal loci are given respectively larger numbers. Particular allozymes are designated

such that "a" represents the fastest migrating band and "b," "c," etc., indicate respectively slower migrating bands.

Specimens examined—Artibeus cinereus: Population 1—Suriname, Nickerie, Kabalebo, 1♂; Suriname, Nickerie, Sipaliwini, 3♀♀, 2♂♂; Population 2—Grenada, St. George, 0.5 km. E Vendome, 1♂; Population 3—Venezuela, Bolívar, 8 km. S, 5 km. E El Manteco, 1♂; Venezuela, Bolívar, 18 km. E El Manteco, 1♀; Venezuela, Bolívar, 28 km. E El Palmar, 1♀; Population 4—Venezuela, Mérida, Mérida, near Hotel Río Prado, 2♀♀, 1♂; Population 5—Venezuela, Barinas, 8 km. by road SW Santa Barbara, 1♂; Populations 6 and 7—Suriname, Para, Zanderij, 4♀♀, 2♂♂. *Artibeus watsoni*: Population 1—Nicaragua, Zelaya, 3 km. NW Rama, 3♀♀, 7♂♂, Nicaragua, Zelaya, 4.5 km. NW Rama, 1♂. *Artibeus toltecus*: Population 1—Costa Rica, Puntarenas, 2.1 mi. S, 1.1 mi. E San Vito, Las Cruces Tropical Botanical Gardens, 1♂; Population 2—México, Sinaloa, 3 mi. E Rosario, 1♂; México, Chiapas, 23.6 mi. N Huixtla, 1♀. *Artibeus phaoetis*: Population 1—México, Sinaloa, 3 km. E Rosario, 1♂; Population 2—México, Nayarit, 0.4 mi. E of Hwy 15 to Acoponeta, 1♀, 1♂; Population 3—México, Guerrero, 24.1 mi. N Río La Union on Hwy 200, 4♀♀, 3♂♂; Nicaragua, Léon, 2.1 mi. SSE Léon on Nic 12, 2♀♀, 3♂♂; Population 4—México, Chiapas, 23.6 mi. N Huixtla, 1♀, 4♂♂; Population 5—Nicaragua, Zelaya, 4.5 km. NW Rama, 2♀♀, 3♂♂. *Artibeus concolor*: Suriname, Para, Zanderij, 1♂. *Artibeus jamaicensis*: Suriname, Commewijne, Niewuwe Grand Plantation, 1♂. *Chiroderma villosum:* Bolivia, Dept. La Pat, 1 mi. W Puerto Linares, 1♂. *Uroderma bilobatum*: Suriname, Brokopondo, Brownsberg Nature Park, 2 km. S Brownsberg, 1♀. *Vampyrops brachycephalus*: Venezuela, Monagas, Carapito, 1♀. All specimens from Suriname and Venezuela are housed in the Carnegie Museum of Natural History. Specimens from near Huixtla and Rama are deposited in either The Museum, Texas Tech University, or the Texas Cooperative Wildlife Collection, Texas A&M University; the remaining specimens are in The Museum, Texas Tech University.

Results

Of the 22 isozymes examined, only one (Mdh-1) was monomorphic for all individuals. The remaining 21 variable loci, or allozymes, and their frequencies are listed in Table 1. From these data, the primitive state of each isozyme was determined using *Artibeus jamaicensis*, *A. concolor*, *Uroderma bilobatum*, *Vampyrops brachycephalus*, and *Chiroderma villosum* as outgroups. Primitive states were found for all loci except Pep-3. Cladistic analysis of the derived character states of each isozyme resulted in the cladogram depicted in Fig. 1, which shows *Artibeus cinereus*, *A. watsoni*, *A. toltecus*, and *A. phaeotis* tied together by three polymorphic synapomorphies [Mdh-2(a), Pep-1(c), and Pep-2(a)]. Interspecific relationships within the small *Artibeus* could not be determined because of either reversals or convergence of character states in Alb(d) and Hb(a). In Fig. 1, the solid line ties together *A. watsoni* and *A. toltecus*, and the broken line ties together *A. watsoni* and *A. phaeotis*. *Artibeus cinereus* has at least twice as many

