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Geographic distribution, ecology, and phylogenetic affinities of *Thyroptera lavali* Pine 1993

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Thyroptera lavali (Chiroptera: Thyropteridae) is a rare Neotropical species that until now has been recorded from only five localities in the Amazonian rainforests of Peru, Ecuador, Venezuela, and Brazil. Fewer than 10 specimens of *T. lavali* exist and, accordingly, little is known about its distribution, natural history, and phylogenetic affinities. We report new records for the species from southeastern Peru. Together with other recently published records, these expand the known range of the species considerably, as well as increase our knowledge of its ecology. *Thyroptera lavali* seems to prefer primary forest near swamps, and probably roosts in palms; its reproductive pattern is similar to that of other Neotropical insectivorous bats, with parturition at the beginning of wet season. Finally, we used two different data matrices to assess its phylogenetic relationships: one of discrete morphological characters, the other of DNA sequences of mitochondrial genes. Both data sets support a sister relationship between *T. lavali* and *T. tricolor*, with *T. discifera* as the basal member of the genus *Thyroptera*.

Key words: disc-winged bats, distribution, ecology, Neotropics, systematics, *Thyroptera lavali*, Thyropteridae

INTRODUCTION

The family Thyropteridae (disc-winged bats) includes three species in the genus *Thyroptera* that are endemic to lowland Neotropical forests (mainly below 1,000 m; Koopman, 1978; Patterson *et al*., 1996). *Thyroptera discifera* and *T. tricolor* have extensive distributions throughout the Amazon basin and beyond (Wilson and Findley, 1977; Wilson, 1978). The third species, *T. lavali*, was described on the basis of four specimens from a single lowland locality in Loreto department, northeastern Peru (Pine, 1993). Previous reports of *T. lavali* include a fossil record in Colombia (as *T. robusta* from Magdalena Valley, Czaplewski, 1996, 1997), a northern record in Napo Province, Ecuador (Reid *et al*., 2000), the type locality (Quebrada Esperanza, Loreto; Pine, 1993), and the first extension southward (Bosque Von Humboldt, Ucayali; Solari *et al*., 1999). These records extended the latitudinal range more than 600 km north and 650 km south of the type locality, clearly indicating that the species has a more widespread distribution than previously known. Two recent records

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of *T. lavali* from the Orinoco Delta, Venezuela (Linares, 1998), and Pará, Brazil (Bernard and Fenton, 2002) extended its known geographic distribution to the northeast by ca. 2100 km.

The purpose of this study is to review and update previous records of *T. lavali* in Amazonian Peru, and to report the first record for Manu Biosphere Reserve (MBR), representing the southernmost record for the species. We also compare *T. lavali* to its congeners (*T. discifera* and *T. tricolor*), update records of sympatry, include additional data on its habitat and ectoparasites, and present the first genealogic hypothesis for the family Thyropteridae inferred from independent analyses of morphological and molecular data.

Methods and Materials

Field Survey

We collected bats during faunal assessments in southeastern Peru; during 1997–1998 in Camisea, Cuzco department, and during 1999–2001 along the Cosñipata and Alto Madre de Dios Rivers, in Cuzco and Madre de Dios departments. The Camisea area is located in La Convención Province, NW Cuzco, in the lower Urubamba Valley, near the border with the Ucayali Department (Solari *et al*., 2001). Lowland forests of the Alto Madre de Dios River are included in the Cultural Zone of Manu Biosphere Reserve (see Pacheco *et al*., 1993). We set mist-nets inside the forests, or across streams and small rivers, or along trails or in manmade clearings. We netted bats in both primary forest and modified habitats, ran our nets for 2-3 consecutive days at most of the locations, and recorded the habitat of capture for every bat caught. We opened nets each night before 1800 h, kept them open until 0600 h of next day, and checked them hourly. Most of the sampling work was completed during the beginning of the wet season (September to December).

