

SYSTEMATICS OF BATS OF THE GENUS *GLOSSOPHAGA*
(CHIROPTERA: PHYLLOSTOMIDAE) AND PHYLOGEOGRAPHY IN
G. SORICINA BASED ON THE CYTOCHROME-*b* GENE

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Systematic relationships within the 5 recognized species of *Glossophaga* were assessed using the complete cytochrome-*b* gene (1,140 base pairs). Our samples from 4 species, *G. commissarisi*, *G. leachi*, *G. longirostris*, and *G. morenoi*, show little intraspecific geographic subdivision. Alternatively, *G. soricina* has a major mtDNA subdivision that may reflect 2 biological species. Our data suggest that *G. soricina* is the sister taxon to the remainder of the genus, *G. leachi* and *G. longirostris* are sister taxa, and the position of *G. morenoi* is unresolved, placed either with the *G. leachi*–*G. longirostris* clade or with the *G. commissarisi* clade. Distance values among *G. morenoi*, *G. commissarisi*, *G. longirostris*, and *G. leachi* were similar, suggesting a similar time of speciation for these 4 species.

Key words: cytochrome-*b*, *Glossophaga commissarisi*, *Glossophaga leachi*, *Glossophaga longirostris*, *Glossophaga morenoi*, *Glossophaga soricina*, Phyllostomidae, phylogeography, systematics

The genus *Glossophaga* comprises 5 species of Neotropical bats: *G. commissarisi* (west-central Mexico to eastern Peru and Brazil), *G. leachi* (western Mexico to Costa Rica), *G. longirostris* (northern South America, including some Caribbean islands), *G. morenoi* (southern Mexico to Central America), and *G. soricina* (Mexico to Northern Argentina, including populations from Jamaica, Trinidad, and Tres Marias Islands; Fig. 1). The genus (Webster 1993) and its species have been systematically reviewed in the last 20 years: *G. commissarisi* (Webster and Jones 1982, 1987), *G. leachi* (Webster and Jones 1980, 1984a), *G. longirostris* (Handley and Webster 1987; Webster and Handley 1986), *G. morenoi* (Gardner 1986; Webster and Jones 1984b, 1985), and *G. soricina* (Alvarez et al. 1991). Although the validity of the name *G. morenoi* has been questioned (Webster 1993), there is no disagreement on the specific validity of the taxon. Karyologic stud-

ies reported the same diploid and fundamental number for all species and individuals studied (Baker 1967, 1979; Webster 1993). Webster (1993), assessing intrageneric and intraspecific relationships based on morphologic and biochemical data, organized the species into 3 different clades: *G. soricina*; *G. commissarisi* and *G. leachi*; and *G. longirostris* and *G. morenoi*. He concluded that climatic and habitat changes during the Quaternary, such as cycles of expansion and contraction of wet and dry habitat, were responsible for relationships within *Glossophaga* and the present distribution of members of the genus. Isozyme analyses found low levels of differentiation within the genus and detected low levels of intraspecific variation in all species but *G. soricina*. We used the complete mitochondrial cytochrome-*b* gene to investigate systematic relationships within the genus *Glossophaga*, patterns of interspecific variation and geographic variation in *G. soricina*.

Previous results using cytochrome-*b*

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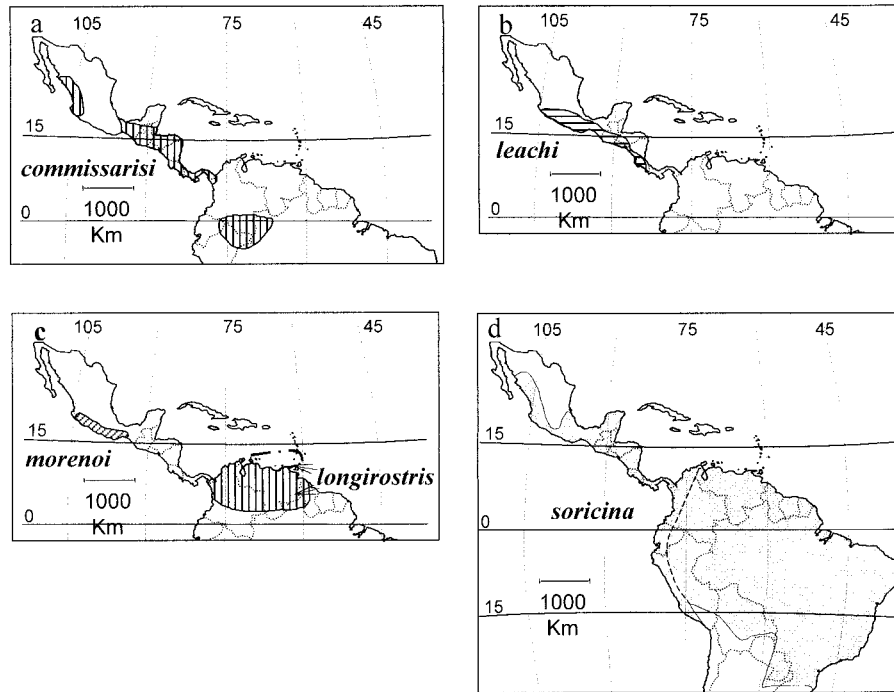