TABLE 1.—*Electrophoretic data for species of* Artibeus *and outgroups. See* Methods and Materials *section for explanation of isozyme and allozyme designations. If a locus is polymorphic for a given population, the allozyme frequencies are given in parentheses.*

	N	Mdh-2	Idh-1	Idh-2	Ldh-1	Ldh-2	Pgi-1	Pgi-2	Pgm-1	Pgm-2	Mpi	Pep-1	Pep-2	Pep-3	6-Pgdh	Alb	Hb	Got-1	Got-2	Adh	Ipo-1	Ipo-2
Artibeus cinereus																						
1	6	a(.17) b(.83)	b	b	a	a	b	b	b	b	b(.17) c(.83)	c(.67) d(.33)	b	c	b	c	c	b	c	c	a	a
2	1	b	b	b	a	a	b	b	b	b	b	c	b	c	b	c	c	b	c	c	a	a
3	3	a(.67) b(.33)	a(.33) b(.67)	a(.67) b(.33)	a	a	b	b	b	b	b(.67) c(.33)	b(.33) c(.33) d(.33)	b(.67) d(.33)	c	b	c(.67) d(.33)	c	b	c	c	a(.33) b(.67)	a
4	3	b	b	b	a	a	b	b	b	b	b(.17) c(.83)	d	a(.17) b(.83)	c	b	d	c	b	c	c	a	a
5	1	b	b	b	a	a	c	b	b	b	b(.50) c(.50)	d	b	c	b	d	d	b	c	c	a	a
6	3	b	a(.17) b(.83)	a	a	a	b	b	b	b	b(.17) c(.83)	d	a(.17) b(.83)	c	b(.67) c(.33)	d(.17) e(.67) f(.17)	b(.33) c(.33) d(.33)	b	c	c	a	a
7	3	a(.67) b(.33)	b	a(.67) b(.33)	a	a	b	b	b	b	b(.67) c(.33)	d	b	c	b	c	c(.67) d(.33)	b	c	c	a(.67) b(.33)	a
Artibeus watsoni																						
1	12	a(.73) b(.27)	b	b	a	a	a	b	b	b	c	c	a(.04) b(.94)	c	b	c	a(.18) b(.82)	b	c	c	a	a
Artibeus toltecus																						
1	1	a	b	b	a	a	b	b	b	b	c	c	a(.50) b(.50)	c	b	b	a	b	c	b	a	a
2	3	a	b	b	a	a	b	a(.33) b(.67)	b	b	c	c	a(.17) b(.83)	c	b	b	a	b	c	b	a	a

TABLE 1.—*Continued.*

Artibeus phaeotis																					
1	1	a	b	b	a	a	b	b	a	b	c	c	b	c	b	d	d	b	c	c	b	a
2	2	a	b	b	a	a	b	b	a	b	a(.25) b(.50) c(.25)	c	b	c	b	d	d	b	c	c	b	a
3	7	a	a(.21) b(.79)	b	a	a	b	b	a	b	a(.07) b(.64) c(.29)	c	a(.07) b(.93)	c	b	d	d	b	c	c	b	a
4	5	a	b(.90) c(.10)	b	a	a	b	b	a	b	b(.90) c(.10)	c	a(.10) b(.90)	c	b	d	d	b	c	c	a(.40) b(.60)	a
5	8	a	a(.13) b(.74) c(.13)	b	a	a	b	b	a	b	b(.25) c(.69) d(.06)	c	b	c	b	c(.13) d(.87)	d	b	c	c	a(.62) b(.38)	a
Artibeus concolor	1	b	b	b	a	a	b	b	b	a	b	a	b	a	a	e	b	a	c	e	a	c
Artibeus jamaicensis	1	b	a	b	a	a	b	b	b	c	b(.50) c(.50)	b	b	a	b	d(.50) e(.50)	c	a	a	c	b	a
Vampyrops brachycephalus	1	b	c	b	a	a	d	b	a	b	b(.50) c(.50)	c	c	b	b	d	c	b	c	b	a	a
Chiroderma villosum	1	b	b	c	b	a	b	b	b	c	c	a	f	b	b	a(.50) b(.50)	d	a	c	a	b	b
Uroderma bilobatum	1	b	b	c	a	b	b	b	a	c	d	a	e	b	b	a	d	b	b	d	b	a

