Phylogenetic Relationships of the New World Bat Genus *Sturnira* (Chiroptera: Phyllostomidae)

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ABSTRACT

Phylogenetic relationships of New World leaf-nosed bats of the genus *Sturnira* were analyzed using allozymic and morphological characters. Seven species of *Sturnira* were included in the genetic analyses, and 14 species were included in the morphological survey. Genetic analyses of the monophyly and intergeneric relationships of *Sturnira* utilized a variety of taxa to root trees at different stages of the analysis, including *Sturnira bidens, S. nana, Vampyrops dorsalis, Uroderma bilobatum, Carollia perspicillata, Glossophaga soricina, Desmodus rotundus,* and *Micronycteris megalotis,* all from the family Phyllostomidae. *Sturnira* proved to be more closely related to *Uroderma bilobatum* and *Vampyrops dorsalis* than to *Carollia perspicillata* or *Glossophaga soricina.* These results confirm its current placement with the Stenodermatinae rather than with the Carolliinae or Glossophaginae. The monophyly of *Sturnira* was substantiated, and the subgenus *Corvira* was found to be distinct both genetically and morphologically. Consensus between genetic and morphological analyses further reveals at least two lineages within the subgenus *Sturnira,* the first comprising *S. tildae, S. lilium, S. luisi,* and *S. thomasi,* and the second *S. magna* and *S. erythromos.* Additional materials and analyses will be needed to resolve the positions of other species in the genus.

INTRODUCTION

The genus *Sturnira* is currently placed in the subfamily Stenodermatinae (Chiroptera: Phyllostomidae), which is endemic to the New World tropics. Externally, members of this genus may be recognized by their lack of a tail and the highly reduced interfemoral membrane. *Sturnira* inhabits lowland and humid montane forest from southern Mexico to eastern Brazil, Uruguay, and the West Indies. Eleven or 12 species are currently recognized in two subgenera, *Corvira* and *Sturnira* (Davis, 1980; Honacki et al., 1982).

The species within the genus *Sturnira* appear to be a monophyletic group (Gardner and O'Neill, 1969, 1971; Owen, 1987), but the higher-level relationships of this genus are still enigmatic. Substantial evidence supports its current placement within the Stenodermatinae (de la Torre, 1961; Smith, 1976). (All members of this traditional group were included within the tribe Stenodermatini, subfamily Phyllostominae, in the recently proposed classification of Baker et al. [1989].) Nevertheless, alternative classifications of *Sturnira* have been suggested. For example, Straney et al. (1979) concluded from electrophoretic evidence that *Sturnira* is not a stenodermatine. Following Miller (1907), Walton and Walton (1968) placed the genus in a separate subfamily, Sturnirinae, based on postcranial characters (see also Hall, 1981; Linares, 1986). Slaughter (1970) concluded from tooth structure that *Sturnira* was related to the Glossophaginae. Recently, Phillips et al.

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(1987) found that the parotid secretory granules of *Sturnira* differed widely from those of the other stenodermatines they examined (*Artibeus* and *Ariteus*), being more similar to those of *Trachops* of the Phyllostominae (genus allocated to the Vampyrinae by Baker et al., 1989).

Phylogenetic relationships of *Sturnira* were recently evaluated using discrete-state and mensural characters (Owen, 1987), but many interspecific relationships remained unresolved. Recently, Owen (1988) presented a systematic arrangement of species based on phenetic analyses of mensural data. No other phylogenetic or systematic studies are known to us. Unfortunately, revision of the entire genus *Sturnira* has not been attempted since the study of de la Torre (1961), and several new forms have been subsequently discovered and described.

Without pretending to review all *Sturnira*, this paper investigates phylogenetic relationships of a set of species in the subgenus *Sturnira* using morphological and allozymic sets of data. In addition, we assess the phylogenetic relationships of the genus *Sturnira* within the Phyllostomidae using the allozymic data, and we determine whether the genus *Sturnira* and its subgenera *Corvira* and *Sturnira* are monophyletic. Lack of materials for several taxa makes this analysis incomplete, but it is a first step toward a comprehensive revision of relationships within this diverse and perplexing genus.

Materials and Methods

Cladistic Analysis of Discrete Morphological Characters: A set of cranial, dental, and external characters was analyzed cladistically using the method developed by Hennig (1966). Multiple outgroup taxa were used to polarize the character states, enhancing the prospect of correctly identifying autapomorphic character states in the outgroup. Such uniquely derived characters might otherwise be confused with plesiomorphic character states.

For analyses of interspecific relationships within the subgenus *Sturnira*, *S. bidens* Thomas, 1915, and *S. nana* Gardner and O'Neill, 1971, of the subgenus *Corvira* were used as outgroups. *Corvira* is considered the sister group for the subgenus *Sturnira* (Gardner and O'Neill, 1969, 1971). Twelve species composed the ingroup: *S. lilium* (E. Geoffroy, 1810); *S. luisi* Davis, 1980; *S. magna* de la Torre, 1966; *S. oporaphilum* (Tschudi, 1844); *S. ludovici* Anthony, 1924; *S. erythromos* (Tschudi, 1844); *S. bogotensis* Shamel, 1927; *S. mordax* (Goodwin, 1938); *S. tildae* de la Torre, 1959; *S. thomasi* de la Torre and Schwartz, 1966; *S. aratathomasi* Peterson and Tamsitt, 1968; and an undescribed species made available to us through the courtesy of Luis Albuja that is here denoted *Sturnira* sp. A. All were examined in the course of this study, and doubtful character states were recorded as missing values.

The analysis was based on a set of 1 external and 14 cranial characters scored mostly from adult specimens (table 1). Characters are described in Appendix 1. The characters were selected after extensive evaluation of characters from a large series of individuals (Appendix 2) and were assumed to be independent. In descriptions of characters, we follow the dental nomenclature of Van Valen (1966) and Phillips (1971).

The character-state matrix was submitted to PAUP (phylogenetic analysis using parsimony) software for personal computers (Swofford, 1985). Parsimony is used to minimize the number of character-state transformations along the branches of a phylogenetic tree. The PAUP options we used were global branch swapping on the first 100 equally parsimonious trees, swapping the remaining trees. This procedure obtains up to 100 equally short trees. The branch-and-bound option, which guarantees obtaining the most parsimonious tree, was not used because of software limitations to nine or fewer taxa. Multistate characters were treated as unordered, freeing the analysis from unwarranted assumptions of particular transitional series. The use of outgroups enabled unequivocal specification of polarity in binary characters.

The CONTREE program with the strict consensus option (SC of Rohlf, 1982) was used to find a single consensus topology among equally short trees identified by the branch swapping analysis. In addition, the jackknife strict consensus method (JSC of Lanyon, 1985) was used on successive iter-

TABLE 1
Character Data Matrix for a Group of Species of the Genus *Sturnira*
(Character and character states are described in Appendix 1)

Species	Character														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Sturnira bidens[a]	0	1	0	0	9	0	1	0	0	0	0	0	0	0	0
S. nana[a]	0	1	0	0	9	1	1	0	0	0	0	0	0	0	0
S. sp. A	0	0	0	2	1	1	1	0	0	2	1	1	0	0	0
S. luisi	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0
S. lilium	1	0	0	1	0	1	0	1	0	1	1	1	1	1	0
S. tildae	1	0	0	1	0	1	0	1	0	1	1	1	0	1	1
S. mordax	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0
S. ludovici	1	0	1	1	0	1	0	1	0	1	1	1	0	0	1
S. oporaphilum	1	0	1	1	0	1	0	1	0	1	1	1	1	0	1
S. magna	1	0	0	1	0	1	0	1	0	1	1	1	0	0	0
S. erythromos	1	0	1	1	0	1	0	1	0	1	1	0	2	0	0
S. bogotensis	1	0	1	1	0	1	0	1	0	1	1	0	2	0	0
S. thomasi	1	0	0	1	0	1	0	1	1	1	1	1	1	1	0
S. aratathomasi	0	0	0	2	0	1	0	1	0	1	0	1	0	1	1

[a] Species used as outgroups.

ations of the PAUP and CONTREE algorithms to identify strongly and weakly supported portions of the trees. This method employs successive permutations of the data matrix, deleting a different taxon from the analysis each iteration, to produce a single consensus tree for each of the $n - 1$ data matrices. The resulting strict consensus trees are in turn examined for consensus, producing a final tree that retains the nodes common to the $n - 1$ jackknifed trees.

Owen (1987) presented a topology for the Stenodermatinae, including most of the species of *Sturnira*. His study represents the only published phylogenetic analysis for the genus using discrete morphological data. To homogenize our methodological procedures, we also analyzed his data matrix for species of *Sturnira* using the PAUP algorithm and options outlined above.