FIG. 1.—Geographic distribution of the species in *Glossophaga* (modified from Webster 1993). a) *Glossophaga commissarisi*, b) *G. leachi*, c) *G. longirostris* and *G. morenoi*, and d) *G. soricina*. A dashed line indicates the geographic location of the hypothetical split between samples from east and west of the Andes in *G. soricina*.

have proven helpful in understanding specific relationships within the phyllostomid genera *Artibeus*, *Dermanura*, *Phyllostomus*, *Chiroderma*, *Carollia*, and *Rhinophylla* (Baker et al. 1994; Van Den Bussche and Baker 1993; Van Den Bussche et al. 1998; Wright et al. 1999).

MATERIALS AND METHODS

Fifty-seven samples of *Glossophaga* were included in our analyses: 4 *G. commissarisi*, 3 *G. leachi*, 8 *G. longirostris*, 4 *G. morenoi*, and 38 *G. soricina*, covering the geographic localities represented in frozen tissue collections. One species of *Dermanura* (*D. tolteca*) and 2 species of *Artibeus* (*A. obscurus* and *A. planirostris*) were included as outgroups (Genbank accession numbers U66515, U66507, and U66508, respectively), and *Leptonycteris curasoae*, *Monophyllus redmani*, and *M. plethodon* were included as ingroup taxa to determine the sister taxon to *Glossophaga* (Gardner 1977); Genbank accession numbers are AF382830–AF382889. A list

of all specimens examined and their geographic localities are given in Appendix I.

Deoxyribonucleic acid was extracted from liver, kidney, or muscle tissue using either a PCI-phenol protocol (Longmire et al. 1997) or a SDS-proteinase K-NaCl extraction and alcohol precipitation protocol (Maniatis et al. 1992; Miller et al. 1988). The complete mitochondrial cytochrome-*b* gene was amplified using polymerase chain reaction (PCR; Saiki et al. 1988) with primers glo7L (5' CAY CGT TGT ATT TCA ACT RTA AGA AC 3') and glo6H (5' CGG TGT AAT GRA TAT ACT ACA TRG 3') modified from L14724 and H15915 (Irwin et al. 1991). The thermal profile used for amplification consisted of an initial denaturing step at 94°C for 2 min followed by 35 cycles of denaturation at 94°C for 15 s, annealing at 48°C for 20 s and extension at 72°C for 1 min, and a final extension step at 72°C for 2 min. PCR products were purified using QIAquick PCR Purification Kit (Qiagen Inc., Chatsworth, California) following manufacturer's instructions. DNA sequencing was accomplished using ABI Prism dRhodamine

or ABI Big Dye chemistry (Applied Biosystems, Inc., Foster City, California) using the amplification primers and a set of internal sequencing primers: glo1L (5' GTC CTG CCA TGW GGA CAA ATA TC 3'); glo2H (5' GCT CCT CAG AAK GAT ATT TGT CC 3'); glo3L (5' TAY CTC CAY GTA GGY CGA GG 3'); glo5L (5' CCA GAY CTY CTA GGA GAY CCA G 3'); and glo13L (5' TCA ACT RTA AGA ACT AAT CT 3'). DNA sequences were generated using an ABI Prism 310 Genetic Analyzer (Applied Biosystems) automatic sequencer. Sequences were verified and aligned using Sequencher version 3.1.1 (Gene Code Corporation, Ann Arbor, Michigan).