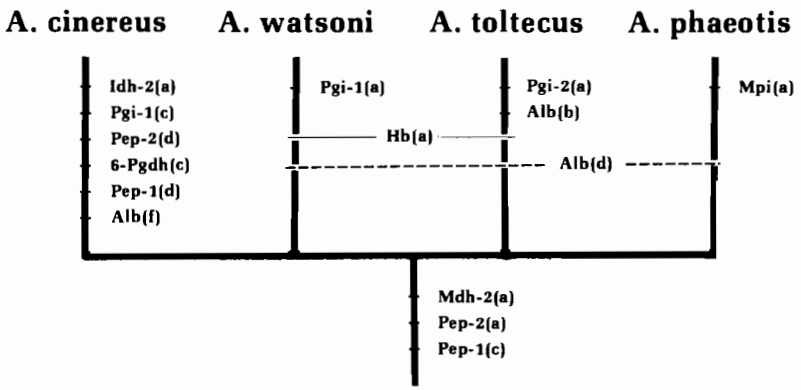

FIG. 1.—A cladogram based on shared derived electrophoretic characters of the small-sized species of *Artibeus*.

unique derived allozymes (6) as any of the other three small species of *Artibeus* examined. However, only *A. watsoni* is characterized by a fixed difference [Pgi-1(a)]. Indeed, the lack of fixed differences in the small species of *Artibeus* is very conspicuous.

In Table 2, polymorphism values, heterozygosity values, number of specimens examined, and number of fixed differences distinguishing a species from its congeners are presented along with results from other studies of species of phyllostomid bats. All calculations exclude values derived from esterases (Straney, 1981).

Clustering analysis based on Rogers' similarity values (Table 3) resulted in a distinct group representing the four species of small *Artibeus* examined in this study. The outgroups, each of which was represented by only a single individual, were significantly separate from the smaller species of *Artibeus* studied. The cophenetic correlation coefficient was 0.924. The maximum distance among the small *Artibeus* was 0.05 and the minimum distance to their nearest neighbor was 0.16 (Fig. 2).

Phylogenetic analysis using the Fitch and Margoliash method (1967) and Rogers' distance value (Rogers, 1972) resulted in two phylogenetic trees having the lowest F value (Prager and Wilson, 1978) and positive branch links (Fig. 3). The relationships among the small *Artibeus* were consistent in both phylogenetic trees. Only the position of *Artibeus concolor* and *A. jamaicensis* varied.

DISCUSSION

Perhaps the most startling aspect of the *Artibeus* data set is the low number of fixed allozymic differences that characterize *Arti-*

TABLE 2.—*Polymorphism, heterozygosity, fixed difference values, and references for various species within the family Phyllostomidae. The asterisk (•) denotes fixed differences relative to the genus* Artibeus. *All values presented exclude esterase variation.*