ELECTROPHORESIS: Electrophoretic analysis of frozen tissues was done by running aqueous extracts of tissues prepared by standard procedures on horizontal starch gels. The procedures and recipes for buffers and stains followed Selander et al. (1971) and Harris and Hopkinson (1976). Composite samples of liver and kidney were prepared with equal amounts of tissues, homogenized in grinding buffer (pH 7.0), and then centrifuged at 12,000 rpm for 40 minutes. Supernatants were removed and preserved at −70°C until used and the precipitates discarded. Composite homogenates were then used in the subsequent electrophoretic runs.

An initial survey using representative individuals was conducted to determine the most appropriate buffer system for each locus. The optimal buffer systems were then used for the initial analysis of each locus. When the identity of specific electromorphs was uncertain, two to four buffer systems were employed and the taxa in question were compared side by side. Buffer systems, loci examined, and the recent Enzyme Commission numbers of these loci are listed in table 2. Scoring and interpretation of gels were based on Harris and Hopkinson (1976) and Richardson et al. (1986). After runs, the gel itself or the overlaid agar was preserved for future reference. Initially, 29 presumptive loci were surveyed, but 10 were later eliminated from further consideration because of ambiguous or inconsistent scores in repetitive runs or because of uncertain discrimination of electromorphs (ALB, PEP-C, GOT-2, GDH, ODH, EST-D, CK, AK, NP, EAP). The results presented here are based on the remaining 19 presumptive loci: ACON-1, ACON-2, αGPD, GPI, GOT-1, ICD-1, ICD-2, LAP, PEP-B, LDH-1, LDH-2, MDH-1, MDH-2, ME, PEPT-D, PGM, 6-PGD, SOD, and SDH.

Sturnira tissue samples came from 131

TABLE 2
Genetic Loci Analyzed by Electrophoresis, Their Symbols, and the Buffer Systems Used

Symbol	Name	Buffer
ACON-1, 2	Aconitase (E.C. 4.2.1.3)	TC III
GOT-1	Glutamate oxalate transaminase (E.C. 2.6.1.1)	Poulik
αGPD	Glycerophosphate dehydrogenase (E.C. 1.1.1.8)	TC III
GPI	Glucose phosphate isomerase (E.C. 5.3.1.9)	Poulik
ICD-1, 2	Isocitrate dehydrogenase (E.C. 1.1.1.42)	TC II
LAP	Leucine aminopeptidase (E.C. 3.4.11)	TC II
LDH-1, 2	Lactate dehydrogenase (E.C. 1.1.1.27)	LiOH
PEP-B	Peptidase B (E.C. 3.4.11)	Poulik
PEP-D	Peptidase D (E.C. 3.4.11)	Poulik
MDH-1, 2	Malate dehydrogenase (E.C. 1.1.1.37)	TC III
ME	Malic enzyme (E.C. 1.1.1.40)	TM
6-PGD	Phosphogluconate dehydrogenase (E.C. 1.1.1.44)	Poulik
PGM	Phosphoglucomutase (E.C. 2.7.5.1)	Poulik
SDH	Sorbitol dehydrogenase (E.C. 1.1.1.14)	Poulik
SOD	Superoxidase (E.C. 1.15.1.1)	TC II

specimens of the subgenus *Sturnira* and seven of the subgenus *Corvira*. In addition, 25 samples of more distantly related taxa including *Uroderma bilobatum* and *Vampyrops dorsalis* (Stenodermatinae), *Carollia perspicillata* (Carolliinae), *Glossophaga soricina* (Glossophaginae), *Desmodus rotundus* (Desmodontinae), and *Micronycteris megalotis* (Phyllostominae) were used as outgroups at different phases of the analyses. Specimens, localities, and codes for populations are described in Appendix 2.

The first analysis included *Glossophaga soricina, Desmodus rotundus,* and *Micronycteris megalotis* as outgroups to identify the phylogenetic relationships of the genus *Sturnira* with the genera *Uroderma, Vampyrops,* and *Carollia*. The second analysis used *Uroderma* and *Vampyrops* as outgroups to evaluate the monophyly of the subgenera *Corvira* and *Sturnira*. Finally, based on the above analysis and other reported works (Gardner and O'Neill, 1969, 1971; Owen, 1987), *S. bidens* was selected as the outgroup taxon for understanding the systematic relationships among species of the subgenus *Sturnira* that were analyzed: *S. lilium, S. tildae, S. magna, S. luisi, S. erythromos,* and *S. oporaphilum*. Thus, analyses of phylogenetic relationships involving the genus *Sturnira* were pursued from higher to lower taxonomic levels. Allele frequencies for the taxa studied here are summarized in table 3.

Rogers's modified genetic distance (Rogers's *D*; Wright, 1978) and Nei's genetic distance *D* (Nei, 1972), two commonly used measures of genetic distances, were employed. Use of two distance measures can identify the extent to which the structure of dendrograms is independent of the specific assumptions of each measure. Rogers's *D* satisfies the triangle inequality, an important feature for the generation of phyletic trees as discussed by Farris (1981), but it is not proportional to evolutionary time (Nei, 1987). On the other hand, Nei's *D* is roughly proportional to the time of historical divergence, but it may fail to satisfy the triangle inequality due to the logarithmic transformation that is involved (Richardson et al., 1986).

Unrooted Fitch-Margoliash networks (Fitch and Margoliash, 1967) were produced from the matrices of Rogers's *D* and Nei's *D* values using Felsenstein's PHYLIP program (1985). This tree-generating method was selected because it does not assume a constant evolutionary rate among lineages. A jackknife manipulation of taxa was performed with both genetic distances to identify unstable nodes that are presumably poorly supported by the data (Lanyon, 1985). Finally, the root for trees generated by the Fitch-Mar-

goliash method was determined by using one outgroup. Because the main objectives here relate to phylogenetic relationships rather than time of divergence, topologies but not branch lengths are discussed.

Acknowledgments

We thank Drs. Scott M. Lanyon, Field Museum of Natural History, and Thomas L. Poulson and Joel S. Brown, University of Illinois, Chicago, for their continued interest and assistance throughout this work. Scott M. Lanyon deserves special recognition here for sharing his technical and theoretical experience in biochemical systematics. Thanks are also due to A. T. Peterson for advice and expertise. Mary Anne Rogers was very helpful during the electrophoretic surveys.

Curators of several museums and institutions loaned us voucher specimens and tissues that made this study possible: Guy G. Musser, American Museum of Natural History; Charles O. Handley, Jr., National Museum of Natural History; Mark S. Hafner, Museum of Zoology, Louisiana State University; James L. Patton, Museum of Vertebrate Zoology, University of California, Berkeley; Robert D. Owen, The Museum, Texas Tech University; Terry L. Yates, Museum of Southwestern Biology, University of New Mexico; Luis Albuja, Escuela Politecnica National, Quito, Ecuador; and Hernando de Macedo, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima. We are grateful to these collectors, especially Linda J. Barkley, Gary L. Graham, and J. L. Patton, who were always available for assistance and advice. Rosa Arana participated in our fieldwork and turned our expedition into a very human, friendly, and unforgettable experience. This work was benefited also from the advice and comments of Philip Hershkovitz, Jack Fooden, and Lawrence R. Heaney.

Several curators offered the senior author great hospitality and assistance on visits to their institutions. Special gratitude is extended to Drs. Sydney Anderson, Charles O. Handley, Jr., John O'Neill, Mark S. Hafner, and James L. Patton.

This research was supported by the Barbara E. Brown Fund for Mammal Research and the Ellen Thorne Smith Bird and Mammal Study Center of the Field Museum of Natural History, as well as a LASPAU–Fulbright grant and a Grant-in-Aid of Research from the American Society of Mammalogists to Pacheco. This work was submitted to the University of Illinois, Chicago, in partial fulfillment of the requirements for the Master's degree of the senior author.

