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EVOLUTION INTO THE ANDES: MOLECULAR EVIDENCE FOR SPECIES RELATIONSHIPS IN THE GENUS *LEPTOPOGON*

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ABSTRACT.—We studied relationships among species of the Neotropical flycatcher genus *Leptopogon* (Tyrannidae), which have modern-day distributions that include a lowland-tropical-zone member, an upper-tropical-zone member, and two subtropical-zone members. Along the eastern slope of the eastern Andes, species inhabiting the different elevational zones occur parapatrically to one another. Both allozymes and restriction-fragment-length polymorphisms of mitochondrial DNA suggest the same phylogenetic hypothesis: the lowland-tropical-zone species (*L. amaurocephalus*) is the basal member of the clade, and the upper-tropical-zone species (*L. superciliaris*) is the sister taxon of the two subtropical-zone species, *L. taczanowskii* and *L. rufipectus.* These data are consistent with diversification into successively higher-elevation habitats in the Andes. The biochemical data also suggest that this genus is substantially differentiated from the genera near it in traditional classifications (*Mionectes, Phyllomyias, Lophotriccus*). *Received 6 August 1992, accepted 31 December 1992.*

RUNNING THE LENGTH of western South America, the Andes mountains were formed by the collision of several tectonic plates beginning approximately 20 million years ago (Zeil 1979). The formation of these mountains had profound effects on the species diversity of the flora and fauna of South America because the newly formed, higher-elevation habitats of these mountains were colonized by taxa that subsequently speciated from their sister taxa in adjacent regions. In his classic monograph on the distribution of birds in Colombia, Chapman (1917) recognized four sources for avian taxa that colonized newly available habitats in the uplifted Andes: (1) the South American tropical lowlands, (2) the Guianan highlands, (3) the Central American highlands, and (4) the southern South American temperate lowlands.

One of many avian genera with representatives in both the lowlands and the Andes is the tyrannid genus *Leptopogon.* The genus includes four forest-dwelling species: (1) *Leptopogon amaurocephalus,* a lowland-tropical species that occurs from northern Argentina to southern Mexico (*L. amaurocephalus* occurs up to elevations of 600 m in the Andes, but up to 1,200 m in the Tepuis in the absence of *L. superciliaris;* Willard et al. 1991); (2) *L. superciliaris,* an upper-tropical-zone (600 to 2,100 m) species that is parapatric with *L. amaurocephalus* along the base of the Andes from Bolivia to Venezuela, and north to Costa Rica (in the absence of *L. amaurocephalus, L. superciliaris* ranges below 600 m on the western slopes of the Andes, extreme north-

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ern Venezuela and Trinidad; Meyer de Schauensee and Phelps 1978, Hilty and Brown 1986, ffrench 1991); and (3 and 4) *L. taczanowskii* and *L. rufipectus*, which are allopatric replacements of one another in Andean subtropical forests (1,600 to 2,700 m) above *L. superciliaris* from Colombia and southern Venezuela to central Peru (Traylor 1979, Fjeldså and Krabbe 1990). *Leptopogon taczanowskii* and *L. rufipectus* are separated by the Río Marañon valley in northern Peru (Parker et al. 1985). Thus, along much of the eastern slope of the Andes, one finds three species of *Leptopogon* occurring parapatrically to one another at successively higher elevations.

We studied differentiation in allozymes and restriction-fragment-length polymorphisms (RFLPs) of mitochondrial DNA (mtDNA) among the four recognized species of the genus *Leptopogon* to determine if evolution in this group was consistent with evolution into the Andes as envisioned by Chapman (1917). If the Andean members of the genus evolved from lowland ancestors, we predict the following relationships: *L. amaurocephalus* should be the most basal member of the genus, followed by a clade containing the upper-tropical-zone species (*L. superciliaris*) and the two subtropical-zone species (*L. taczanowskii* and *L. rufipectus*), which should be sister taxa. The two independent molecular data sets permit tests of congruence that potentially strengthen conclusions about patterns of evolution in the genus (Hillis 1987, Zink and Avise 1990, Miyamoto and Cracraft 1991).