Species	Number examined	Polymorphism P (%)	Heterozygosity H	No. of fixed differences	Reference
Tonatia silvicola	6	16		3	Arnold, 1981
T. bidens	5	16		11	" "
T. carrikeri	1	5		4	" "
T. brasiliense	1	0		1	" "
T. schultzi	1	0		5	" "
T. nicaraguae	1	5		4	" "
T. venezuelae	1	10		7	" "
Micronycteris megalotis	3	16		4	" "
M. daviesi	1	0		3	" "
M. nicefori	6	30		5	" "
M. sylvestris	2	16		3	" "
M. minuta	5	40		10	" "
M. hirsuta	3	20		2	" "
M. schmidtorum	1	0		1	" "
M. brachyotis	1	0		6	" "
Monophyllus redmani	25	17		3	Baker et al., 1981
M. plethodon	10	8		3	" "
Macrotus waterhousii	118	10	.026	5	Greenbaum et al., 1976
M. californicus	100	14	.033	5	" "
Carollia perspicillata	57	24	.037		Straney et al., 1979
Anoura geoffroyi	30	17	.016		" "
Glossophaga soricina	19	6	.018		" "
Artibeus jamaicensis	48	24	.080		" "
A. jamaicensis	1	9	.090	1	This paper
A. concolor	1	0	.000	4	" "
A. cinereus	20	45	.023	0	" "
A. watsoni	12	14	.003	1	" "
A. toltecus	3	14	.030	0	" "
A. phaeotis	23	23	.035	0	" "
Vampyrops brachycephalus	1	5	.045	2•	" "
Chiroderma villosum	1	5	.045	5•	" "
Uroderma bilobatum	1	0	.000	4•	" "

beus cinereus, A. watsoni, A. toltecus, and *A. phaeotis*. Of these four species, only *A. watsoni* has a fixed unique allele [Pgi-1(a)], despite polymorphism levels that equal or exceed those of other phyllostomid species (Straney *et al.*, 1979; Greenbaum and Baker, 1976; calculated from Arnold, 1981). Except for *A. watsoni*, heterozygosity levels are only slightly less then the averages of other phyllostomid species ($P = 0.14$, $\bar{H} = 0.032$, Straney *et al.*, 1979). In comparable data sets from the same family, fixed differences among seven species of *Tonatia* averaged five (of 20 loci) per species. Among eight species of *Micronycteris*, fixed differences averaged 4.25 (of 21 loci) per species (Arnold, 1981), and in two sibling species of *Monophyllus* there were three (of 12 loci) (Baker *et al.*, 1981). The average number of fixed differences among *Artibeus cinereus, A. watsoni, A. toltecus,* and *A. phaeotis* was 0.25 (of

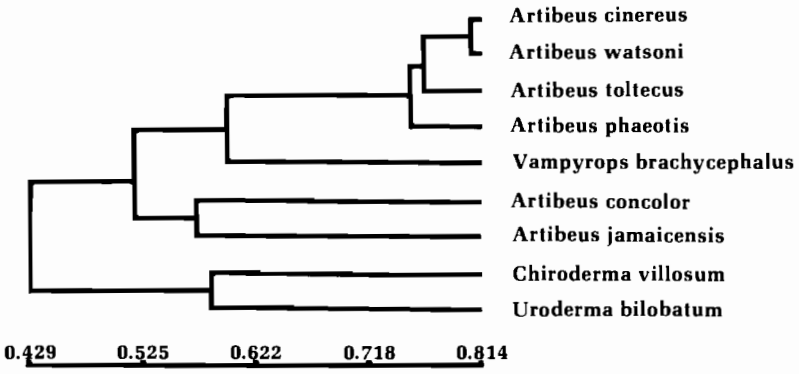

FIG. 2.—A phenogram of *Artibeus* species and outgroup taxa based on Rogers' similarity values.