RESULTS

Morphological Analysis

Phylogenetic analyses of the 12 species of the subgenus *Sturnira* were conducted using *S. bidens* and *S. nana* as outgroups (fig. 1). The position of *Sturnira* sp. A is striking, being intermediate between the subgenera *Sturnira* and *Corvira* in several characters. *Sturnira* sp. A shares the presence of the four lower incisors with members of the subgenus *Sturnira.* However, it shares tooth gaps and the absence of zygomatic arch with members of *Corvira.* The position of *Sturnira* sp. A within the cladogram indicates that it could be recognized as a distinct subgenus. Additional specimens are needed to corroborate this assessment or to indicate that it is better considered a primitive member of the subgenus *Sturnira.*

Within the subgenus *Sturnira,* at least two lineages are apparent. The first is composed of *S. ludovici, S. oporaphilum, S. erythromos,* and *S. bogotensis.* These species are closely related in sharing the bilobate condition in the middle lower incisors (character 3). *S. erythromos* and *S. bogotensis* are joined further by the presence of a flat palate (character 13), whereas *S. ludovici* and *S. oporaphilum* share a developed protolophid (character 15); by parsimony, the same state in *S. tildae* (and *S. aratathomasi*) constitutes a parallelism within the subgenus. The second lineage is composed of *S. lilium, S. luisi,* and *S. thomasi.* They share the derived presence of a well-developed entoconid (character 14) and a slightly depressed palate (character 13). Within this lineage, relationships remain unresolved, as do placements of *S. tildae, S. mordax, S. magna,* and *S. aratathomasi.*

Using Owen's character matrix, PAUP resolved the two subgenera of *Sturnira* but left unresolved relationships within the subgenus

TABLE 3
Allele Frequency Data for Phyllostomid Bats

Locus	op-1[a] (1)[b]	op-2 (6)	op-3 (10)	op-4 (5)	bo-1 (7)	er-0 (8)	er-1 (4)	er-2 (1)
ACON-1	b[c]	a(.083) b(.917)	a(.063) b(.937)	b	d	d	d	d
ACON-2	a	a	a	a	a	a	a	a
αGPD	e	e	e	e	d	d(.833) g(.167)	d	d
		N=1	N=1	N=1	N=3	N=6		
GPI	e	e	b(.150) c(.200) e(.650)	b(.100) e(.800) a(.100)	e	e	e	e
GOT-1	b	b	b	b	b	b	b	b
ICD-1	g	g(.666) d(.334)	g(.750) d(.250)	g(.500) d(.500)	d	d	d	d
ICD-2	d	d	d	d	d	d	d	d
LAP	b	b	b	b(.700) c(.300)	b	b	b	b
		N=3	N=3		N=6	N=6		
PEP-B[d]	c	c	c	c	c(.714) g(.286)	c	c	c
LDH-1	a	a	a	a	a	a	a	a
LDH-2	a	a	a	a	a	a	a	a
MDH-1	a	a	a	a(.900) b(.100)	a	a	a	a
MDH-2	b	b	b	b	b	b	b	b
ME	g	g	g	g	d	d	d	d
PEP-D[e]	c	c	c	c	c	c	c	c
PGM	f	f	f	f	f	f	f	f
6PGD	—	c	c	c	c	b(.125) c(.875)	c	c
SOD	b	b	b	b	e	e	d(.125) e(.875)	e
SDH	e	e	e	e	b	b	b	b

[a] Codes for taxon name and population number are described in Appendix 2.
[b] Sample size for all loci unless mentioned in a specific locus.
[c] Allele frequency equals one unless mentioned in parentheses.
[d] Using leucine-glycine-glycine as substrate.
[e] Using phenylalanine-proline as substrate.

TABLE 3—(*Continued*)

Locus	er-3 (9)	er-4 (1)	er-5 (5)	er-6 (10)	er-7 (2)	er-8 (19)	ma-1 (4)	ma-2 (5)
ACON-1	d(.944) g(.056)	d	d	d	d	d	d(.250) g(.625) i(.125)	d(.100) g(.900)
ACON-2	a	a	a	a	a	a	a	a
αGPD	d N=4	—	d	d(.950) a(.050)	d N=1	d(.816) a(.184)	b	b
GPI	b(.056) e(.944)	e	e(.900) g(.100)	e	e	c(.026) e(.947) h(.027)	e	e
GOT-1	b	b	b	b	b	b	b	b
ICD-1	b(.056) d(.833) a(.111)	d	d(.900) a(.100)	b(.050) d(.950)	d	a(.026) d(.974)	b	b(.800) d(.200)
ICD-2	d	d	d	d	d	d	d	d
LAP	b	b	b	b	b	b	b	b
PEP-B[d]	c	c	b(.100) c(.900)	c	c	b(.026) c(.974)	c	c
LDH-1	a	a	a	a	a	a	a	a
LDH-2	a	a	a	a	a	a	a	a
MDH-1	a	a	a	a	a	a(.974) b(.026)	a	a
MDH-2	b	b	b	b	b	b	b	b
ME	d	d	d	d(.950) i(.050)	d	d(.895) i(.105)	d	d
PEP-D[e]	c	c	c	c	c	c	c	c
PGM	c(.056) f(.944)	f	d(.100) f(.900)	d(.050) f(.950)	f	f(.974) i(.026)	c(.875) f(.125)	c(.800) a(.200)
6PGD	c	c	c	b(.100) c(.900)	c	c	c	c
SOD	e	e	e	e	e	e	e	e
SDH	b	b	b	—	—	—	b	b N=1

TABLE 3—(*Continued*)

Locus	ti-1 (1)	ti-2 (4)	li-1 (1)	li-2 (1)	li-3 (3)	li-4 (6)	li-5 (7)	li-6 (7)
ACON-1	d	b(.125) d(.875)	c(.500) f(.500)	h	c(.667) f(.167) h(.166)	c(.917) f(.083)	c(.500) f(.500)	c(.786) f(.071) e(.143)
ACON-2	a	a	a	a	a	a(.750) b(.250)	a	a
αGPD	d	d	d	d	d	d	d N=6	d N=3
GPI	e	e	e	e	e	e	e	e
GOT-1	b	b	b	b	b	b	b	b(.929) c(.071)
ICD-1	d	g(.375) d(.625)	g(.500) i(.500)	g	g(.667) i(.333)	g(.667) i(.333)	g(.571) i(.429)	g(.929) c(.071)
ICD-2	d	d	d	d	d	d	d	d
LAP	b	b	b	b	b	b	b	b
PEP-B[d]	c	c	c	c	c(.500) e(.333) g(.167)	c(.917) e(.083)	c	c(.929) f(.071)
LDH-1	a	a	a	a	a	a	a	a
LDH-2	a	a	a	a	a	a	a	a
MDH-1	a	a	a	a	a	a	a	a
MDH-2	b	b	b	b	b	b	b	b
ME	g	g	g	g	g	g	g	g
PEP-D[e]	c	c	c	c	c	c	c	c
PGM	f	f	h	f(.500) i(.500)	f(.500) h(.333) i(.167)	f(.250) h(.667) i(.083)	f(.143) h(.786) i(.071)	f(.429) h(.571)
6PGD	c	c	c	c	c	c	c	c
SOD	b	b	d	d	d	b(.167) d(.833)	b(.286) d(.714)	d
SDH	—	g N=2	—	e	e	e(.833) f(.167)	e	—

TABLE 3—(*Continued*)

Locus	lu-1 (2)	bi-1 (7)	vd-1 (5)	ub-1 (7)	cp-1 (10)	dr-1 (1)	gs-1 (1)	mm-1 (1)
ACON-1	c	l	c	j	l	k	—	l
ACON-2	a	a	b	b	b	—	—	—
αGPD	d	a	d	c	d	g	e	f
GPI	e	g	f	f	N=7 g	c	i	a(.500) d(.500)
GOT-1	b	b	b	d	a	e	c	f
ICD-1	d	e	f	c(.214) e(.786)	h	i	e	g
ICD-2	d	c	a	a	a	a	a	b
LAP	b	b	b(.700) a(.300)	b	b	—	—	—
PEP-B[d]	c	b(.357) c(.571) e(.072)	c	e(.071) g(.786) h(.143)	b	d	a	i
LDH-1	a	a	a	a	b	c	c	c
LDH-2	a	a	a	a	b	c	e	d
MDH-1	a	a	a	a	a	a	a	a
MDH-2	b	b(.714) c(.143) a(.143)	b	b	b	b	b	b
ME	i	e	h	f	c	b	j	a
PEP-D[e]	c	c	d	d	b	d	d	a
PGM	f(.750) b(.250)	f	h	g(.071) h(.929)	f	d	b(.500) e(.500)	c
6PGD	c	c	c(.667) f(.333) N=3	c(.929) e(.071)	c	c	d	a
SOD	b	c	a	d	f	f	g	e
SDH	—	b	b	b	a	d	—	c