METHODS

Specimens were collected by Louisiana State University Museum of Natural Science (LSUMNS) personnel in Panama, Peru, Bolivia, and Puerto Rico (see Appendix) between 1980 and 1989. Voucher study skins are in the LSUMNS. Samples of heart, liver, and breast muscle collected in the field and stored in liquid nitrogen (Johnson et al. 1984) were later cataloged into the LSUMNS Frozen Tissue Collection and stored at −70°C.

Allozymes.—Sample sizes for allozymes were: *L. amaurocephalus* ($n = 3$), *L. superciliaris* (2), *L. taczanowskii* (2), and *L. rufipectus* (1). In addition, the following species were included because they have been placed near *Leptopogon* in other classifications (Traylor 1977, 1979, Sibley and Ahlquist 1985): *Mionectes olivaceus* ($n = 1$), *Phyllomyias plumbeiceps* (1), and *Lophotriccus eulophotes* (1). Finally, *Tyrannus dominicensis* ($n = 3$) was included as an outgroup because the genus has been placed in a separate subfamily (Traylor 1977, Sibley and Ahlquist 1985). Methods for starch-gel electrophoresis followed those of Harris and Hopkinson (1976) and Richardson et al. (1986). The computer program BIOSYS-1 (Swofford and Selander 1981) was used to calculate Nei's (1978) and Rogers' (1972) genetic distances (*D*), as well as UPGMA and distance-Wagner phenograms. Although not without problems, genetic distances are useful because they can be compared directly to distances generated from other avian studies to assess relative degrees of divergence. The FITCH and KITSCH options in the computer program PHYLIP (Felsenstein 1986) were used to estimate trees (Fitch and Margoliash 1967) based on Rogers' (1972) *D*. Trees generated using FITCH do not assume equal rates of evolutionary change in all lineages, whereas those generated using the KITSCH option do. Although Archie et al. (1989) have demonstrated that small sample sizes can bias estimates of genetic distance in allozymic studies, the degree of divergence among these taxa may minimize problems related to this bias.

Cladistic analyses of allozyme data were performed in two ways: (1) by constructing data matrices coding loci as characters and alleles as unordered character states (polymorphisms in terminal taxa were treated as true polymorphisms and not as uncertainties); and (2) by considering the presence (1) or absence (0) of alleles across all loci. Note, however, that the validity of the second approach has been questioned (Mickevich and Mitter 1981, Swofford and Berlocher 1987, Murphy 1993; for a defense of the approach, see Rogers and Cashner 1987). Trees were rooted using *Tyrannus dominicensis*. The data matrices were analyzed using the exhaustive-search routine of the computer program PAUP 3.0L for the Macintosh (Swofford 1989), which generated most-parsimonious cladograms and their consistency indices (*CI*) excluding uninformative characters. In addition, both matrices were subjected to bootstrap analyses to assess relative confidence in nodes (Felsenstein 1985).

MtDNA.—We isolated mtDNA for RFLP analysis using established protocols (Lansman et al. 1981, Avise and Zink 1988). *Leptopogon* tissue was from the same individuals used in the allozyme analysis. The *Phyllomyias plumbeiceps* specimen from the allozyme study was chosen as an outgroup for the mtDNA study based on allozyme results. An individual of an additional species, *Pogonotriccus orbitalis*, was also included because it is a member of a group of small Andean cloud-forest flycatchers that shares characteristics with *Leptopogon*, such as a penchant for wing flipping and mottled auriculars (Hilty and Brown 1986, J. Fitzpatrick pers. comm.). Several members of *Pogonotriccus* were originally described in *Leptopogon* (Traylor 1977, Traylor 1979), so inclusion of this species provided a further test of the monophyly of *Leptopogon*.

Thirteen restriction enzymes produced patterns that

TABLE 1. Allelic frequencies for variable loci (loci abbreviations follow Richardson et al. 1986). Letters designate alleles (numbers in parentheses are allele frequencies where polymorphisms occur). Taxa as follows: Td (*Tyrannus dominicensis*), Mo (*Mionectes olivaceus*), Le (*Lophotriccus eulophotes*), Pp (*Phyllomyias plumbeiceps*), Lr (*Leptopogon rufipectus*), Lt (*L. taczanowskii*), Ls (*L. superciliaris*), La (*L. amaurocephalus*).