Morphological Analysis

We assessed phylogenetic relationships among extant species of *Thyroptera* through cladistic analysis of discrete morphological characters that we presume reflect evolutionary change. These included the following cranial, dental, and external characters discussed in the original description of *T. lavali* (Pine, 1993) or in other accounts of species of *Thyroptera* (Miller, 1907; Wilson and Findley, 1997; Wilson, 1978):

1. Length of dorsal fur between shoulders: (0) very long; (1) short.
2. Degree of countershading: (0) inconspicuous; (1) conspicuous, venter brown to yellowish; (2) conspicuous, venter white or whitish.
3. Hair pattern on proximal edge and dorsal surface of uropatagium: (0) dispersed along the dark transverse veins; (1) sparsely haired; (2) densely covered with long hairs.
4. Hair pattern along distal margin of uropatagium: (0) short, pale hairs along border, but not in central margin; (1) long, pale hairs scattered near central margin; (2) fringes of dark hairs near central margin.
5. Hair pattern on elbow and proximal one-third of forearm: (0) underdeveloped, not hairy; (1) densely furred.
6. Fusion of toes 3 and 4: (0) undeveloped, feet normal; (1) developed, toes 3 and 4 with single claw.
7. Development of suction-disc on thumb: (0) undeveloped, no suction-disc present; (1) developed, disc-shaped; (2) developed, oblong-outline (Fig. 1).
8. Number of lappets in calcar: (0) no lappets; (1) one lappet; (2) two lappets. [This character shows some variation (Pine, 1993), but none was detected in our samples.]
9. Slope of skull between braincase and rostrum: (0) steep, angle < 90°; (1) gentle, angle > 90°.
10. Shape of braincase, as determined by relative height and width of braincase in comparison to interorbital constriction: (0) globular; (1) low and less globular.
11. Shape of mesopterygoid fossa: (0) U-shaped; (1) V-shaped.
12. Length of mesopterygoid fossa: (0) extremely long, reaching the anterior half of the palate; (1) long, extending to the posterior half of the palate; (2) very short.
13. Development of transverse ridge between pterygoids: (0) absent; (1) low ridge, not reaching hamulars; (2) high ridge, reaching hamulars.
14. Shape of transverse ridge between pterygoids: (0) wall-like or thick lamina; (1) hill-like, with bump in middle. The character is scored as missing (-) in species without a transverse ridge.
15. Size of foramen ovale: (0) very large; (1) large; (2) small.
16. Number of cusps of first upper incisor and resultant orientation of axis: (0) single cusp, main axis converging anteriorly; (1) two-cusps, axis converging

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FIG. 1. Specimen of *Thyroptera lavali* (FMNH 174916) caught in Maskoitania, Alto Madre de Dios River, Manu Biosphere Reserve, Peru. Notice the size and oblong shape of the suction-disc (photo by B. D. Patterson)

anteriorly; (2) two-cusps, axis parallel to sagittal axis; (3) three-cusps, axis converging anteriorly.
17. Number of cusps of second upper incisor and resultant orientation of axis relative to sagittal axis of skull: (0) single cusp, main axis oblique; (1) two-cusps, axis oblique; (2) two-cusps, axis perpendicular.
18. Gaps between upper canine and first premolar, and between first and second upper premolar: (0) two gaps, no apparent contact; (1) no gaps, partial or complete contact.
19. Size of third lower incisor relative to first and second lower incisors: (0) subequal; (1) larger.
20. Cusp development on third lower incisor: (0) unicuspidate; (1) faintly trilobate; (2) conspicuously trilobate.
21. Contact between lower premolars: (0) complete contact; (1) no contact.

We scored the 21 characters for specimens representing all three species of *Thyroptera* and species of *Furipterus, Amorphochilus*, and *Natalus* (see Specimens Examined and Table 1). We used two species of *Natalus* as outgroups (Simmons and Geisler, 1998; Hoofer *et al*., 2003; Van Den Bussche and Hoofer, 2004). We conducted phylogenetic analyses in PAUP* software (test version 4.0b10; Swofford, 2002) using a branch-and-bound tree-searching method. We evaluated repeatability of clades on the most parsimonious tree via bootstrapping (Felsenstein, 1985) with 1,000 iterations.