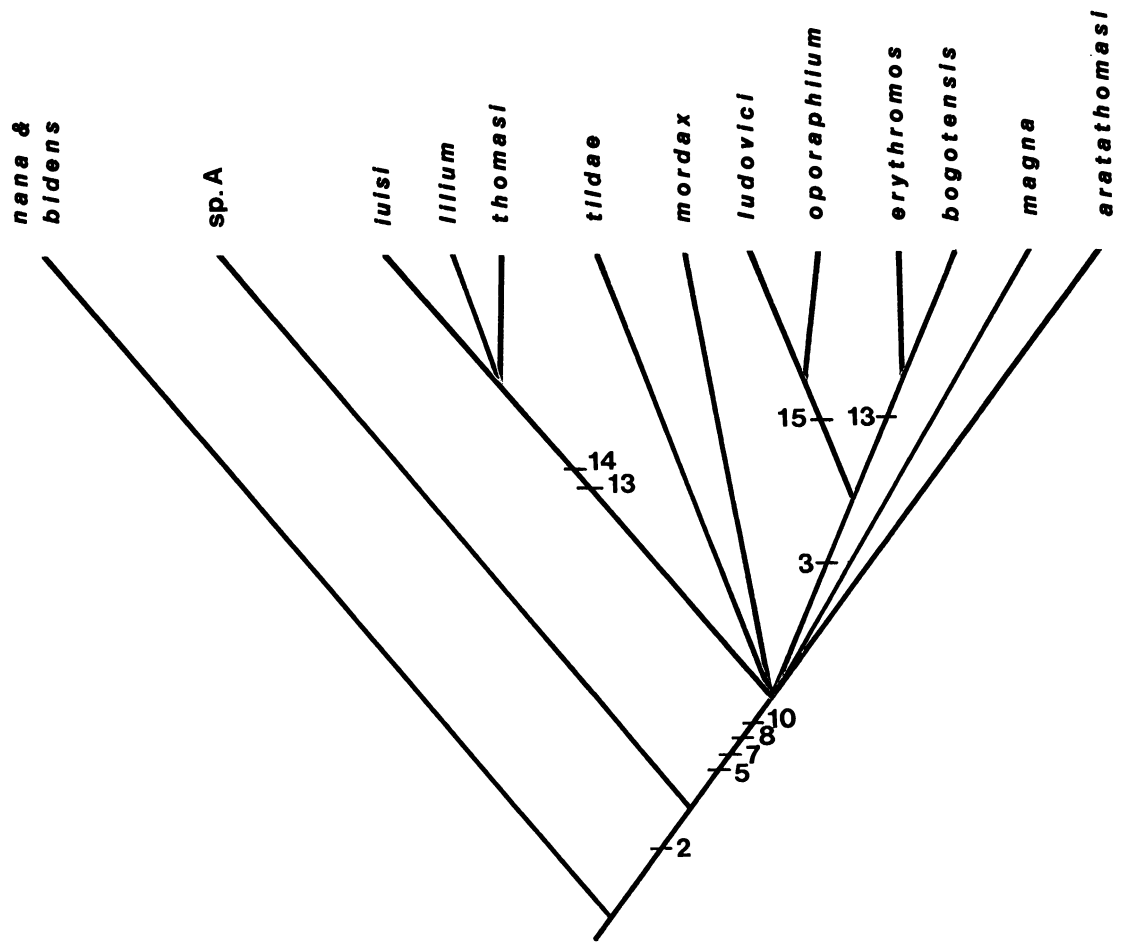

Fig. 1. Final strict consensus cladogram of species of the subgenus *Sturnira*, based on discrete morphological characters (table 1). *Sturnira bidens* and *S. nana* were used as outgroups. Numbers refer to derived morphological characters described in Appendix 1.

Sturnira (see also Owen, 1987, and his fig. 17). Because Owen's characters were selected for assessing higher-level relationships within the Stenodermatinae, they are not as useful for discerning interspecific relationships within speciose genera like *Sturnira*. Apparently, different sets of characters are needed to resolve relationships at different taxonomic levels.

Electrophoretic Analyses

Interspecific Variability: Loci with allelic frequencies higher than 0.95 were considered monomorphic (LDH-1, LDH-2, PEPT D). The average polymorphism value for *Sturnira* species was $P = 0.134$, with a range from 0.053 to 0.237 (table 4). These values are comparable to the value $P = 0.147$ given for mammals (Nevo, 1978) and are similar to an average of $P = 0.164$ that we have obtained from data for 25 phyllostomid bats (Koop and Baker, 1983) or $P = 0.141$ from a broader group of Neotropical bats (Straney et al., 1979). Heterozygosity values, H, ranged from 0.0197 in *S. luisi* to 0.0963 in *S. lilium*. These H values are also comparable to $H = 0.036$ given for mammals (Nevo, 1978), to $H = 0.037$ obtained from data for phyllostomid bats (Koop and Baker, 1983), and $H = 0.032$ from data in Straney et al. (1979).

Matrices of genetic distance values (Nei's *D* and Rogers's *D*) for all the Phyllostomidae analyzed here were based on 15 loci (table 5). Four loci (ACON-1, ACON-2, LAP, SDH) were not included because they were not shared by all the taxa. The same distance values for the stenodermatine species were based on 19 loci (table 6), accounting for minor differences between pairwise distance estimates in the two tables. The range of Nei's *D* among species of the subgenus *Sturnira* was 0.329–0.541 (Rogers's *D*, 0.121–0.358), whereas the distance between species of the subgenus *Sturnira* and the subgenus *Corvira* was higher, 0.615–0.656 (Rogers's *D*, 0.513–0.603). These values are grossly comparable to those of other mammalian taxa (Avise and Aquadro, 1982).

GENETIC DISTANCE ANALYSES: Relationships of taxa were inferred from genetic distance matrices of Nei's *D* and Rogers's *D* using the Fitch-Margoliash algorithm. Analysis of *Sturnira* was initially conducted using non-stenodermatine taxa (*Micronycteris megalotis, Desmodus rotundus, Glossophaga soricina*) to root the trees (fig. 2) and later using the stenodermatines *Vampyrops dorsalis* and *Uroderma bilobatum* for this purpose (fig. 3). Trees generated with Nei's *D* and Rogers's *D* differed in branch length but had identical topologies; only trees using Nei's *D* are shown.

The depicted pattern of relationships among the genera showed a closer relationship of *Sturnira* to other stenodermatines (*Uroderma, Vampyrops*) than to *Carollia* or *Glossophaga,* supporting the inclusion of *Sturnira* within the Stenodermatinae. In addition, these dendrograms showed the genus *Sturnira* as a natural group and consistently placed *S. bidens* at the base of the remaining *Sturnira* species. These analyses support the use of *S.* (*Corvira*) *bidens* as an outgroup for investigating relationships among species of the subgenus *Sturnira.*

Relationships within the subgenus *Sturnira* were evaluated using *S. bidens* to root the trees (fig. 4). The average percent standard deviation for 45 trees was 5.09 for Nei's *D* and 8.65 for Rogers's *D.* Because we are inferring phylogenetic relationships from topologies, branch distances were not analyzed. Two lineages were identified in figure 4: *S. oporaphilum* clusters with *S. tildae,* followed by *S. lilium* and *S. luisi,* whereas *S. erythromos* and *S. magna* compose a second group.

TABLE 4

Proportion of Polymorphic Loci and Heterozygosity Based on 19 Loci for the Species Here Examined

Species	N	Polymorphism, *P* (%)	Heterozygosity, *H*
Sturnira bidens	7	10.5	0.0521
S. oporaphilum	16	15.8	0.0530
S. erythromos	55	17.6	0.0304
S. magna	9	13.2	0.0413
S. tildae	4	15.8	0.0362
S. lilium	23	23.7	0.0963
S. luisi	2	5.3	0.0917
Vampyrops dorsalis	5	10.5	0.0455
Uroderma bilobatum	7	21.1	0.0503
Carollia perspicillata	10	0	0

Finally, pseudoreplicates were calculated to assess the robustness of these associations (Lanyon, 1985). As before, topologies of trees based on the two genetic distances were identical. The grouping of *S. tildae* and *S. oporaphilum* was not retained, and *S. tildae, S. oporaphilum, S. luisi,* and *S. lilium* composed an unresolved group. However, the node comprising *S. erythromos* and *S. magna* was retained in pseudoreplicates and appears to signify the special affinities of these taxa (fig. 5).

DISCUSSION

The position of *Sturnira* with respect to other phyllostomids and interspecific and subgeneric relationships within the genus are illuminated by cladistic analyses of morphology and genetics. Rather than cede superiority to one of these data sets, we have emphasized congruence in our analyses. Congruence among character sets is likely to reveal underlying historical patterns of relationship (Hillis, 1987).