	Taxon							
Locus	Td	Mo	Le	Pp	Lr	Lt	Ls	La
ACON	E	F (0.50) G (0.50)	D	C	A	A	A	A (0.33) B (0.67)
AK	B	A	A	B	A	A	A	A
CK1	B	A	A	A	A	A	A	A (0.83) C (0.17)
CK2	B	A	C	D	E	E (0.75) F (0.25)	E	D
GOT1	A	B	C	A	A	A (0.50) B (0.50)	A	A
GPI	B (0.17) D (0.83)	B	B	B	B	B	B (0.75) C (0.25)	A (0.33) B (0.67)
ICD1	B (0.83) A (0.17)	A (0.50) C (0.50)	D	A	A	A	A	A
ICD2	B (0.33) C (0.67)	D	C	A	A	A	A	A
LDH1	B	A	A	A	A	A	A	A
LDH2	A	A	B	C	A	A	A	A
ME	A	A	B	B	A	A	C	B
MPI	F	D	A (0.50) B (0.50)	G	C	C	E	E
NP	F (0.33) G (0.67)	E	D	C	A	A	A (0.75) B (0.25)	A (0.83) B (0.17)
PEP-A	E	A (0.50) B (0.50)	A	C (0.50) D (0.50)	E	E	E	E
PEP-B	D	F	E	G	A (0.50) B (0.50)	A (0.25) B (0.25) C (0.50)	A (0.50) B (0.50)	C
PEP-C	D	A	B	C (0.50) E (0.50)	B	B	C	B (0.17) C (0.83)
6PGD	D	C	B	E	A	A	A	A
PGM1	A	A	A	A	A	A	A (0.75) C (0.25)	B
PGM2	D	E	C	B	A	A	A	D
SOD1	C	B	B	A	A (0.50) D (0.50)	A	A	B

could be scored for most of the study individuals; relative restriction-site maps could be inferred for nine of these enzymes. We combined restriction-site data and restriction-fragment data (for the four enzymes with digestion patterns too complex to determine sites), and coded sites and fragments as present or absent. This matrix was analyzed cladistically using PAUP 3.0L. Missing data were coded as "?". We calculated *P*-values (Nei and Li 1979) as estimates of percent sequence divergence from the restriction-site data using computer programs written by M. Ball and J. Neigel (the matrix of *P*-values is available from the authors or can be computed from the restriction-site data). In several cases (all in *L. amaurocephalus*), there were polymorphisms in terminal taxa; these characters were assigned the character state agreeing with the presumed sister taxon to calculate *P*-values.

RESULTS

Allozyme data.—Across all taxa, 20 of 24 loci surveyed were polymorphic (Table 1); four (GLUD, FUM, MDH2, GOT2) were monomorphic. UPGMA analysis (Fig. 1) of Rogers' (1972) *D* (matrix available upon request) generated the same intrageneric branching sequence for *Leptopogon* as distance-Wagner, KITSCH and FITCH analyses (not shown): (1) all members of *Leptopogon* clustered together; (2) *L. amaurocephalus* was the most basal taxon; (3) *L. superciliaris* was the next most basal taxon; and (4) *L. taczanowskii* and *L. rufipectus*, the two allopatric subtropical-zone species, were sister taxa. The only differences among trees produced by these al-

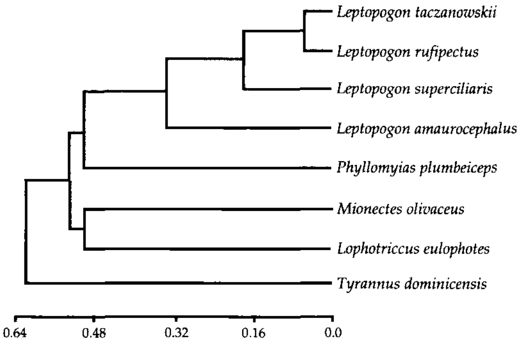
Leptopogon taczanowskii
Leptopogon rufipectus
Leptopogon superciliaris
Leptopogon amaurocephalus
Phyllomyias plumbeiceps
Mionectes olivaceus
Lophotriccus eulophotes
Tyrannus dominicensis
0.64
0.48
0.32
0.16
0.0
Rogers' (1972) D