Pairwise distance comparisons were calculated using the uncorrected percentage of sequence divergence. Three different methods were used to estimate phylogenetic relationships: neighbor joining, maximum parsimony, and maximum likelihood. All phylogenetic analyses were estimated using PAUP* version 4.02 (Swofford 1999). Arlequin version 2000 (Schneider et al. 2000) was used to perform an analysis of molecular variance (AMOVA) to investigate genetic variation within and among geographic samples of *G. soricina*. Sequence divergence for the neighbor-joining (Saitou and Nei 1987) analysis was calculated using Tamura-Nei (Tamura and Nei 1993) distance, which allows for bias in base composition and independent rates for different types of nucleotide substitutions. In maximum parsimony, a number of different transition:transversion ratios (2:1, 5:1, 6:1, and 10:1) were applied to explore sensitivity of results to variation in substitution model. Heuristic searches were performed with 10 random additions of taxa. Support for the nodes was evaluated using 1,000 bootstrap replicates in the fast heuristic mode. In the case of maximum likelihood, the consensus tree from a parsimony unweighted heuristic search was used to evaluate the likelihood of different models of DNA substitution (Huelsenbeck and Crandall 1997). Parameter values were then set to those of a complex model (HKY+ Γ) that optimized 3 parameters: proportion of each base, transition:transversion ratio, and shape (alpha) of the gamma distribution. A maximum likelihood heuristic search with 10 random additions of taxa was then performed using the complete data set.

RESULTS

Description of data.—Of the 1,140 base pairs of the complete cytochrome-*b* gene, 702 were invariant and 70 were autoapomorphic, leaving 368 potentially parsimony informative characters within our complete data set. There were 77 changes at 1st codon positions, 35 at 2nd positions, and 326 at 3rd positions. Among sequences of *Glossophaga*, 787 characters were invariant and 58 changes were autoapomorphic, leaving 295 as parsimony informative characters. Within *Glossophaga* there were 54 changes at 1st positions, 23 at 2nd positions, and 267 at 3rd positions. Average distance values (using uncorrected percentage of sequence divergence) for pairwise comparisons within species ranged from 0.7% \pm 0.08 SE in *Glossophaga longirostris* to 4.6 \pm 0.07% in *G. soricina*; whereas comparisons among species within *Glossophaga* averaged 12.4 \pm 0.04% (Table 1).

Phylogenetic analyses.—A maximum-parsimony heuristic search using all variable positions and weighting substitutions equally resulted in 1,130 equally-parsimonious trees of 1,369 steps (Fig. 2). Those trees differed from those obtained with different transition:transversion ratios only in topology within species. The g_1 -statistic obtained from 10,000 random trees was highly significant ($P < 0.01$), which indicated a strong phylogenetic signal in the data set (Hillis 1991; Hillis and Huelsenbeck 1992; Huelsenbeck 1991). Results from neighbor joining, maximum parsimony, and maximum likelihood agree that *G. soricina* was sister to the remainder of the genus. Neighbor joining placed *G. morenoi* sister to the *G. leachi*-*G. longirostris* clade (Fig. 3); whereas parsimony (Fig. 2) and likelihood (Fig. 4) analyses placed *G. morenoi* sister to *G. commissarisi*. The strict consensus parsimony tree was used to evaluate the likelihood of different models of nucleotide substitution. A maximum-likelihood analysis of the complete data set, setting parameter values to the HKY+ Γ (Hasegawa et al.

TABLE 1.—Pairwise uncorrected percentage of sequence divergence ($\bar{X} \pm SE$) among *Aritebus* (which includes *Aritebus* and *Dermanura*), *Glossophaga*, *Leptoncyterys*, and *Monophyllus*. W = samples from North America and South America west of the Andes, E = samples from South America east of the Andes.