Various workers (de la Torre, 1961; Baker, 1973; Smith, 1976; Gardner, 1977; Owen, 1987) have concluded that *Sturnira* is a member of the Stenodermatinae, while others have placed the genus outside the sub-

TABLE 5

Matrix of Genetic Distances for Phyllostomid Species Generated from Allele Frequency Data (table 3)

(Above the diagonal are modified Rogers's *D*, below Nei's *D*)

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. *Sturnira oporaphilum*	—	0.1839	0.2659	0.1954	0.3743	0.0852	0.5337	1.2990	1.0562	1.5586	1.5717	1.6804	0.7709
2. *S. lilium*	0.3948	—	0.2433	0.2294	0.3515	0.1190	0.6095	1.2016	0.7695	1.4785	1.9402	1.6426	0.5451
3. *S. erythromos*	0.4712	0.4491	—	0.1474	0.1836	0.1524	0.5390	1.1066	1.0605	1.5889	1.9835	1.5755	0.6573
4. *S. luisi*	0.4129	0.4399	0.3639	—	0.3611	0.0822	0.5774	1.1372	1.0673	1.5968	1.9247	1.9853	0.6435
5. *S. magna*	0.5464	0.5276	0.4017	0.5426	—	0.3615	0.6639	1.5745	1.0634	1.5929	1.9814	1.3308	0.7794
6. *S. tildae*	0.2800	0.3255	0.3693	0.2772	0.5424	—	0.5452	1.0844	1.0658	1.5952	1.9838	1.8440	0.6419
7. *S. bidens*	0.6233	0.6485	0.6277	0.6471	0.6792	0.6330	—	1.0503	0.9483	1.6754	1.6584	2.1180	0.8751
8. *Carollia perspicillata*	0.8410	0.8171	0.8093	0.8190	0.8832	0.8079	0.7930	—	1.3067	1.0986	1.5925	1.9980	1.1526
9. *Uroderma bilobatum*	0.7832	0.7037	0.7866	0.7918	0.7894	0.7909	0.7568	0.8403	—	1.0800	1.0924	1.9649	0.5143
10. *Desmodus rotundus*[a]	0.8763	0.8585	0.8825	0.8874	0.8853	0.8866	0.8866	0.8165	0.7997	—	1.0817	1.5925	1.1526
11. *Glossophaga soricina*[a]	0.8702	0.8961	0.9108	0.9106	0.9131	0.9143	0.8771	0.8851	0.7952	0.8062	—	1.5755	1.2898
12. *Micronycteris megalotis*[a]	0.8819	0.8697	0.8734	0.9152	0.8435	0.9033	0.9144	0.9220	0.9044	0.8851	0.8756	—	1.9829
13. *Vampyrops dorsalis*	0.7174	0.6286	0.6814	0.6794	0.7242	0.6783	0.7452	0.8210	0.6192	0.8210	0.8378	0.9139	—

[a] Species used as outgroups.

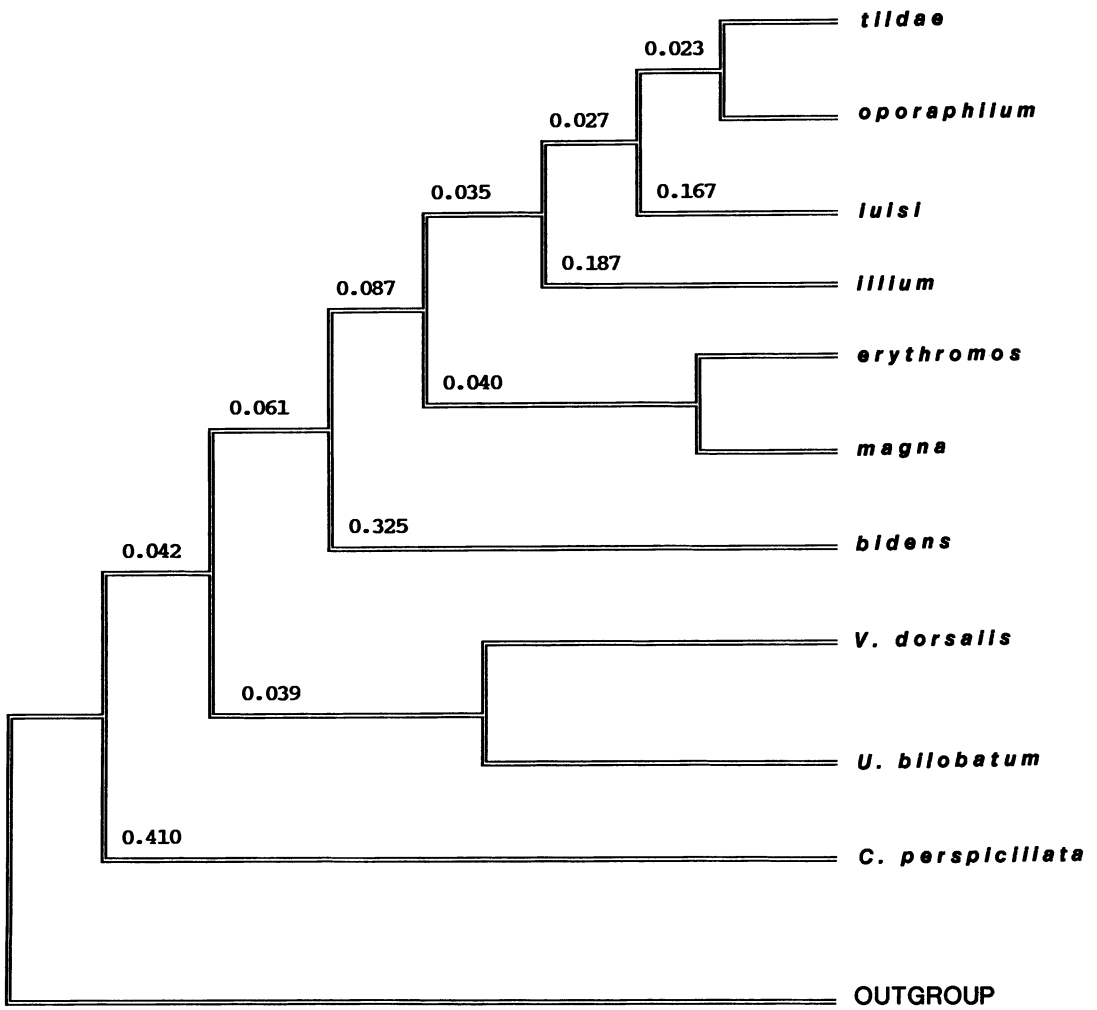

Fig. 2. Fitch-Margoliash dendrogram based on Nei's genetic distances, depicting phylogenetic relationships of four genera of Phyllostomidae. *Glossophaga soricina, Desmodus rotundus,* and *Micronycteris megalotis* were used as outgroups. Dendrogram was derived from table 5.

TABLE 6

Matrix of Genetic Distances Generated from Allele Frequency Data (Table 3)
(Above the diagonal are modified Rogers's *D*, below Nei's *D*)

	1	2	3	4	5	6	7	8	9
1. *Sturnira oporaphilum*	—	0.2061	0.2888	0.2285	0.3705	0.1213	0.5130	1.0757	0.8511
2. *S. lilium*	0.4128	—	0.2561	0.1941	0.3371	0.1445	0.5580	0.7945	0.5455
3. *S. erythromos*	0.4882	0.4582	—	0.1867	0.1953	0.1259	0.5140	1.0666	0.7440
4. *S. luisi*	0.4426	0.4072	0.4068	—	0.3580	0.1253	0.5454	1.0727	0.6181
5. *S. magna*	0.5408	0.5139	0.4123	0.5392	—	0.3409	0.6034	1.0590	0.8446
6. *S. tildae*	0.3299	0.3544	0.3379	0.3385	0.5266	—	0.5144	1.0663	0.7246
7. *S. bidens*	0.6145	0.6267	0.6193	0.6360	0.6557	0.6200	—	0.9732	0.9425
8. *Uroderma bilobatum*[a]	0.7877	0.7098	0.7914	0.7960	0.7876	0.7920	0.7671	—	0.5113
9. *Vampyrops dorsalis*[a]	0.7356	0.6226	0.7089	0.6672	0.7369	0.7032	0.7609	0.6165	—

[a] Species used as outgroups.

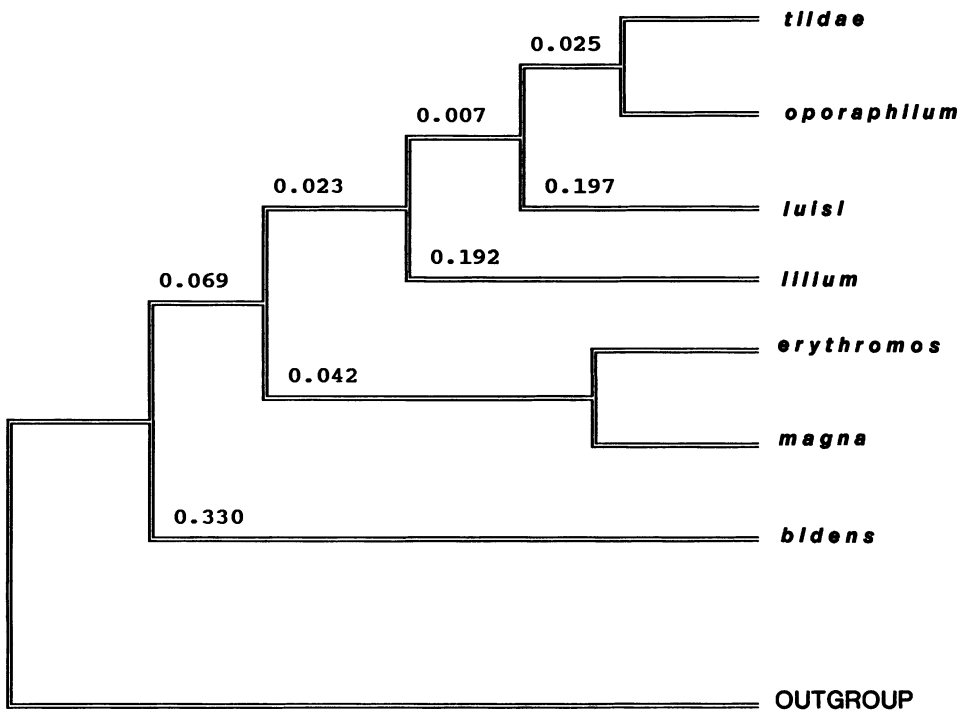

Fig. 3. Fitch-Margoliash dendrogram of the genus *Sturnira* based on Nei's genetic distances in table 6. *Uroderma* and *Vampyrops* were used as outgroups.