Fig. 1. UPGMA phenogram, based on Rogers' (1972) *D* values, of relationships among *Leptopogon* and selected outgroups. Cophenetic correlation coefficient equals 0.992. Results of other phenetic and cladistic analyses of allozyme data showed same intrageneric relationships in *Leptopogon*.

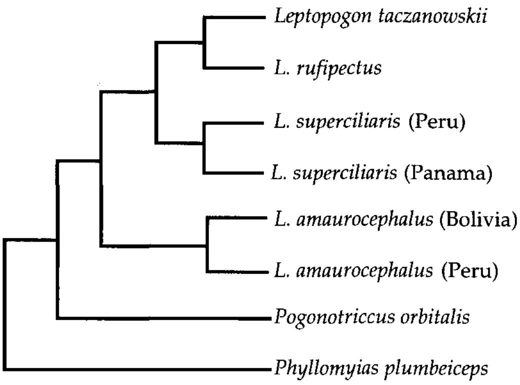
Leptopogon taczanowskii
L. rufipectus
L. superciliaris (Peru)
L. superciliaris (Panama)
L. amaurocephalus (Bolivia)
L. amaurocephalus (Peru)
Pogonotriccus orbitalis
Phyllomyias plumbeiceps

Fig. 2. Most-parsimonious tree (141 steps, *CI* = 0.689) for relationships among *Leptopogon* flycatchers based on restriction-fragment-length polymorphisms of mtDNA (Table 2).

gorithms involved relationships among the outgroup genera.

The cladistic analysis using loci as characters and alleles as unordered character states (the data matrices for this and the following analysis can be constructed from Table 1) produced 76 most-parsimonious trees (*CI* = 0.903) and no resolution in a 50% majority-rule consensus tree (not shown). One of these trees was the tree supported by the phenetic analyses. The analysis using the presence or absence of alleles as characters resulted in only two most-parsimonious trees (45 steps, *CI* = 0.622, trees not shown) that differed only in the placement of outgroups. Thus, in this analysis *Leptopogon* was monophyletic and exhibited the same intrageneric branching sequence found by the distance analyses (Fig. 1). Relationships within *Leptopogon* also were well supported after bootstrapping these data (nodes supporting relationships in *Leptopogon* appeared in 81% or more of 1,000 bootstrapped replicates). Thus, although allozymes provided little resolution of relationships among outgroups, relationships in *Leptopogon* were well supported.

MtDNA data.—All 13 restriction enzymes produced two or more restriction-fragment profiles within *Leptopogon*. Parsimony analysis of data from nine restriction enzymes for which sites could be inferred combined with fragment data from the other four restriction enzymes (Table 2) yielded a single most-parsimonious tree (141 steps, *CI* = 0.689, Fig. 2) that was identical to the allozyme tree in the relationships among *Leptopogon*. Due to the potential lack of independence among restriction fragments (Swofford and Olson 1990), these data were not bootstrapped.

For the 28 restriction sites scored for all eight taxa, mean *P*- values between *Phyllomyias* and *Leptopogon* were 0.123 ± SD of 0.017 ($n = 6$), and between *Pogonotriccus* and *Leptopogon* were 0.183 ± 0.019 ($n = 6$), whereas the mean *P*-value among taxa in *Leptopogon* was only 0.044 ± 0.018 ($n = 15$). Mean *P*-values between *Pogonotriccus* and *Leptopogon*, and among *Leptopogon*, based on 50 restriction sites (seven enzymes; Table 2) were 0.169 ± 0.015 ($n = 6$) and 0.054 ± 0.019 ($n = 15$), respectively. Thus, based on percent sequence divergence, the mtDNA data suggest that *Leptopogon* is highly differentiated from other flycatcher genera.

