The Auk 113(3):709–714, 1996

Why the Yungas Tody-Tyrant (*Hemitriccus spodiops*) is a *Snethlagea*, and Why it Matters

MARIO COHN-HAFT[1]

Museum of Natural Science and Department of Zoology and Physiology, 119 Foster Hall, Louisiana State University, Baton Rouge, Louisiana 70803, USA

Recognition of biogeographical patterns depends on accurate knowledge of phylogenetic relationships. In tropical South America, where species richness is very high, but knowledge of relationships is rudimentary, numerous biogeographic patterns await discovery. Work to date has focused mostly on patterns in lowland Amazonia (see Haffer 1993 and references therein), although a few other patterns have been identified, such as the "circum-Amazonian" pattern (Remsen et al. 1991), Andean "leapfrog" pattern (Remsen 1984), and a variety of patterns associated with dry forest species (Willis 1992). With few exceptions (e.g. Cracraft and Prum 1988, Hackett 1993), pattern recognition has not been based on explicit phylogenies, but has made use of uncontroversial monophyletic taxa, such as single polytypic species, obvious species pairs, or allospecies groups. As knowledge of distributions and systematics of South American birds improves, we can expect new patterns to appear and old ones to be revised.

Here, I present evidence from external morphology and voice that *Hemitriccus spodiops* (Yungas Tody-Tyrant) and lowland Amazonian *H. minor* (Snethlage's Tody-Tyrant) are sister taxa, and that both species equally and exclusively meet criteria for membership in the subgenus *Snethlagea*. This contradicts earlier views of relationships of *H. spodiops* and suggests a novel biogeographic link between the Amazonian lowlands and adjacent Andean foothills that is supported by several other presumed sister-species pairs.

Hemitriccus spodiops is a tiny flycatcher endemic to Bolivia, known only from the lower montane moist forests (*yungas*) of the eastern slope of the Andes between 800 and 1,600 m. Published data on its natural history are limited to two brief species accounts (Remsen et al. 1982, Parker et al. 1991), and its taxonomic history also is relatively brief and straightforward. After its original description as *Euscarthmus spodiops* (Berlepsch 1901), it has been placed in a sequence of genera (*Euscarthmornis, Idioptilon*, and finally *Hemitriccus*; see Lanyon 1988b). These nomenclatural changes, however, apply to tody-tyrants in general and do not reflect any change in thinking about the position of *spodiops* within this group.

Three authors have addressed the phylogenetic relationships of *H. spodiops* within the tody-tyrants. In the type description of the species, Berlepsch (1901) stated that its closest relative is probably *H. zosterops*, based on a single specimen of each. Later, after the taxon *minor* was described as a new subspecies of *zosterops* (Snethlage 1907), Berlepsch (1909) recognized that the *zosterops* specimen to which he had previously compared the type of *spodiops* belonged to this new form. Thus, Berlepsch may have considered *spodiops* closest to *minor*, but he never stated so explicitly. On the contrary, although Berlepsch (1909) considered *minor* to be so distinct from nominate *zosterops* that he erected a new genus for the former (see below), he apparently never re-evaluated the relationships of *spodiops* or considered its placement in the new genus.

Hellmayr (1927) took a different position, which persists in current classifications, placing *spodiops* immediately after *H. nidipendulus*. Based on examination of the type specimen, he proposed that *spodiops* is "allied to [*H.*] *nidipendulus* with which it agrees in absence of wing-bands and coloration of abdomen" (Hellmayr 1927). These characters, however, are not especially convincing evidence of close relationship. Weak wingbars (neither *spodiops* nor *nidipendulus* actually entirely lacks wingbars) and yellow-tinged, white bellies are found in numerous *Hemitriccus* species, including *H. minor* (see below). The same brief account lists more differences than similarities between the purported "allies." The continued placement of *spodiops* next to *nidipendulus* in modern classifications (Traylor 1979, Sibley and Monroe 1990) is apparently a case of uncritical acceptance of Hellmayr's proposal and ignores the third published suggestion.