family (Walton and Walton, 1968; Slaughter, 1970). Herein, the placement of *Sturnira* within the Stenodermatinae is supported by allozymic data. Figure 2 shows that *Sturnira* is more closely related to the stenodermatines *Vampyrops* and *Uroderma* than to *Carollia* or *Glossophaga*. The latter two genera have traditionally been placed in separate subfamilies (Carolliinae and Glossophaginae, respectively), but Baker et al. (1989) included both in their Phyllostominae, *Carollia* as a member of the Stenodermatini and *Glossophaga* in the Glossophagini. Results in figure 2 indicate that, if *Carollia* is a member of a broadened stenodermatine clade, it is a basal member less closely related to typical stenodermatines than is *Sturnira*. Our alignment of *Sturnira* with *Vampyrops* and *Uroderma* contradicts earlier allozymic evidence that *Sturnira* is not a stenodermatine (Straney et al., 1979), but that study may be unreliable concerning relationships of *Sturnira* (Straney, personal commun.).

Owen (1987) demonstrated the monophyly of the genus *Sturnira* in his phylogenetic analyses of Stenodermatinae using discrete and continuous morphological characters. Here, the monophyly of *Sturnira* is supported by allozymic data. Although few other species of Phyllostomidae were analyzed in this study, their representation among subfamilies or tribes permits reliable tests of the monophyly of *Sturnira*. All seven species of the genus *Sturnira* cluster together in analyses using both the stenodermatines *Uroderma* and *Vampyrops* (fig. 3) and nonstenodermatine taxa to root the trees (fig. 2). Monophyly of the genus justifies our subsequent analyses of intrageneric relationships.

Within the genus *Sturnira*, *S.* (*Corvira*) *bidens* differed genetically from all species of the subgenus *Sturnira*. Nei's *D* and Rogers's *D* between *S. bidens* and other *Sturnira* were always greater than between any pair of species of the subgenus *Sturnira* (table 6). These results support the recognition of the subgenera *Corvira* and *Sturnira*.

Several discrete morphological character

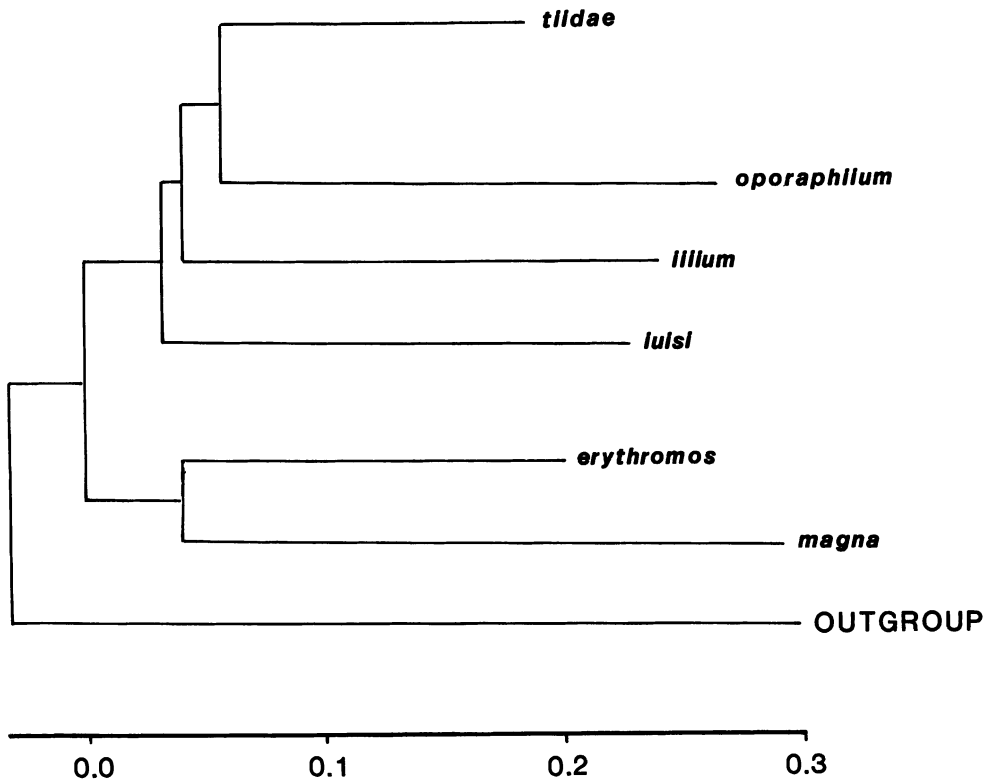

Fig. 4. Fitch-Margoliash dendrogram of the subgenus *Sturnira* based on Nei's genetic distances in table 6. *S.* (*Corvira*) *bidens* was used as the outgroup.

states differentiate the species of the subgenus *Sturnira* from the two species of the subgenus *Corvira* (fig. 1). Using different discrete characters, Owen (1987) arrived at the same conclusion, but the distinctiveness of *Corvira* was not apparent in phenetic analyses of continuous characters (Owen, 1987, 1988). He retained the subgeneric status of *Corvira,* following Gardner and O'Neill (1969, 1971). Genetic and morphological results here suggest that the subgenus *Corvira* is well defined and highly differentiated from other *Sturnira.* Based on our morphological analyses, *Sturnira* sp. A also appears to be a distinct but unnamed subgenus that is somewhat more closely related to the subgenus *Sturnira.* Additional specimens of this species are needed to substantiate this conclusion.

Some of the morphological characters used in our analysis were previously reported (de la Torre, 1961; Davis, 1980) but had been used mostly in the context of identification keys rather than in a formal phylogenetic analysis. For example, de la Torre (1961) used the lingual notch in the lower molar series to divide all *Sturnira* into "serrated" or "not serrated" species, treating *Sturnira bidens* as another "not serrated" species. On the other hand, Davis (1980) employed the same character only after removing *S. bidens* and *S. nana* (the subgenus *Corvira*) by their possession of two lower incisors. Here, 15 selected characters were used for the first time in an unweighted parsimony approach to construct a phylogeny. After comparing the resulting cladogram with a corresponding genetic dendrogram, we generated a hypothesis of phylogenetic relationships within the genus.

In the morphological cladogram, *Sturnira lilium, S. luisi* and *S. thomasi* compose a single lineage. *S. thomasi* was not included in the genetic analysis, which separated *S. lilium, S. luisi, S. tildae,* and *S. oporaphilum* as a distinct lineage. The close relationship

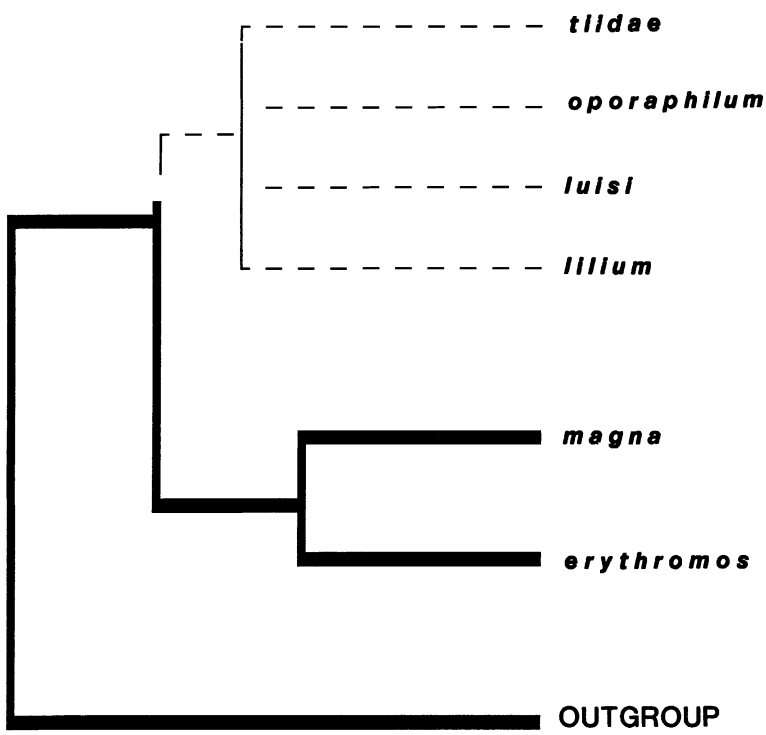

Fig. 5. Jackknife strict consensus tree based on figure 4 for species of the subgenus *Sturnira*. Bold lines indicate nodes that were stable to all permutations of the data matrix; dashed lines indicate unstable relationships.

of *S. lilium* and *S. luisi* is thus supported by both morphological and genetic data, although jackknife analyses of the genetic data call this association into doubt.