	<i>G. soricina</i> W	<i>G. soricina</i> E	<i>G. longirostris</i>	<i>G. leachi</i>	<i>G. morenoi</i>	<i>G. commissarisasi</i>	<i>M. plethodon</i>	<i>M. redmani</i>	<i>L. curasoae</i>
<i>G. soricina</i> W	2.8 ± 0.09								
<i>G. soricina</i> E	6.3 ± 0.02	2.7 ± 0.08							
<i>G. longirostris</i>	12.5 ± 0.02	12.6 ± 0.02	0.7 ± 0.08						
<i>G. leachi</i>	13.2 ± 0.06	12.5 ± 0.05	8.4 ± 0.05	0.9 ± 0.02					
<i>G. morenoi</i>	13.7 ± 0.03	13.3 ± 0.03	10.3 ± 0.06	10.1 ± 0.09	0.9 ± 0.02				
<i>G. commissarisasi</i>	12.8 ± 0.04	12.6 ± 0.04	10.2 ± 0.04	10.2 ± 0.04	10.7 ± 0.08	2.2 ± 0.04			
<i>M. plethodon</i>	16.5 ± 0.06	16.4 ± 0.06	15.8 ± 0.07	15.4 ± 0.05	16.8 ± 0.08	15.5 ± 0.08			
<i>M. redmani</i>	16.6 ± 0.06	16.0 ± 0.06	15.9 ± 0.09	15.6 ± 0.08	16.6 ± 0.1	16.3 ± 0.1	10.3		
<i>L. curasoae</i>	16.9 ± 0.05	17.0 ± 0.06	16.1 ± 0.09	15.5 ± 0.06	16.1 ± 0.04	16.0 ± 0.1	16.1	15.4	
<i>Aritebus</i>	17.2 ± 0.06	17.6 ± 0.06	17.1 ± 0.2	17.1 ± 0.2	17.8 ± 0.3	17.7 ± 0.1	15.7	17.1	17.2

1985) model of nucleotide substitution (empirical base frequencies, transition to transversion ratio of 6.3, $\alpha = 0.21$; Table 2), resulted in a tree with likelihood value of $-\ln L = 7799.04$ (Fig. 4). However, topology within *Glossophaga* was the same. A heuristic search using the same settings and constrained to find the shortest tree supporting the hypothesis of Webster (1993) resulted in a tree $-\ln L = 7808.33$ (tree not shown). Two tests, a Kishino–Hasegawa (1989) and a Shimodaira–Hasegawa (1999) did not detect significant differences in the likelihood scores among our neighbor-joining tree, our likelihood tree, and Webster’s tree. In all cases, *G. soricina* was defined by 2 well-supported lineages, that corresponded to an Andean split. An eastern clade (supported in 88% of the bootstrap iterations) consisted of individuals from South America east of the Andes Mountains; whereas a western clade (supported by 96% bootstrap iterations) included individuals from Central and North America, Jamaica, and the western slope of the Andes Mountains. Mean sequence divergence within *G. soricina* from North America, plus individuals from Jamaica and 3 specimens from western Peru (hereafter referred to as western clade), was 2.8%; whereas comparisons within samples east of the Andes (eastern clade), including Trinidad, was 2.7%. *G. soricina* samples from Chachapoyas, Peru, presented the greatest nongeographic variation (6.5%). The average pairwise distance between the 2 lineages was 6.3%. Molecular variance within *G. soricina* was partitioned into, within, and between lineage components by the AMOVA. The 1st component accounted for 44% of the total variance, and the 2nd component accounted for 56% ($P < 0.001$).

DISCUSSION

Highly supported interspecific relationships.—Most nodes were highly supported by bootstrap analyses, particularly monophyly of *Glossophaga* (bootstrap = 97%) and all recognized species within the genus