Fitzpatrick (1976) included *spodiops* in his "green" group of *Hemitriccus* species, along with *zosterops, minor, nidipendulus*, and numerous other species. Of these, he proposed that "*minor* is closest to [*H.*] *spodiops* and [*H.*] *zosterops*. . .based on similarities between the bill and nostril structures in these three species" (Fitzpatrick 1976). This statement, which contradicts previous treatments distinguishing *minor* from *zosterops* by nostril shape, was not further explained or justified by Fitzpatrick (1976). As I will show, *minor* has an unusually shaped bill and nostrils, distinctly different from those of *zosterops*, but very similar to those of *spodiops*.

Morphology.—The following is based on examination of museum specimens of all known *Hemitriccus*

[1] E-mail: zocohn@lsuvm.sncc.lsu.edu

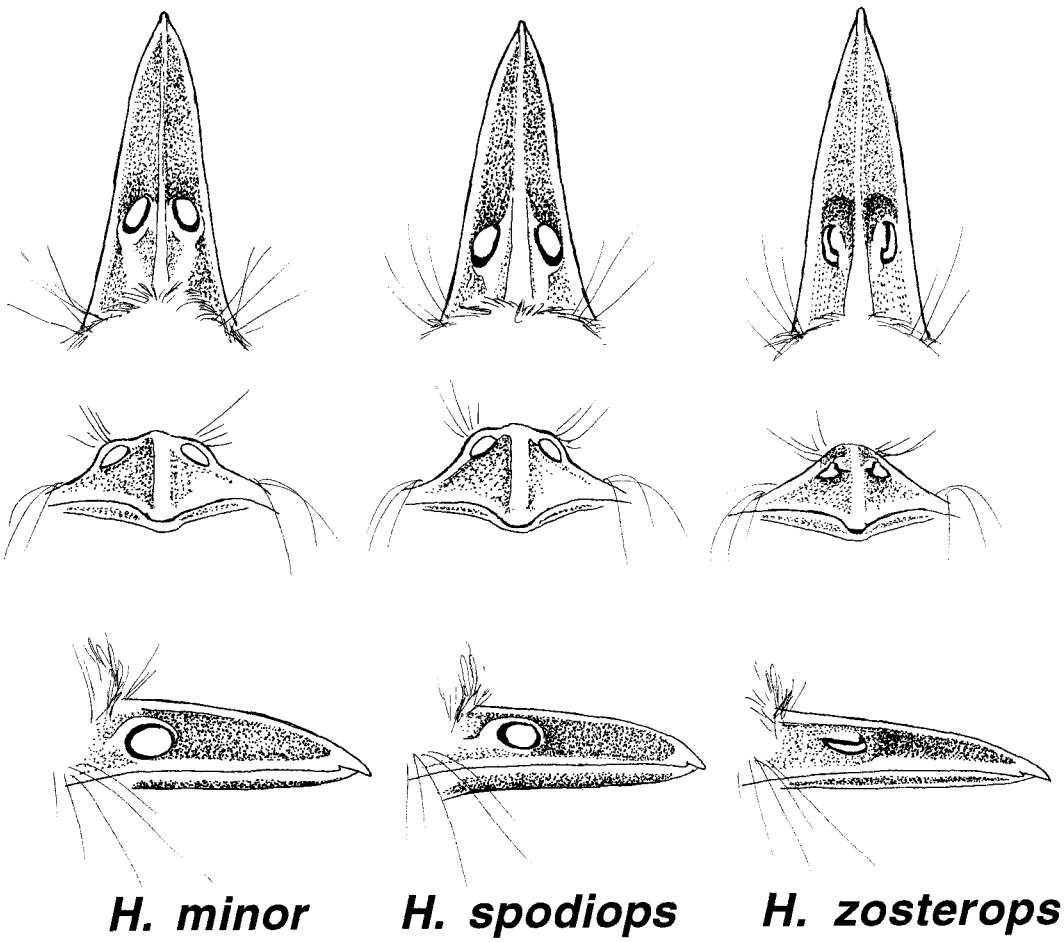

Fig. 1. Bill and nostrils of three *Hemitriccus* species: *H. minor* (LSUMZ 137562), *H. spodiops* (LSUMZ 157505), and *H. zosterops* (LSUMZ 117240) viewed from above (top row), from front (middle row), and from side (bottom row). Drawn to scale; length of exposed culmen of *H. minor* equals 9 mm.