Molecular Analyses

We extracted genomic DNA from tissue of *T. lavali* (FMNH 174916) following standard protocols (Longmire *et al*., 1997). We amplified and sequenced the entire mitochondrial 12S rRNA, 16S rRNA, and intervening $tRNA^{Val}$ following the methods of Van Den Bussche and Hoofer (2000). We downloaded from GenBank orthologous 12S rRNA, $tRNA^{Val}$, and 16S rRNA sequences for *T. discifera* (AF345923), *T. tricolor* (AF263233), *Noctilo albiventris* (AF263223), *N. leporinus* (AF263224), and *Mystacina tuberculata* (AF263222) that we generated in previous studies (Van Den Bussche and Hoofer, 2000, 2001).

We aligned DNA sequences using CLUSTAL X software (Thompson *et al*., 1997) following methods of Hoofer *et al*. (2003), and imported the alignment into MacClade (Maddison and Maddison, 1992) for visual inspection. We excluded regions of the aligned sequence potentially violating the assumption of positional homology following methods of Hoofer and Van Den Bussche (2003). We coded all nucleotides as one of four discrete character states (A, C, G, T) and gaps as missing data. For phylogenetic analysis, we polarized character-state changes by designating *Mystacina* as the outgroup. The most appropriate model of DNA sequence evolution and model parameters as determined in Modeltest (Posada and Crandall, 1998) were: General time reversible (GTR) with allowance for gamma distribution of rate variation (Γ) and for proportion of invariant sites (I); base frequencies = 0.3620, 0.2081, 0.1865, 0.2434; R-Matrix = 3.6519, 6.8557, 2.1310, 0.0009, 23.6564; shape parameter (α) of the gamma distribution = 0.3711, and proportion of invariable sites = 0.3411. We used these model parameters in a Maximum Likelihood analysis in PAUP* software. The starting tree was obtained via random addition with the

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TABLE 1. Morphological data matrix for species of *Thyroptera*, Furipteridae, and Natalidae used in the phylogenetic analysis. Characters are numbered as shown in the Materials and Methods. *A.* = *Amorphochilus*; *F.* = *Furipterus*; *N.* = *Natalus*; *T.* = *Thyroptera*

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
N. stramineus	0	0	0	0	0	0	0	0	1	1	0	1	0	-	0	2	0	1	0	1	0
N. tumidirostris	0	0	0	0	0	0	0	0	1	1	0	0	0	-	0	2	0	1	0	1	0
A. schnablii	0	0	0	0	0	0	0	0	0	0	1	2	0	-	2	0	0	0	0	0	0
F. horrens	0	0	0	0	0	0	0	0	0	0	0	1	0	-	2	1	1	0	0	0	0
T. discifera	0	2	2	1	1	1	1	1	0	1	0	2	2	0	2	3	1	0	0	2	1
T. tricolor	0	1	1	2	0	1	1	2	0	0	1	1	1	0	1	2	1	1	1	1	0
T. lavali	1	2	1	2	0	1	2	1	1	1	1	1	1	1	1	2	2	1	1	0	0

exhaustive-search option and tree-bisection-reconnection (TBR) branch-swapping. We evaluated reliability of clades on the optimal tree through bootstrap analysis with 1,000 iterations.

We also performed a Bayesian phylogenetic analysis (MRBAYES; Huelsenbeck and Ronquist, 2001) using the GTR + I + Γ model of sequence evolution. However, we did not define values for model parameters a priori, but treated them as unknown variables with uniform priors to be estimated in each analysis. We conducted Bayesian analyses with random starting trees without constraints, four simultaneous Markov chains were run for 2 x 10^6 generations, trees were sampled every 10 generations, and temp was set to 0.02. We determined resulting burn-in values (the point at which model parameters and tree scores reach stationarity) by empirical evaluation of likelihood scores. Finally, we conducted three independent Bayesian analyses to help ensure that final trees converged upon the same topology (Huelsenbeck *et al*. 2002).