The *P*-value between the two allopatric highland taxa (*L. taczanowskii* and *L. rufipectus*) was 0.046. Between geographically separated samples of the other two members of the genus, *P*-values were 0.004 for *L. amaurocephalus* (samples from Peru and Bolivia) and 0.026 for *L. superciliaris* (samples from Panama and Peru).

DISCUSSION

Congruence between data sets.—Although the mtDNA analysis provides a "gene" tree of evolution (Neigel and Avise 1986, Pamilo and Nei 1988), the most-parsimonious mtDNA tree matches the topology of the best-supported allozyme tree for relationships among *Leptopogon* species (Figs. 1 and 2). This suggests that mtDNA in *Leptopogon* is tracking phylogeny in

TABLE 2. Matrix of 129 mtDNA characters. Data include restriction-site combined with fragment data. Characters correspond to order of enzymes; numbers of characters for each restriction enzyme in parentheses. Site data: *Ava*I (8), *Bcl*I (13), *Bgl*I (6), *Bgl*II (3), *Eco*R I (7), *Nco*I (5), *Nde*I (4), *Pst*I (6), *Pvu*II (9); Fragments: *Bam*H I (17), *Hin*D III (12), *Msp* I (18), *Stu* I (21). ? = missing data, a = polymorphism (0,1).

Phyllomyias plumbeiceps
101000011100001111000?????????1010110??1000000000101000001001

Pogonotriccus orbitalis
0000011011000000001110001111001000001?????1110??????00000011100000000000000111???

Leptopogon rufipectus
111000000100000000000110000100110000001000011001001001100000011111000000000000111110000000011111110000000000111111100000000000000

L. taczanowskii
111000000110000000000111000100101100011100110011101010100000001011001000000001001111111000000111110111000000001110111000000000000

L. superciliaris (Panama)
111000000111100000000100000100100000001000011111010001011000000011000110000000000000000110000011100011110000000110010111110000000

L. superciliaris (Peru)
111010001100110000000100000100100000001000011101001001011000000101100101000010000000000110000011100011110000000101000110010000000

L. amaurocephalus (Peru)
111000000110110000000100000111100000001011111101010001000100000000000000111110000100000011000101000100010011000000010100001011000

L. amaurocephalus (Bolivia)
111a0000110110000000010000011a10000000101101110111000100011000001100000011a00000100000011000100000010001110000000101000000011111 0

the same manner as nuclear characters (allozymes). It is unlikely that this happened by chance alone. There are 15 possible topologies for a rooted four-taxon statement such as that in *Leptopogon* (Simberloff 1987); thus, the probability that one four-taxon statement will match another, independently derived, four-taxon statement is only 1 in 15, or 0.067.

Although divergences based on allozymes (Nei's D) and mtDNA (P-values) are highly correlated ($r^2 = 0.796$) for pairs of taxa in common, levels of differentiation measured by the two types of data can be different. For instance, there are no fixed allelic differences (Nei's $D = 0.022$) between the sister taxa *L. taczanowskii* and *L. rufipectus;* however, these taxa differed at 13 of 50 mtDNA restriction sites (Table 2) and exhibited different fragment profiles for 10 of 13 restriction enzymes. The estimated mtDNA sequence divergence between these two allopatric sister taxa (4.6%) is high compared to many pairs of avian sister species (Avise and Zink 1988). The 2.6% mtDNA sequence divergence between the two individual *L. superciliaris* from Panama and Peru is also as high as that found between many species of birds (Avise and Zink 1988, Avise and Ball 1991); however, high levels of genetic divergence may be typical within sedentary Central and South American "species" as suggested by recent studies employing either mtDNA (Zink et al. 1991, Bates 1993, Seutin et al. 1993) or allozymes (Capparella 1988, Hackett and Rosenberg 1990, Peterson et al. 1992, Bates 1993, and Hackett 1993).