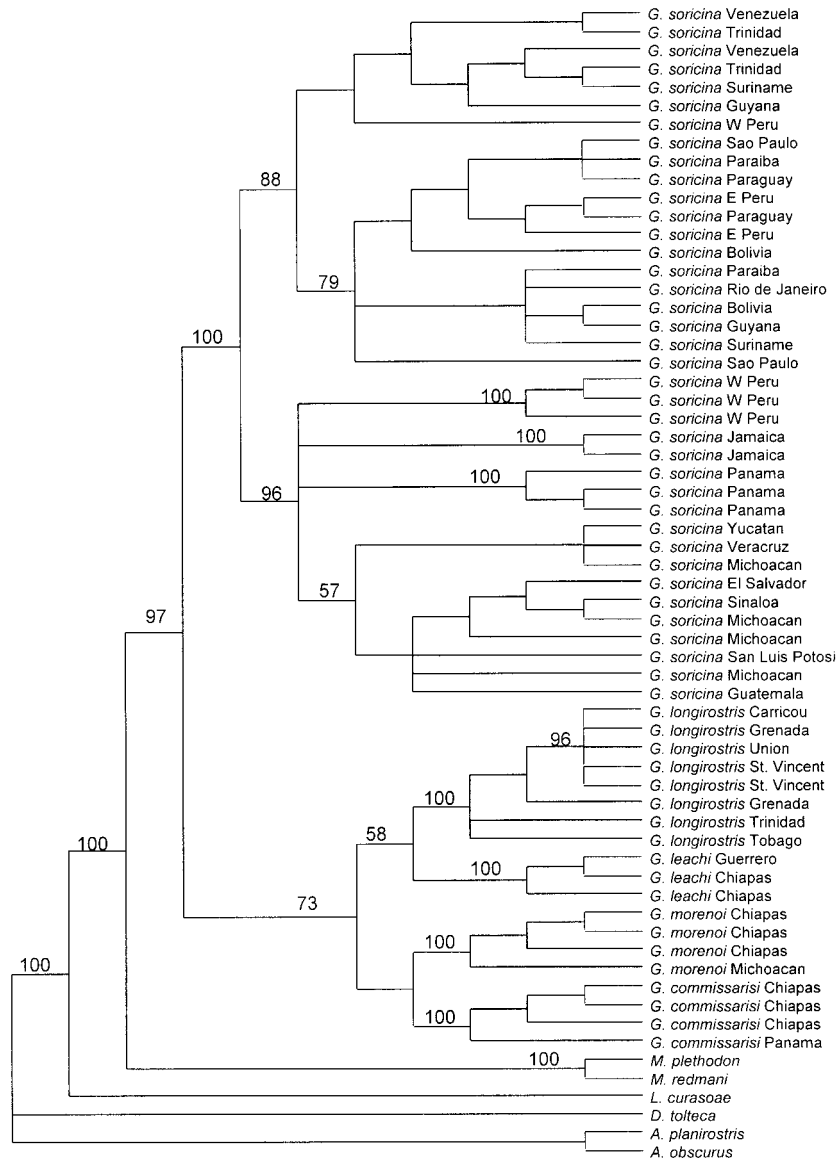


FIG. 2.—Strict consensus of 1,130 trees 1,369 steps long, result of an unweighted parsimony heuristic search. Bootstrap values are next to the most relevant nodes.

(100%). Weaker bootstrap values in both likelihood and parsimony analyses supported the position of *G. soricina* as the sister group to the remainder of the genus and the sister species relationship between *G. longirostris* and *G. leachi*. Disagreement with the neighbor-joining analysis probably was due to few changes resolving that node. When *Leptoncyteris* was excluded from un-

weighted parsimony, *G. morenoi* was sister to the *G. leachi*–*G. longirostris* clade, as in the neighbor-joining analysis.

Distance values among *G. morenoi*, *G. commissarisii*, *G. longirostris*, and *G. leachi* were similar, suggesting a rapid speciation event at the base of this clade. This pattern might account for the lack of statistical resolution among competing trees. If a molec-