Specimens Examined

We collected two individuals of *T. lavali* at Camisea, Cuzco; both came from Cashiriari-3 (11°53'S, 72°39'W, 700 m), an oil-well site where gas exploration was being carried out by Shell Prospecting and Development Peru (Solari *et al*., 2001). We netted a young male on 21 November 1997 (MUSM 13966), and an adult female on 6 December 1997 (MUSM 13967). We netted another adult male on 19 September 2001 (FMNH 174916; Fig. 1) near Maskoitania, a tourist lodge in the lowland forests of the Alto Madre de Dios River. During comparisons, we detected another male of *T. lavali* that had been misidentified as *T. discifera* in the samples of the Centro de Investigaciones Jenaro Herrera (CIJH), Loreto, northeast Peru (Ascorra *et al*., 1993).

Specimens and tissues used for morphological and molecular analyses are deposited in the Museum of Texas Tech University (TTU), Field Museum of Natural History (FMNH), and Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM). The following were examined for morphological comparisons: *Natalus stramineus*: Dominica, St. John Parish (TTU 31464, 31469, 31475); Dominica, St. Paul Parish (TTU 31486). *N. tumidirostris*: Trinidad, St. George (TTU 5436, 5445, 9822, 9823, 9824). *Amorphochilus schnablii:* Peru, Piura (FMNH 81054, 81057); Peru, Lima (MUSM 964, 965, 966). *Furipterus horrens*: Peru, Madre de Dios (MUSM 9811). *Thyroptera discifera*: Colombia, Valle del Cauca (FMNH 140791);

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Colombia, Cordoba (FMNH 69509); Peru, Loreto (MUSM 5546). *T. lavali*: Peru; Loreto (MUSM 5944); Peru, Ucayali (MUSM 8463); Peru, Cuzco (MUSM 13966, 13967); Peru, Madre de Dios (FMNH 174916). *T. tricolor*: Peru, Madre de Dios (MUSM 745, 6834, 6835); Trinidad, St. George (TTU 5439, 5440); Ecuador, Esmeraldas (TTU 85356, 85386).

Results

Morphological Analyses

Five of the 21 morphological characters that we scored (Table 1) were phylogenetically uninformative, primarily because the states were autapomorphic for *T. discifera* or *T. lavali*. Parsimony analysis recovered two equally-parsimonious trees of 40 steps (consistency index [CI] = 0.83; retention index [RI] = 0.71). Bootstrap analysis provided strong support [bootstrap support (BS) ≥ 70%) for most clades, including monophyly of *Thyroptera* and a sister relationship between *T. tricolor* and *T. lavali* (Fig. 2). The only topological difference between the two equally-parsimonious trees is in regard to the paraphyletic nature of Furipteridae, with *Furipterus* being basal to *Thyroptera*.

Molecular Analyses

The complete 12S rRNA, $tRNA^{Val}$, 16S rRNA gene sequence from *T. lavali* has been deposited in GenBank (accession number AY786557). Alignment of the 12S rRNA, $tRNA^{Val}$, and 16S rRNA genes from the six taxa examined resulted in 2,676 aligned positions, of which 361 were excluded from phylogenetic analysis due to potentially violating the assumption of positional homology. Of the remaining 2,315 characters, 284 were variable. Maximum Likelihood analysis resulted in an optimal