The jackknife strict-consensus tree based on allozymes strongly supported the node linking *Sturnira magna* and *S. erythromos*. However, in the cladogram based on morphology, the position of *S. magna* could not be resolved, and *S. erythromos* was joined to *S. ludovici, S. oporaphilum,* and *S. bogotensis*. Additional evidence supports the phylogenetic relationship of *S. magna* and *S. erythromos*. Both species possess an acrocentric Y chromosome, whereas *S. lilium* and *S. ludovici* have a subtelocentric Y chromosome (Gardner, 1977; Baker et al., 1982). Furthermore, the first lower molars of *S. magna* and *S. erythromos* are quite similar, with a small metaconid present and the protolophid and entoconid both absent.

In the cladistic analyses of morphology, *Sturnira bogotensis* was allied with *S. erythromos* rather than *S. oporaphilum,* despite the similar size of *S. bogotensis* and *S. oporaphilum. S. bogotensis* can be easily differentiated from *S. oporaphilum* and *S. ludovici* by the absence of the protolophid in the first lower molar (character 15). Detailed studies of the status of these taxa and their geographic variation will be reported elsewhere (Pacheco, in prep.).

The genetic dendrograms suggest that *Sturnira tildae* is related to *S. lilium* and *S. luisi,* but its position in the morphological cladogram is unresolved. Similarly, consensus is lacking for the placement of *S. oporaphilum*: morphology places it in a lineage with *S. ludovici, S. erythromos,* and *S. bogotensis,* while genetic data place it with *S. tildae, S. lilium,* and *S. luisi.*

We cannot choose on logical grounds between statements of relationship based on morphological characters and those summarized in the genetic dendrograms. A hypothesis of phylogenetic relationships within

Sturnira based on congruence of these analyses identifies two lineages: *Sturnira tildae, S. lilium, S. luisi,* and *S. thomasi* form one lineage, and *S. erythromos* and *S. magna* compose the second. Positions of other species in the subgenus *Sturnira* relative to these groups cannot be resolved. However, based on morphological similarities, *S. ludovici–S. oporaphilum* and *S. bogotensis–S. erythromos* seem to be sister pairs. Obviously, additional studies including the species not analyzed here are needed.

Morphologically, *Corvira* is distinguished mainly by the loss of characters distinguishing other taxa of *Sturnira,* rather than by the acquisition of novel apomorphic character states. Examples include the reduction or lack of zygomatic arch, the gaps among the cheek teeth, the reduced molar cusps, and the tendency for reduced number of lower incisors (Miller, 1907; Gardner and O'Neill, 1969, 1971). Instances of evolutionary loss complicate the identification of character states in common ancestors, whose existence can be inferred from monophyly. Based on the morphology of typical stenodermatines and of mammals generally, it seems probable that species of the subgenus *Corvira* were derived from an ancestor that resembled members of the subgenus *Sturnira.* In turn, this implies that the species of *Corvira* have undergone faster evolutionary differentiation (i.e., more rapid acquisition of apomorphic states in the characters under study) than members of the subgenus *Sturnira.*

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APPENDIX 1: DESCRIPTION OF MORPHOLOGICAL CHARACTERS

1. Shoulder glands: Externally indicated by a tuft of stiff modified hairs at front of shoulders, occurring mostly in adult males (Miller, 1907). 0, absent; 1, present.

2. Number of lower incisors: The outer lower incisors may sometimes be present as simple spicules (Gardner and O'Neill, 1971), in which case only the inner incisors were counted. This suggests that four teeth represents the primitive condition. 0, four present; 1, two present.

3. Number of lobes of inner lower incisors (i1): Scores from juveniles and subadults were used when the adult scores were misleading because of tooth wear. The outer lower incisors were not scored because they were apparently more prone to wear than the inner ones. 0, three lobes present; 1, two lobes present.

4. Inner lower incisors (i1) with median lingual cusp: This structure appears to be a modification of the posterior border of the cingulum; in old specimens it is affected by wear. 0, present; 1, small; 2, absent.

5. Shape of lower incisors: Defined by the shape of outline. Curved shape means a slight convexity outlined by the anterior border of the teeth; triangular shape is caused by highly protruded incisors. When only two incisors were present, we scored it as a missing value because the shape produced by two teeth did not logically apply (Swofford, 1985). 0, curved; 1, triangular.

6. Cingulum of the lower canines: Two canine types are apparent among the species of *Sturnira*: slender and broad. The latter is apparently the result of greater development of the cingulum. 0, slender; 1, broad.

7. Tooth gaps: These are spaces between premolars and molars apparently produced by the reduction of the paracone(id). We scored *Sturnira mordax* as not having gaps, although the scored specimen presented an incipient or vestigial gap among the molars, but the paracone(ids) were not reduced. Other *Sturnira* species rarely presented indications of gaps, especially between molars, either in the upper or the lower jaw. 0, gaps absent; 1, gaps present.

8. Zygomatic arch: An incomplete zygomatic arch among the *Sturnira* was considered homologous based on the underlying similarities of the squamosal bone. The absence of zygomatic arches in the presumably related genera such as *Carollia* seems not homologous to that character in *Sturnira*. The two taxa differ in the orientation of the squamosal, being mainly horizontal in *Sturnira* and vertical in *Carollia*. 0, absent; 1, present.

9. Posterior third lower molar (m3): Although the absence of the third lower molar can be correlated with other tendencies for reduction, such as dental gaps, it is considered uncorrelated with other characters. Some individual variation was noted. 0, present; 1, absent.

10. Posterior internal basal cusp in inner upper incisor (I1): This character could be homologous with the lingual cusp of the lower incisors (character 4). However, because of the distinct shape of these structures they were considered independent. 0, present; 1, intermediate; 2, absent.

11. Lobes of inner upper incisors (I1): This character was difficult to score in some taxa because it is quickly worn. Linares (1986) indicated that *bogotensis* differs from *erythromos* in tending to have entire incisors, not the distinct bilobate incisors of *erythromos*. We have observed the bilobate state in juveniles and subadults of *bogotensis* and entire incisors in adults of *erythromos*. Whenever available, juveniles or subadults were scored. Number of lobes (one or two) was scored without consideration of their size. 0, one lobe; 1, two lobes.

12. Orientation of upper inner incisors (I1): The direction of the incisors was considered relative to the course of the upper canines. Incisors following the curve of the upper canines were called curved and those oriented more forward or separate from the upper canines were termed protruded. This character was also difficult to score because it is affected by sexual dimorphism. The males of some species have more protruded incisors than do females (e.g., *Sturnira magna*). 0, curved; 1, protruded.

13. Palate depth: Adults have either a "depressed" or a "flat" palate. Depressed indicates a concavity in transverse view, usually with a conspicuous but narrow longitudinal groove; a flat palate is more planar or slightly concave but without a narrow groove. An intermediate score was included because it proved to be constant in the observed series. This character is strongly affected by age, with juveniles and subadults having a more depressed and narrow palate than adults. This developmental variation can confuse identification, in which case states may be recognized by the width of the palate. 0, depressed palate; 1, slightly depressed with rare presence of narrow groove; 2, flat palate.

14. Entoconid of first lower molar (m1): We have chosen this character because it seems to represent a complex molar pattern in a simple way. It partially corresponds to the "serrated or not serrated" lower molars of Davis (1980) and to the "vertical division" between the metaconid and en-

toconid of de la Torre (1961). 0, absent; 1, developed.

15. Protolophid in first lower molar (m1): Ridge between the protoconid and the metaconid of the first lower molar. It is also associated with the distance between the two cusps. The protoconid and metaconid are much closer together when the protolophid is present than when it is not. When the protolophid was not clearly observable, the distance between the cones indicated the pattern. The character was observed in all age classes and was still visible (when present) in worn teeth. 0, absent; 1, developed.

APPENDIX 2: SPECIMENS EXAMINED IN THE CLADISTIC AND ELECTROPHORETIC ANALYSES

Codes used in table 3 are in boldface type in parentheses. * Specimens used only in the cladistic analysis. † Specimens used only in the electrophoretic analysis. Museum acronyms are as follows: AMNH, American Museum of Natural History; EPN, Escuela Politécnica Nacional, Ecuador; FMNH, Field Museum of Natural History; LSUMZ, Museum of Zoology, Louisiana State University; MSB, Museum of Southwestern Biology, University of New Mexico; MVZ, Museum of Vertebrate Zoology, University of California; MZUSP, Museu de Zoologia, Universidade de São Paulo, Brazil; TTU, The Museum, Texas Tech University; USNM, National Museum of Natural History (United States).