species. Because the distinction between *Hemitriccus* and related genera is poorly defined (see Discussion), I also examined specimens of all species in *Myiornis, Lophotriccus, Atalotriccus,* and *Oncostoma.* Together with *Hemitriccus,* these genera form a monophyletic group (based on syringeal morphology; Lanyon 1988b), which I refer to throughout as the "tody-tyrants." Comparison derives primarily from the series at the Louisiana State Museum of Natural Science (LSUMZ), particularly of *H. spodiops* (six specimens), *H. minor* (31 specimens), *H. zosterops* (34 specimens), and *H. nidipendulus* (two specimens).

Hemitriccus spodiops and *H. minor* share a bill and nostril shape not found in any other tody-tyrants (Fig. 1). Their culmens tend to be more arched than in other species, although in some individuals this distinction is subtle and never is so accentuated as in the bentbills (*Oncostoma*). More striking are the shape and position of the nostrils. In *H. spodiops* and *minor,* the nostrils are large and nearly round, with the long axis set diagonally relative to the culmen. In contrast, the external nasal openings of all other tody-tyrants (including *H. zosterops;* see Fig. 1) are shaped more like longitudinal slits, roughly parallel to the culmen. The slit shape is formed by a covering of the nasal fossa along its length adjacent to the culmen. The nostrils of *minor* and *spodiops,* however, appear to be fully exposed to the air, with only a suggestion of a covering in the form of a raised posterior rim, best seen from the bill tip. The lateral nostril covering in most *Hemitriccus* species also makes their nostrils appear to be set farther apart than those of *spodiops* or *minor* when viewed from above.

Berlepsch (1909) considered this nostril shape so distinctive that he erected the monotypic genus *Snethlagea* for *minor.* Additional characters listed by Berlepsch (1909) as diagnostic of *Snethlagea* relative to *Hemitriccus* were a shorter bill, more graduated

(rounded) tail (vs. only slightly rounded to slightly forked in other species), and, in males, greatly elongated rictal bristles extending nearly to the bill tip. Except for the rictal bristles (which are not exceptionally long in all *minor* specimens; pers. obs.), all of these characteristics are shared by *spodiops*.

In addition to sharing all the diagnostic features of *Snethlagea*, *spodiops* and *minor* are similar in several other morphological characteristics. Both have dark-centered crown feathers nearly long enough to form a short crest, a character considered typical of *Snethlagea* by Hellmayr (1927), but also found in *H. minimus* and *H. inornatus*. The wings of both species are relatively rounded, lacking the unusual "double-rounded" wing formula found to varying degrees in *zosterops* and several other species (see Zimmer 1940). Both have a beige tinge to their whitish irides (vs. greenish white in *zosterops*; based on specimen labels and field observations in Bolivia and Brazil), blurry throat streaks (vs. nonexistent to distinct streaks in other species), and faint wingbars (except in *H. m. pallens*). Also, the two are nearly identical in size, having unflattened wing chord and tail lengths, respectively, of 49.3–51.2 mm and 36.6–39.2 mm for *spodiops* ($n = 2$ adult males), and of 48.1–53.3 mm and 36.6–41.6 mm for *minor* ($n = 12$ adult males). They are among the smallest species in the genus, in which sizes range from the tiny *H. minimus* (male wing 42–45 mm, tail 30–33.5 mm; Stotz 1992) to the large *H. obsoletus* (male wing 57–59 mm, tail 52–54 mm; Hellmayr 1927). In sum, *spodiops* looks just like *minor*, but with a brown wash to the head and breast.

Vocalizations.—The following is based on comparison among all known tody-tyrant species. Principal sources are my own field recordings, recordings archived at the Library of Natural Sounds (LNS) at Cornell University, unarchived recordings made by colleagues (see Acknowledgments), and, in a few cases, published written descriptions. Recordings of *H. spodiops* include LNS catalog numbers 17121, 17129, 17149, 33708, 33713, recorded by T. A. Parker III; LNS 65392 recorded by B. M. Whitney; and my own unarchived recordings, available on request.