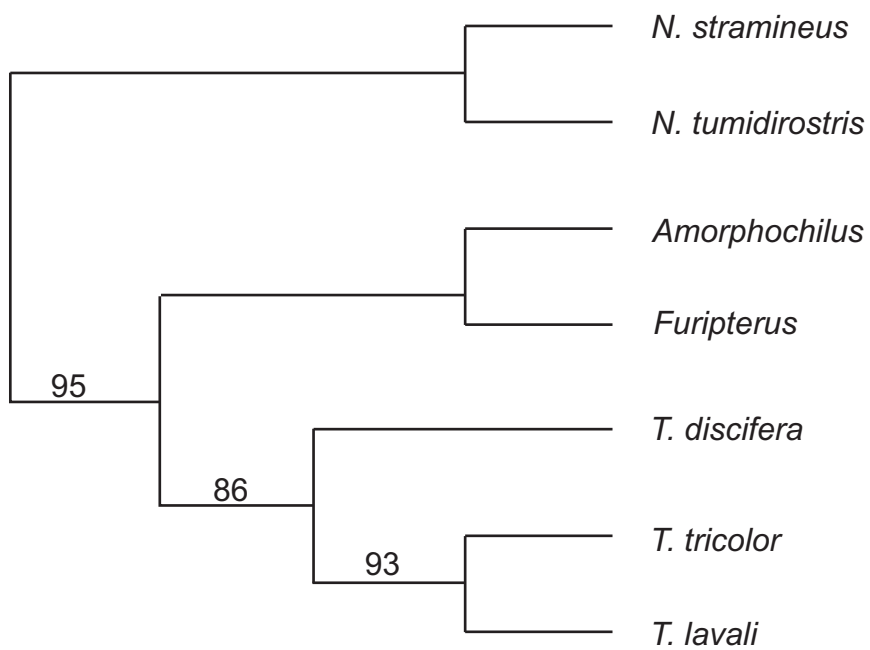


FIG. 2. One of two equally-parsimonious trees (40 steps; CI = 0.83; RI = 0.71) from phylogenetic analysis of morphological data, with *Natalus* spp. used as outgroups. The other equally-parsimonious tree indicated paraphyly of Furipteridae. Numbers above branches represent bootstrap percentages based on 1,000 replications. *N.* = *Natalus*, *T.* = *Thyroptera*

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tree (Ln = -6966.37) that supported monophyly of *Thyroptera* (BS = 100%) as well as a sister relationship between *T. lavali* and *T. tricolor* (BS = 100%; Fig. 3). Bayesian analyses agreed between the three independent runs. Burn-in values for each run were 3,000 trees, resulting in 197,000 trees for phylogenetic analysis. Results of Bayesian analysis produced a topology identical to that from Maximum Likelihood analysis, supporting monophyly of *Thyroptera* (P = 1.00) and sister relationship between *T. lavali* and *T. tricolor* (P = 1.00; Fig. 2).

Discussion

Distribution and Ecology

There was little known about the natural history of *T. lavali* at the time of its description (Pine, 1993). Solari *et al*. (1999) reported that the single individual of *T. lavali* from Ucayali probably was roosting in a palm frond, and field notes describe the collecting area as an open formation with few large trees near to a small creek. We collected the two Camisea specimens in a mixed upland forest characterized by few shrubs, scarce understory, and rolling hills. The aborescent palm *Iriartea deltoidea* (Arecaceae) and species of *Miconia* (Melastomataceae) dominated the hilly forest (Comiskey *et al*., 2001). We also collected a single individual of *T. tricolor* during the same field season at this site, making Cashiriari-3 the fourth locality where *T. lavali* and *T. tricolor* are sympatric (Pine, 1993; Reid *et al*., 2000; Bernard and Fenton, 2002). Reid *et al*. (2000) collected two of their *T. lavali* specimens from Ecuador in low-level mist nets set in terra firme forest adjacent to a *Mauritia* palm swamp; the third specimen was netted directly over the swamp.

The specimen from Manu was netted over a small creek (ca. 2 m wide) inside a relatively mature forest, during the first half of a clear night with new moon. Tree canopy was above 20 m, and few arborescent palms were present. This individual (Fig. 1) represents the southernmost locality of record for *T. lavali*, nearly 200 km south of Camisea and 920 km south of the type locality in Loreto. Although we did not find *T. lavali* sympatric with *T. tricolor* at any locality of Manu Biosphere Reserve, *T. tricolor* has been recorded at Hacienda Amazonia (Pacheco *et al*., 1993), which is only 10 km from Maskoitania. The specimen of *T. lavali* collected in Pará, Brazil, was netted within a forest fragment surrounded by grass savanna (Bernard and Fenton, 2002). Finally, according to Ascorra *et al*. (1993), the single *T. lavali* from Jenaro Herrera, Loreto, also was collected with a mist net.