Carollia perspicillata†: PERU: Amazonas, 3 km E Balzas, FMNH 128764–128768; Río Utcubamba, 15 km (by road) N of Pedro Ruiz, FMNH 128773–128777 (**cp-1**).

Desmodus rotundus†: PERU: Lima, San Bartolomé, Rímac Valley, FMNH 129204 (**dr-1**).

Glossophaga soricina†: PERU: Amazonas, 3 km E Balzas, FMNH 128681 (**gs-1**).

Micronycteris megalotis†: BRASIL: Rondônia, Cachoeira Nazaré, W bank Rio Ji-Paraná, BDP 2103 (MZUSP uncatalogued) (**mm-1**).

*Sturnira aratathomasi**; COLOMBIA: Valle del Cauca, Pance, ca. 20 km SW Cali, USNM 395158.

Sturnira bidens: PERU: Piura, "Batan" on Zapalache–Carmen trail, LSUMZ 26920–26922; "Machete" on Zapalache–Carmen trail, LSUMZ 26915–26916; "Lucuma" on Zapalache–Carmen trail, LSUMZ 26919; Cerro Chinguela, ca. 5 km NE Zapalache, LSUMZ 26924 (**bi-1**).

*Sturnira bogotensis**: COLOMBIA: Bogotá, La Uribe, USNM 251986–251987. Santander, Puente Nacional, AMNH 207851. Bogotá, Base de Monserrate, AMNH 207852–207857. Cundinamarca, Bogotá, AMNH 207858–207860; Mesitas del Colegio, AMNH 207861–207862; Sibate, AMNH 212276; Usaguen, N of Bogota, AMNH 62798; Choachi, Bogotá region, AMNH 61556; Bogotá, USNM 251988. Bogotá, Estacion La Uribe, USNM 251989. VENEZUELA: Merida, Montes de Lourdes, AMNH 24378; Tachira, 35 km S, 22 km W of San Cristobal (Buena Vista), USNM 440088.

Sturnira erythromos: PERU: Lima, San Bartolomé, FMNH 128789–128792; Bosque de Zarate, FMNH 128935, 128793–128794 (**bo-1**). Ancash, Río Mosna, FMNH 128781–128788 (**er-0**). Amazonas, 19 km (by road) E Balzas, FMNH 128796–128799 (**er-1**); Río Utcubamba, between Churuja and Pedro Ruiz, FMNH 128809 (**er-2**); ca. 20 km (by road) W Leymebamba, FMNH 128800–128808 (**er-3**). Cajamarca, Río Zaña, 2 km N Monteseco, FMNH 128811 (**er-4**). Cuzco, 32 km NE Paucartambo (km 112), MVZ 171436–171437, 171440–171442 (**er-5**). Piura, Cruz Blanca, 33 km road SW Huancabamba, LSUMZ 26930–26933; Cerro Chinguela, 5 km NE Zapalache, LSUMZ 26925–26927; Machete on Zapalache Carmen trail, LSUMZ 26928–26929 (**er-6**). San Martín, Puerto del Monte, 30 km NE los Alisos, LSUMZ 27280–27281 (**er-7**). Huánuco, Unchog, pass between Churubamba and Hacienda Paty, NNW Acomayo, LSUMZ 28167–28168, 28173, 28179–28180, 28182, 28185–28188 (**er-8**).

Sturnira lilium: SURINAM: Marowijne, Oelemarie, TTU-TK 21008 (**li-2**). PERU: Cajamarca, Limón, W of Balzas, FMNH 128837–128839 (**li-3**); Río Zaña, 2 km N Monteseco, FMNH 128856, 128858, 128888–128889, 128891–128892, 128894 (**op-5**). Amazonas, 19 km (by road) E Balzas, FMNH 128812 (**li-1**). Río Utcubamba, 15 km (by road) N of Pedro Ruiz, FMNH 128814, 128819–128820, 128823, 128825, 128829 (**li-4**); Río Cenepa, vicinity of Huampaní, MVZ 154839–154841; ca. 0.5 mi W of Huampaní, Río Cenepa, MVZ 153362–153365 (**op-6**).

*Sturnira ludovici**: COLOMBIA: Huila/Cauca, 1 mi S Moscopas, Río La Plata, USNM 483510. Magdalena, Sierra Negra, Villanueva, Valledupar, USNM 281259–281261, 281264. Valle del Cauca, Dapa, 15 km NW Cali, USNM 483511; 2 km S de Pance, ca. 20 km SW Cali, USNM 483512–483516. ECUADOR: Cañar, San Jose, 12 mi SW Huicra, FMNH 48785; San Juan, 15 mi W Huicra,

FMNH 48786. Carchi, Maldonado, EPN 7975. Esmeraldas, ca. Río Cauce, FMNH 44296–44297. Pichincha, Gualea, W side Pichincha, AMNH 67329. Loja, Santa Barbara, EPN 2485. Near Mindo, FMNH 48343–48348, 48784; Zapadores, USNM 513448–513449. Pastaza, Mera, USNM 548146; 1.5 km E Mirador, USNM 513456–513457. Imbabura, Paramba, USNM 113370. Zamora-Chinchipe, 3 km NE Cumbaratza, USNM 513452–513455; 4 km NE Sabanilla, USNM 513451. VENEZUELA: Barinas, Altamira, 2 km SW of La Vega del Río Santo Domingo, USNM 440134–440148. Carabobo, San Esteban, FMNH 29440. Distrito Federal, Caracas, 5 km N of Los Venados, USNM 370374–370387, 370389.

Sturnira luisi: PERU: Lambayeque, Las Juntas in Quebrada La Pachinga, ca. 14 km N, 25 km E Olmos, LSUMZ 27256–27257 (**lu-1**); 16 km N, 25 km E Olmos*, MVZ 135569. Piura*, 15 road km E Canchaque, LSUMZ 18982.

Sturnira magna: PERU: Amazonas, ca. 0.5 mi W of Huampaní, Río Cenepa, MVZ 153368–153369, 153371–153372 (**ma-1**). Loreto, Quebrada Orán, 5 km N Río Amazonas, 85 km NE Iquitos, LSUMZ 28288–28289, 28260–28262 (**ma-2**).

*Sturnira mordax**: COSTA RICA: Cartago, Rio Chitaria (above highway), LSUMZ 12788. San José, Fila La Maquina, 7.5 km E Canaan, LSUMZ 12784–12787; Colorado, LSUMZ 11454–11456; San Gerardo, LSUMZ 12781, 12783. Puntarenas, Finca Las Cruces, 2 km S San Vito, FMNH 124092.

*Sturnira nana**: PERU: Ayacucho, Huanhuachayo, AMNH 219138, 219171–219173; LSUMZ 16522–16524, 15683; Río Santa Rosa, San Jose, LSUMZ 16519.

Sturnira oporaphilum: PERU: Amazonas, 3 km E Balzas, FMNH 128919 (**op-1**); Río Utcubamba, 15 km (by road) N of Pedro Ruiz, FMNH 128920–128925 (**op-2**). Cajamarca, 2 km N of Monteseco, Río Zaña, FMNH 128926–128934, 128795 (**op-3**). BOLIVIA: Santa Cruz, San Rafael de Amboro, MSB 55904, 56184–56185; 4.5 km N, 1.5 km E Cerro Amboro, Río Pitasana, MSB 56177–56178 (**op-4**).

*Sturnira thomasi**: LESSER ANTILLES: Guadaloupe Basse Terre, Grande Etang, AMNH 234950. French Leeward Ids., USNM 361883.

Sturnira tildae: BRASIL: Rondônia, Cachoeira Nazaré, W bank Rio Ji-Paraná, BDP 2128 (MZUSP uncatalogued) (**ti-1**). PERU: Ucayali, Balta, Río Curanja, MVZ 136449, 136487–136489. SURINAM: Marowijne, Oelemarie, TTU-TK 21007. Saramacca, Tafelberg, SE side Arrowhead Basin, TTU-TK 17702, 17703. TRINIDAD: Mayaro, 1 mi S, 2 mi W Guayaguayare, TTU-TK 25221 (**ti-2**).

Sturnira sp. A*: ECUADOR: Chimborazo, Pallatanga, EPN E-6722.

Uroderma bilobatum†: BRASIL: Rondônia, Cachoeira Nazaré, W bank Rio Ji-Paraná, BDP 2107, 2158, 2182, 2198, 2210, 2215, ALG 14924 (MZUSP uncatalogued).

Vampyrops dorsalis†: PERU: Amazonas, 19 km (by road) E Balzas, FMNH 129133–129134, 129137–129138. Cajamarca, Limón, W of Balzas, FMNH 129143 (**vd-1**).