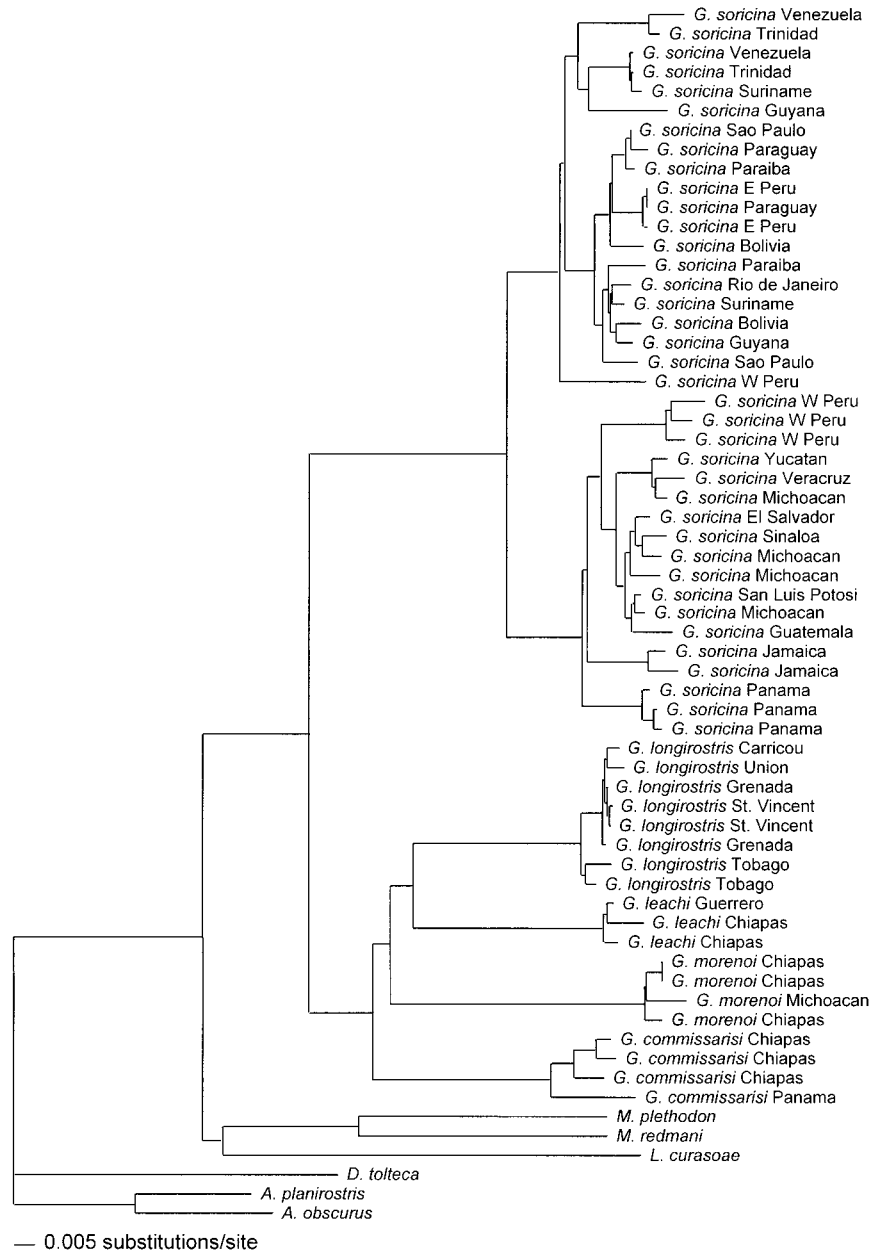


FIG. 3.—Neighbor-joining tree based on the Tamura-Nei distance matrix.

ular clock is assumed, with rates ranging from 2.3% to 5%/10⁶ years ago (Arbogast and Slowinski 1998; Smith and Patton 1999), the speciation event would have occurred about 2–4 × 10⁶ years ago. Furthermore, all species in the genus appear to have had relatively long, independent his-

tories, with interspecific comparisons averaging about 10%.

Analyses of morphologic, morphometric, and isozyme variation by Webster (1993) identified 3 different clades: *G. soricina*; *G. commissarisi* and *G. leachi*; and *G. longirostris* and *G. morenoi*. Our results support