22 loci). If genic evolution is progressing in a clocklike fashion in *Artibeus, Tonatia, Micronycteris,* and *Monophyllus,* then the divergence of *Artibeus cinereus, A. watsoni, A. toltecus,* and *A. phaeotis* was extremely recent relative to the speciation events in *Tonatia* and *Micronycteris.* Calculation of time since divergence based on fixed allozymic differences would suggest that either *Artibeus cinereus, A. watsoni, A. toltecus,* and *A. phaeotis* have only just diverged because they have even fewer fixed differences than sibling species of *Monophyllus* or perhaps because they are incipient species. If time since divergence was based on genetic similarity or distance (which uses polymorphic systems in measuring evolutionary distance), then the average age of species within the genera *Tonatia* and *Micronycteris (Nei's* I = 0.34 and 0.28, respectively, Arnold, 1981) would be greater than the average age of the small *Artibeus* (Rogers' S = 0.77). However, each of these small *Artibeus* species would then be older than the sibling species *Monophyllus redmani* and *M. plethodon* (Rogers' S = 0.83, Baker *et al.,* 1981), indicating that the number of fixed differences between congeners is not in all cases correlated with genetic distance, polymorphism, or heterozygosity. Species of *Tonatia, Micronycteris,* and *Monophyllus* all exhibit normal polymorphism levels and extensive allelic fixation. The small species of *Artibeus* do not exhibit extensive allelic fixation and exhibit higher than average polymorphism levels, particularly *Artibeus cinereus.*

Basing their hypothesis on electrophoretic analysis of several species within the family Phyllostomidae, Straney *et al.* (1979) suggested that *Artibeus* was a basal taxon for the rest of the sub-

TABLE 3.—*Rogers' genetic similarity and distance coefficients for species of* Artibeus *and outgroup taxa. Above the diagonal line are Rogers'* S *values and below the line are Rogers'* D *values.*

		1	2	3	4	5	6	7	8	9
Artibeus cinereus	1	—	.81	.75	.78	.56	.49	.64	.45	.66
Artibeus watsoni	2	.19	—	.80	.76	.52	.41	.56	.36	.52
Artibeus toltecus	3	.25	.20	—	.75	.50	.45	.58	.38	.48
Artibeus phaeotis	4	.22	.24	.25	—	.46	.44	.62	.51	.57
Artibeus concolor	5	.41	.48	.50	.54	—	.48	.41	.35	.57
Chiroderma villosum	6	.51	.59	.55	.56	.52	—	.38	.59	.51
Vampyrops brachycephalus	7	.36	.44	.42	.38	.59	.62	—	.44	.54
Uroderma bilobatum	8	.55	.64	.62	.49	.65	.41	.56	—	.45
Artibeus jamaicensis	9	.34	.48	.52	.43	.43	.49	.46	.55	—

family Stenodermatinae and that it represented a paraphyletic taxon. Further cladistic analysis based on a transformation series of the same data set (Straney, 1981) corroborated this hypothesis. Chromosomal data comparing species within the subfamily Stenodermatinae indicated that *Artibeus* has a conserved primitive karyotype (Baker *et al.*, 1979; Johnson, 1979). It is also important to note that between the small *Artibeus* examined and *Artibeus jamaicensis* there was only one fixed allozymic difference. Straney *et al.* (1979) also reported a high heterozygosity level (H = 0.08) in *Artibeus jamaicensis*. It is surprising to see so few fixed differences between *Artibeus jamaicensis* and *A. cinereus*, *A. watsoni*, *A. toltecus*, and *A. phaeotis*, despite a substantial genetic distance among them (Rogers' D = 0.24). A possible explanation is that *Artibeus* represents a basal taxon retaining primitive exophenotypic conditions and that the genus is a composite or paraphyletic taxon. If this proposal is correct and the genus is old relative to other genera in the family and subfamily—and if genic evolution behaves in a clocklike fashion—then one would predict that the genic distance among the species of *Artibeus* would be relatively large. As noted above, the genic divergence for the small species of *Artibeus* examined here is generally lower than in other genera of the Phyllostomidae. Thus, small species of *Artibeus* do not appear to be paraphyletic.