Morphologic studies of Leptopogon.—Lanyon (1988), using specimens collected from the same sites as individuals used in our study, found that Panamanian *L. superciliaris transandinus* had a syrinx structure similar to *L. taczanowskii* and *L. rufipectus,* whereas the syrinx of the Peruvian *L. s. albidiventer* resembled *L. amaurocephalus.* Considering that this variability exceeded normal intrageneric variability, he suggested that there may be two lineages in *Leptopogon* and that *L. superciliaris,* as currently recognized, may be polyphyletic. Two lineages of *L. superciliaris* are also supported by our data; however, in our analyses these lineages are monophyletic (based on our mtDNA data set, the tree supporting Lanyon's suggestion of polyphyly in *L. superciliaris* has 149 steps, 8 more than the shortest tree). We agree with Lanyon (1988) that further study of both molecular and morphological characters in this taxon is warranted.

Testing Chapman's hypotheses.—If the two molecular data sets do accurately reflect relationships within *Leptopogon,* it is still possible that these relationships support evolution into the Andes by chance alone. Again, the cladogram suggested by our data is 1 of only 15 possible four-taxon statements (Simberloff 1987). Only one other of these 15 topologies (one with a *taczanowskii/rufipectus* clade and an *amaurocephalus/superciliaris* clade) would also be consistent with evolution directly into the Andes without also suggesting multiple origins of *taczanowskii* and *rufipectus;* thus, the probability of obtaining a cladogram consistent with evolution into the Andes is only 0.133 (2/15). However, we cannot distinguish among three of Chapman's possible source areas, because the South American lowlands, the Central American highlands, and the Guianan highlands could all be source areas for the *Leptopogon* lineage. An additional taxon at the base of the clade would distinguish among the three possibilities. For example, the tropical lowlands would be favored as a source area if an additional lowland taxon, like *L. amaurocephalus,* were found to be basal to the three higher elevation taxa. With no apparent relatives close to the genus, it may be impossible to resolve this question, although additional populations of *L. amaurocephalus* could be informative.

Although all four of Chapman's four proposed areas of origin may apply to some species, there are currently few phylogenetic hypotheses of relationships among South American sister taxa separated along elevational gradients. Gerwin and Zink's (1989) allozyme data for the hummingbird genus *Heliodoxa* suggest that the ancestor of tropical lowland species *H. schreibersii* (lowlands to 1,000 m, elevation data from Hilty and Brown 1986) and *H.* [*Polyplancta*] *aurescens* (lowlands to 400 m) may have given rise to higher-elevation species, *H. jacula* (500–1,500 m), *H. leadbeateri* (1,300–2,400 m), and *H. rubinoides* (1,800–2,600 m). Patton and Smith (1992) used mtDNA sequence data to study relationships of subtropical forest members of the rodent genus *Akodon* and suggested that forest species evolved from ancestors inhabiting the puna grasslands above the forests. It has been proposed based on allozymic data that the puna-inhabiting species in this genus evolved from ancestors in Central America (Hoffstetter 1986, Apfelbaum and Reig 1989). Finally, Fjeldså (1985) presented morphological and behavioral data that supported southern-temperate South America as the area of origin for high Andean coot species. These data sets illustrate that three of Chapman's four areas of origin (all except the Guianan highlands) could have been source areas for these taxa; however, additional phylogenetic studies of more speciose taxa are needed.

Patterns and timing of speciation.—Members of *Leptopogon* occur parapatrically, but do not have distributions that correspond to hypothesized Pleistocene refugia (Haffer 1969, Cracraft 1985). Using published estimates of molecular-clock calibrations for both mtDNA (Shields and Wilson 1987) and allozymes (Gutiérrez et al. 1983, Marten and Johnson 1986), differentiation between *L. amaurocephalus* and other members of the genus occurred 6 to 9 million years ago (mya.), and the two subtropical species diverged from *L. superciliaris* 3 to 6 mya. These values are in accord with the timing of uplift in the Bolivian Andes and the faunal turnover in the mammalian fossil record leading to the appearance of taxa adapted to higher-elevation habitats (Hoffstetter 1986). Pre-Pleistocene divergence has also been suggested for other South American suboscine taxa (Capparella 1988, Hackett and Rosenberg 1990).