With a new locality record for *Lampronycteris brachyotis* (Solari *et al*., 1999), the description of a new species of *Micronycteris* (*M. brosseti*; Simmons and Voss, 1998), and now a new locality record for *T. lavali,* the documented bat diversity of Jenaro Herrera has increased to 65 species. Moreover, this site also is the first to document sympatry of *T. discifera* and *T. lavali*. Interestingly, capture of *T. lavali* has been mostly with mist nets whereas *T. discifera* and *T. tricolor* are usually collected from their peculiar roosts, inside curled *Heliconia* leaves (Findley and Wilson, 1974; Wilson, 1978; Pine, 1993; Ascorra *et al*., 1996).

From the information presented by Solari *et al*. (1999) and Reid *et al*. (2000), it is possible to infer a reproductive pattern for *T. lavali*. In northeast Ecuador, one female caught in October was pregnant, and two females caught in January and February were lactating. This contrasts with the female caught in September (southeast

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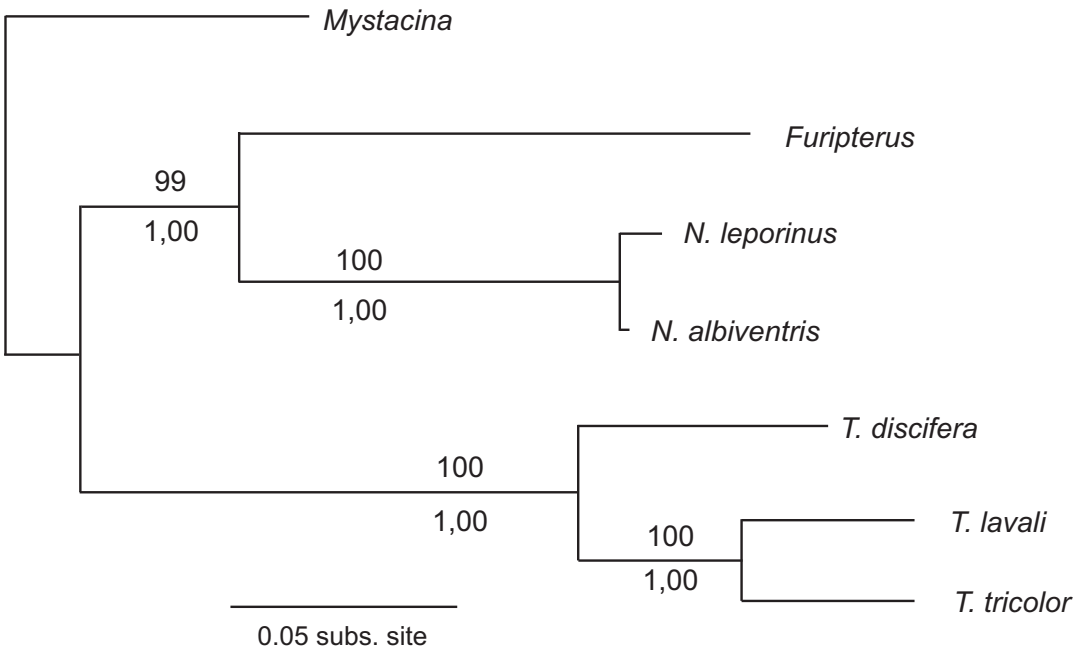


FIG. 3. Optimal topology resulting from maximum-likelihood analysis of mitochondrial 12S rRNA, $tRNA^{Val}$, and 16S rRNA sequences (Ln = -6966.37), with *Mystacina tuberculata* used as outgroup. Numbers above branches represent bootstrap percentages based on 1,000 replications; numbers below branches are Bayesian posterior probabilities. *N = Noctilio*, *T = Thyroptera*

Peru), which was carrying a newborn. The difference in time of parturition for these individuals might be related to latitudinal and seasonal differences between Ecuador (00°40'S) and Peru (08°47'S). As in other bats from the Amazon Basin, parturition in *T. lavali* appears to occur at the beginning of the wet season (Graham, 1987).