Systematically, the electrophoretic data indicate a close similarity among *A. cinereus*, *A. watsoni*, *A. toltecus*, and *A. phaeotis*, implying that these four species once shared a common ancestor after diverging from *A. jamaicensis*, *A. concolor*, *Chiroderma villosum*, *Vampyrops brachycephalus*, and *Uroderma bilobatum*.

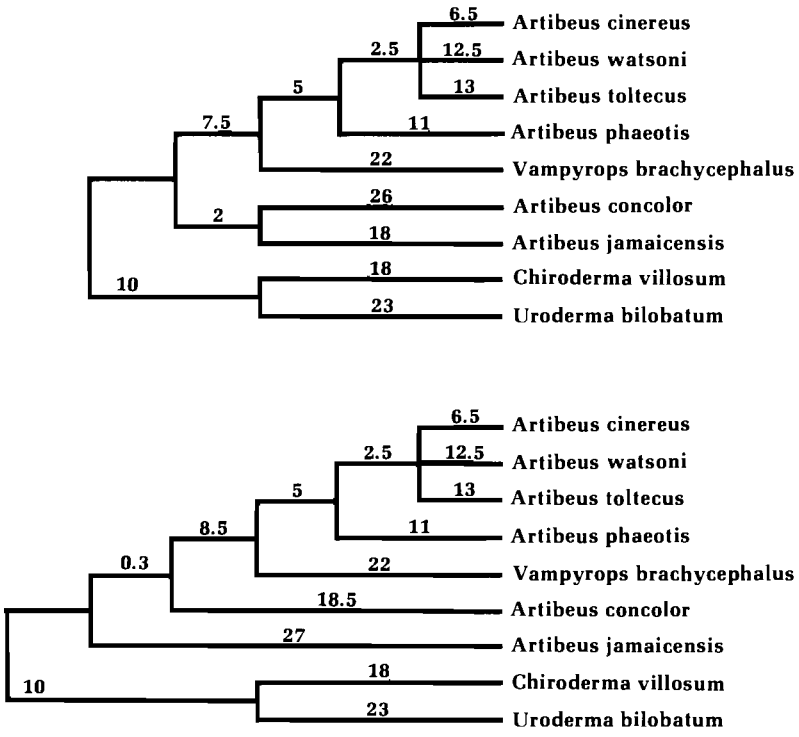

FIG. 3.—Fitch-Margoliash phylogenetic trees of *Artibeus* species and outgroup taxa. The F value for both trees is 6.4.

The common ancestry of these four species is documented by three polymorphic synapomorphies—Mdh-1(a), Pep-1(c), and Pep-2(a). However, the electrophoretic data do not document a common ancestry for the larger (*Artibeus jamaicensis* and *A. concolor*) and smaller (*A. cinereus, A. watsoni, A. toltecus,* and *A. phaeotis*) species of the genus *Artibeus* to the exclusion of the genus *Vampyrops*. If these electrophoretic data were used to define the systematics of the taxa examined, then either the genus *Artibeus* would include *Vampyrops brachycephalus*, or, within the currently recognized genus *Artibeus*, there would be at least two sister lineages to the genus *Vampyrops*. This is consistent with views suggesting that *Artibeus* is a paraphyletic taxon maintaining primitive exophenotypic conditions. Certainly the lack of fixed differences between the small *Artibeus* and *Artibeus jamaicensis* does not refute this stance.

Any attempt to analyze population differences electrophoretically, particularly in the widespread *Artibeus cinereus*, must rely

solely upon polymorphic differences. For this type of study, large sample sizes are necessary from each population. Although not the purpose of the present study, it is interesting to note that populations 6 and 7 (Table 1), collected at the same locality, differed in seven of the nine polymorphic loci found at that location. The two populations were separated on the basis of ear color. Though the sample size is too small to draw conclusions, in a genus where species are differentiated electrophoretically on the basis of polymorphic differences, these figures represent a substantial difference. Larger sample sizes are needed to determine if there is a difference between these two groups.

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