The differentiation between *L. taczanowskii* and *L. rufipectus* could have been as recent as 0.3 mya. based on allozyme data or as ancient as 4 mya based on mtDNA data. Parker et al. (1985) included *L. taczanowskii* and *L. rufipectus* in a list of pairs of presumed sister taxa separated by the deep, dry Marañon river valley. Because the molecular data support a sister relationship for these two species, we suggest that a vicariance event separated them after they differentiated from *L. superciliaris.* Thus, the ancestor of *L. taczanowskii* and *L. rufipectus* probably occurred across northern Peru before the formation of the valley. Unfortunately, we know of no geologic data that address the timing of the formation of the Marañon valley.

Position of Leptopogon *in relation to other tyrannids.*—Although they were not the focus of this study, several of the outgroups were chosen because they have been considered by systematists to be closely related to *Leptopogon.* Lanyon (1988) concluded that *Leptopogon* and *Mionectes* were sister taxa based on derived cranial and syringeal characters, and Traylor (1977) placed the two genera together because of shared characters that included pendant globular nests and the penchant for single-wing flicking (a trait that has also been observed in *Phyllomyias* and *Pogonotriccus;* Hilty and Brown 1986). Traylor placed *Phyllomyias* and *Lophotriccus* along with *Leptopogon* and *Mionectes* in the Elaeniinae, and placed *Tyrannus* in the Tyranninae. Sibley and Ahlquist (1985) placed *Mionectes* and *Leptopogon* in the same subfamily (Mionectinae) based on DNA-DNA hybridization data, but their $T_{50}H$ value between the two genera is quite large. Using their molecular clock, Sibley and Ahlquist (1985) suggested that the two genera may have been evolving separately for over 20 million years. This age of separation is similar to the 14 to 19 million years predicted by our allozyme data based on published clock calibrations (Gutiérrez et al. 1983, Marten and Johnson 1986). Although our data sets include too few taxa to assess intergeneric relationships of the tyrannids, both allozymes and mtDNA suggest *Leptopogon* is quite differentiated from many of the genera near it in classifications (Traylor 1979).

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APPENDIX. Specimens used. Specimen numbers refer to LSUMNS frozen-tissue-collection catalog numbers (voucher specimens also are housed at the LSUMNS).

Leptopogon amaurocephalus (6), 10700, 10721, 10764 (PERU: Dpto. Ucayali; W Bank Río Shesha, ca. 65 km ENE Pucallpa). 9093 (BOLIVIA: Dpto. Pando; Prov. Nicolás Suarez, ca. 12 km by road S Cobija, ca. 8 km W on road to Mucden, 325 m). 14461 (BOLIVIA: Dpto. Santa Cruz; Serranía de Huanchaca, 21 km S Catarata Arco Iris, 670 m). 14744 (BOLIVIA: Dpto. Santa Cruz: Serranía de Huanchaca, 25 km S Catarata Arco Iris, 670 m).

L. superciliaris (2), 5408 (PERU: Dpto. San Martin; 20 km by road NE Tarapoto on road to Yurimaguas, 1,050 m). 2160 (PANAMA: Darien; Caña).

L. taczanowskii (2), 1765, 1831 (PERU: Dpto. Pasco; Santa Cruz, ca. 9 km SSE Oxapampa, 2,050 m).

L. rufipectus (1), 273 (PERU: Dpto. Cajamarca; "Batan" on Sapallache-Carmen trail, 2,000 m).

Tyrannus dominicensis (3), 11353, 11433, 11487 (PUERTO RICO: Municipio Cabo Rojo; Barrio Llanos Costa, 0.75 km E mouth of Arroyo Cajúl).

Mionectes olivaceus (1), 11910 (ECUADOR: Prov. Esmeraldas; El Plácer, ca. 670 m).

Phyllomyias plumbeiceps (1), 8139 (PERU: Dpto. Pasco; Cushi, 1,800 m).

Lophotriccus eulophotes (1), 9303 (BOLIVIA: Dpto. Pando; Prov. Nicolás Suarez, ca. 12 km by road S Cobija, ca. 8 km W on road to Mucden, 325 m).