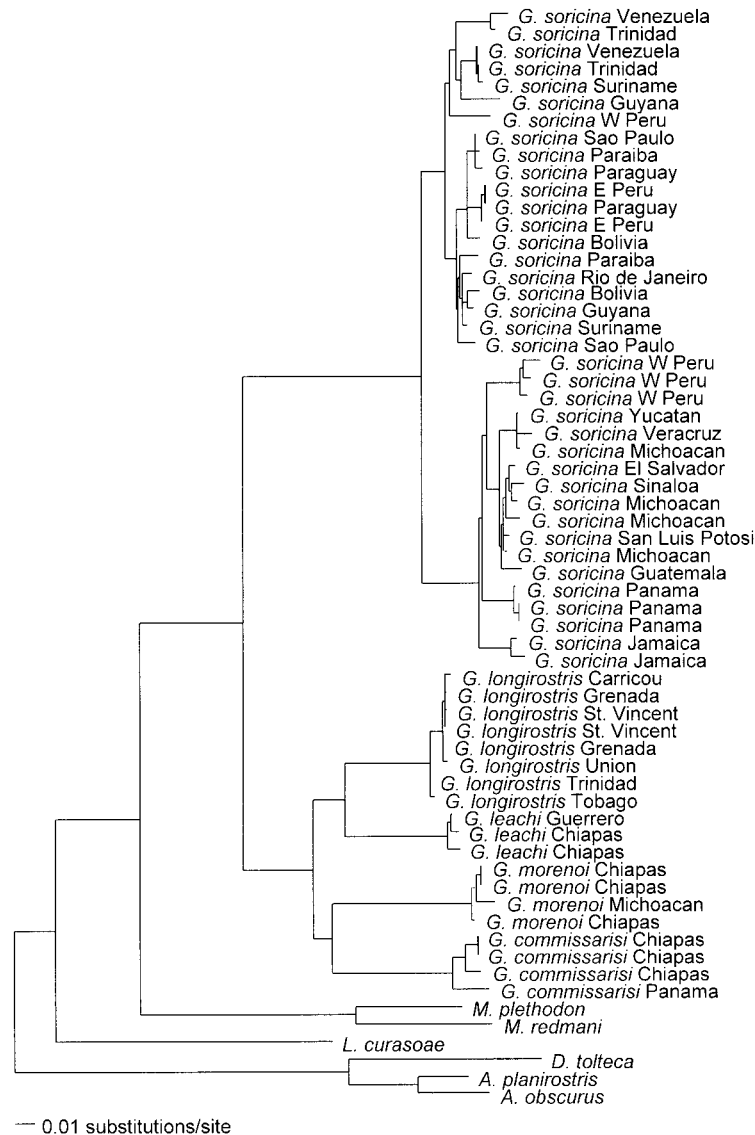


FIG. 4.—Phylogram from a heuristic maximum likelihood search, following the HKY85+ Γ model ($-\ln L = 7799.04$; transition:transversion ratio = 6.3, gamma shape parameter (α) = 0.21).

a slightly different scenario, with *G. soricina* as the sister taxon to a large clade, including the *G. longirostris*–*G. leachi* clade, *G. morenoi*, and *G. commissarisi*. At present, we lack statistical resolution to favor either of them.

Intraspecific geographic variation.—Monophyly of all 5 species was highly supported by bootstrap analyses (100% in all cases). In a recent synthesis of cytochrome-

b data, Avise and Walker (1999) found agreement between mtDNA lineages and traditionally recognized taxonomic units. They also reported that 56% of the species were represented by >1 deep mitochondrial lineage possibly representing distinct biological species. In our study, only *G. soricina* showed such a pattern. Within *G. commissarisi*, *G. leachi*, *G. longirostris*, and *G. morenoi*, distance values between individ-

TABLE 2.—The ln-likelihood scores of the different substitution models tested; rate heterogeneity indicated by Γ .

Model ^a	Base frequencies	Ts : v ratio (κ)	Among site rate variation (α)	ln likelihood
JC69	Equal	1	No	-9615.27
K80	Equal	Estimate from data	No	-8892.35
HKY85	Empirical	Estimate from data	No	-8737.76
JC69+ Γ	Equal	1	Estimate from data	-8927.57
K80+ Γ	Equal	Estimate from data	Estimate from data	-8135.37
HKY85+ Γ	Empirical	Estimate from data	Estimate from data	-7990.51

^a Model abbreviations: JC69, Jukes and Cantor (1969); K80, Kimura (1980) two-parameter model; HKY85, Hasegawa et al. (1985).

uals from different localities were low (average pairwise distance about 1%). These results provide evidence in favor of Webster's conclusion (Webster 1993) of Quaternary changes in habitat accounting for the present distribution and degree of intraspecific variation within those 4 species. Unfortunately, small samples were available from these 4 species; additional samples might reveal the presence of greater intraspecific variation.

Glossophaga soricina, however, shows considerable genetic variation (average pairwise distance within the whole species about 5%). In all cases, *G. soricina* is represented by 2 well-supported lineages. The 1st clade (supported in 88% of the bootstrap iterations) consists of individuals from South America east of the Andes Mountains, whereas the 2nd clade (supported by 96% bootstrap iterations) includes individuals from Central and North America, Jamaica, and the western slope of the Andes Mountains. Pairwise distance comparisons between the 2 lineages are similar to pairwise comparisons between sister species in other phyllostomid genera such as *Carollia* (Wright et al. 1999) and *Chiroderma* (Baker et al. 1994). The 2 lineages were collected sympatrically in Chachapoyas, in the Departamento Amazonas in Peru (FMNH 128675 and 128676). Interestingly, this region has been recognized as a major species boundary for *Artibeus* (*fraterculus* + *jamaicensis*) and may present a similar suture zone for other taxa (Patterson et al. 1992). As argued by Patterson et al. (1992) on the

basis of ATPase sequence variation and subsequently supported by Van Den Bussche et al. (1998) using cytochrome-*b*, *A. fraterculus* is sister to *inopinatus* + *hirsutus* of the Pacific Coast, and this clade is sister to all Amazonian diversity within *Artibeus*.