Ectoparasites were also collected from specimens of *T. lavali* captured at Camisea and Manu. We collected three bat flies (two females, one male) of the genus *Hershkovitzia* (Nycteribiidae) from the Camisea specimens. Morphological comparisons suggest that these ectoparasites represent an undescribed species of *Hershkovitzia* (J. Chavez, pers. com.). Likewise, one additional bat fly (female) of the same species was collected from the Manu specimen. Other external parasites include mites of the family Macronyssidae (C. W. Dick, pers. com.).

Phylogenetic Affinities and Morphological Characteristics of Thyroptera *Species*

Independent phylogenetic analyses of morphological and molecular characters, using different outgroup taxa and different methods for tree construction were congruent for phylogenetic relationships within *Thyroptera* (Figs. 2 and 3). Both data sets strongly support a sister relationship between *T. lavali* and *T. tricolor*, with *T. discifera* as the basal member of the clade. Indeed, when Pine (1993) described *T. lavali*, some characteristics and measurements showed certain resemblance to those of *T. tricolor*, although no formal hypothesis of relationships was stated. At this time we cannot offer an appropriate account of the biogeographic patterns for the Thyropteridae without assessing more thoroughly geographic variation in each lineage. However, current distributions of *T. lavali*

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and *T. discifera* appear more similar than those of *T. lavali* and *T. tricolor* (see Wilson, 1978).

If *T. lavali* and *T. tricolor* are represented in fossils from the middle Miocene of Colombia, as suggested by Czaplewski (1997), then they diverged from *T. discifera* at least 12 Mya. There is no fossil record for *T. discifera* (see Wilson, 1978) to confirm this hypothesis.

Several authors have compared species of *Thyroptera* in an attempt to find distinguishing morphological characteristics (Hershkovitz, 1949; Husson, 1962; Findley and Wilson, 1974; Wilson and Findley, 1977, Wilson 1978; Pine, 1993). Although external coloration appears to be the simplest to use (venter white or whitish in *tricolor*, brown to yellowish in *discifera* and *lavali*), traits like external projection of tail beyond uropatagium (longer in *tricolor*, shorter in *discifera*) or forearm length ($\geq$ 38 mm in *lavali*, $\leq$ 38 in *discifera* and *tricolor*) might also help in distinguishing species. Wrist suction disks of *T. lavali* are large (5 $\times$ 4 mm) and, as recognized by Pine (1993), oblong in shape (Fig. 1); these are distinctive with regard to the more circular disks of *discifera* and *tricolor* (Reid *et al*., 2000).

The present study describes and characterizes several important morphological characters that help to distinguish species of *Thyroptera*. Furthermore, most contain phyletic information, as judged by congruence between phylogenetic analyses of the morphological and molecular data sets. In our limited morphological analysis, monophyly of *Thyroptera* is supported by seven synapomorphies: conspicuous countershading, sparse or dense hairs on the proximal end of the uropatagium, long hairs near the central free margin of the uropatagium, fusion of toes 3 and 4, development of thumb suction-discs, presence of 1 or 2 lappets on calcar, and development of a transverse ridge between pterygoids. The sister relationship between *T. lavali* and *T. tricolor* is supported by three additional synapomorphies: black, long hairs near the central margin of uropatagium, large foramen ovale, and third lower incisors larger than first and second ones.

The Red List of IUCN lists *T. lavali* as vulnerable because of severe fragmentation of populations, decline in area extent and/or quality of habitat, and population restricted to fewer than five localities (Hutson *et al*., 2001). Our records show that this geographic restriction may not be true, and we can expect more records of this species in undisturbed flooding forests along the main tributaries of the Amazon River (Pastaza in Ecuador, Ucayali in Peru, and the Solimoes in Brazil). Increasing our knowledge on geographic patterns of species and their genealogical relationships might help to update the conservation status of little known groups, like *Thyroptera* or other insectivorous bats (see Hutson *et al*., 2001). However, the inclusion of representatives of the recognized subspecies of *T. tricolor* and *T. discifera* in future analyses should give us a better picture of these patterns.

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