Our results are consistent with Webster's morphometric analyses (Webster 1993), including the subspecies *G. s. antillarum* (from Jamaica), *G. s. handleyi* (from northern Mexico southward through Central America up to northern and western Colombia), and *G. s. valens* (western Ecuador and Peru) in 1 clade, and *G. s. soricina* (from South America east of the Andes) in the other one. Webster (1993) also reported presence of *G. s. soricina* and *G. s. valens* in Amazonas, Peru, but he did not find evidence of intergradation between the two, further suggesting that the 2 clades may represent species. Further analyses of morphologic variation and nuclear DNA markers would aid in elucidating the matter.

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APPENDIX I

Specimens examined and their geographic localities.—TK numbers correspond to samples from the frozen tissue collection at the Natural Science Research Laboratory from Texas Tech University, Lubbock, Texas; MVZ numbers correspond to samples from the Museum of Vertebrate Zoology, Berkeley, California; FMNH numbers correspond to samples from the Field Museum of Natural History, Chicago, Illinois, and NMNH numbers correspond to samples from the National Museum of Natural History, Washington, D.C.

Glossophaga commissarisi.—TK 20562, Mexico, Chiapas, Tonalá; TK 20586, TK 20600, Mexico, Chiapas, Huixtla; NMNH 578998, Panama, Bocas del Toro, Isla Popa.

Glossophaga leachi.—TK 4812, Mexico, Guerrero, El Carnzal; TK 20567, TK 20569, Mexico, Chiapas, Tonalá.

Glossophaga longirostris.—TK 18501, Grenada, St. George, Confer, Chemin River; TK 18585, Grenada, St. George, St. Paul's; TK 18613, Grenadines, Union Island, Clifton; TK 18667, Grenadines, Carriacou Island, Hillsborough; TK 25150, Trinidad and Tobago, Tobago, St. Patrick, Grange; TK 25157, NMNH 580656, NMNH 580658, St. Vincent, St. George Parish.

Glossophaga morenoi.—TK 20563, TK 20564, TK 20579, Mexico, Chiapas, Tonalá; TK 43176, Mexico, Michoacán, Aquila, Maruata.

Glossophaga soricina.—TK 34707, El Salvador, Santa Ana; TK 41573, Guatemala, Zocalpal; TK 9251, Jamaica, St. Catherine Parish, Watermount; TK 11040, Jamaica, St. Ann Parish, Discovery Bay, Green Grotto; TK 4728, Mexico, Sinaloa, Rosario; TK 13173, Mexico, Veracruz, Córdoba, Ojo de Agua, Río Atoyac; TK 14159, Mexico, San Luis Potosí, Ciudad Valles; TK 13594, Mexico, Yucatán; TK 43138, TK 43178, TK 43189, TK 43208, Mexico, Michoacán, Aquila; NMNH 578997, Panama, Bocas del Toro, Isla Popa; NMNH 579009, NMNH 579010, Panama, Bocas del Toro, Isla Escudo de Veraguas; FMNH 128675, FMNH 128676, Peru, Amazonas, Chachapoyas; FMNH 128713, FMNH 128718, Peru, Cajamarca, Santa Cruz; TK 14605, TK 14610, Bolivia, La Paz, Puerto Linares; MVZ 185583, MVZ 185585, Brazil, Paraíba; MVZ 185566, Brazil, Rio de Janeiro; MVZ 185874, MVZ 185875, Brazil, São Paulo; TK 86578, TK 86579, Guyana, N.W. District, Baramita; TK 56869, TK 57056, Paraguay, Canindeyu, Mbaracayu; TK 22602, TK 22631, Peru, Huanuco, Leoncia Prado; TK 17476, Suriname, Nickerie, Kabalebo; TK 17544, Suriname, Marowijne, Albina; TK 25071, Trinidad and Tobago, Trinidad, Nariva, Ecclesville; TK 25212, Trinidad and Tobago, Trinidad, Mayaro, Guayaguayare; TK 15154, TK 15194, Venezuela, Guarico, Calabozo.

Leptonycteris curasoae.—TK 45107.

Monophyllus plethodon.—TK 15607.

Monophyllus redmani.—TK 27694.