Vocal comparisons support a sister relationship between *spodiops* and *minor*. Vocalizations of most *Hemitriccus* species consist of high-pitched "tick" notes and, in some species, these are delivered in rapid succession as a short trill. Both *spodiops* and *minor* have songs consisting of a fast trill, dropping slightly in frequency throughout the roughly 0.6-s duration (Fig. 2). A typical song bout in both species consists of two to four such trills separated by silent intervals roughly the length of a single trill (Remsen et al. 1982; pers. obs.). The number of notes per trill and speed of delivery of these notes are greater in *spodiops* than in *minor*, but their frequency range is very similar in the two (Fig. 2). No other species of *Hemitriccus* has such a song or song bout pattern. The most similar song in the genus is that of the form of *H. zosterops* found near Manaus, Brazil (*H. z. zosterops*; following Traylor 1979). This song is also a rapid trill of similar duration, but it is lower in frequency than *spodiops* and *minor* songs, slows down considerably toward the end (vs. maintaining uniform speed throughout), and is always preceded by a separate, single tick note (Fig. 2). Songs of *H. minor* are sometimes preceded by tick notes (calls), but these are not an obligatory introduction to the trill as in the song of *zosterops* (pers. obs.). Song bouts by *zosterops* (and other *Hemitriccus* species) normally consist of single songs given either sporadically at long intervals, often interspersed with tick calls, or in indeterminately long series of closely spaced songs. The other purported relative of *spodiops*, *H. nidipendulus*, has a distinctive song consisting of a syncopated series (E. O. Willis recording) that is entirely unique among *Hemitriccus*.

Hemitriccus spodiops and *H. minor* sound more like several *Lophotriccus* species (*L. pileatus, vitiosus,* and *galeatus*) than they do other *Hemitriccus* species (Remsen et al. 1982; B. Whitney pers. comm.; pers. obs.). The relationship of *Lophotriccus* to *Hemitriccus* is controversial (see Lanyon 1988a, Sibley and Ahlquist 1990) and will be considered briefly below. However, regardless of how close these two genera may be, *Lophotriccus* species do not share the unusual bill morphology of *Snethlagea*. Therefore, I argue that *H. spodiops* and *H. minor* are more closely related to each other than either is to any *Lophotriccus* species.

Discussion.—Taxonomy of *spodiops* and *minor* should reflect their sister relationship and their phylogenetic relationships to other taxa. Placing both species in *Snethlagea* achieves the former objective. It is conceivable that some or all of the three *minor* subspecies (*minor, snethlageae,* and *pallens*; Traylor 1979, Stotz 1992) represent taxa of equal stature to *spodiops* (which is monotypic). However, testing this hypothesis must await further analysis of geographic variation.

The relationship of *Snethlagea* to other tody-tyrants is ambiguous, and, in light of available information, I cannot suggest any entirely satisfactory taxonomic treatment. The vocal similarities between *Snethlagea* and *Lophotriccus* noted above suggest that the two are sister taxa. If true, then *Hemitriccus* cannot contain *Snethlagea* and still be monophyletic. In fact, *Hemitriccus* as currently delimited (Traylor 1979) is not defined by any synapomorphies. Rather, a number of previously recognized genera, including *Snethlagea*, were lumped in *Hemitriccus* for their lack of certain derived characters distinguishing other genera in the group (e.g. *Lophotriccus*, crest; *Oncostoma*, "bent" bill), and the result is expressly paraphyletic (see Fitzpatrick 1976:fig. 4; Traylor 1977:157). Lanyon (1988b), too, defined *Hemitriccus* by symplesiomorphy. Lanyon's (1988b) *Hemitriccus* contains all those tody-tyrants (including *minor*; *spodiops* was not examined) that lack the derived syringeal morphology distinguishing a *Lophotriccus-Oncostoma* clade. Simply resurrecting *Snethlagea* as a genus would not eliminate

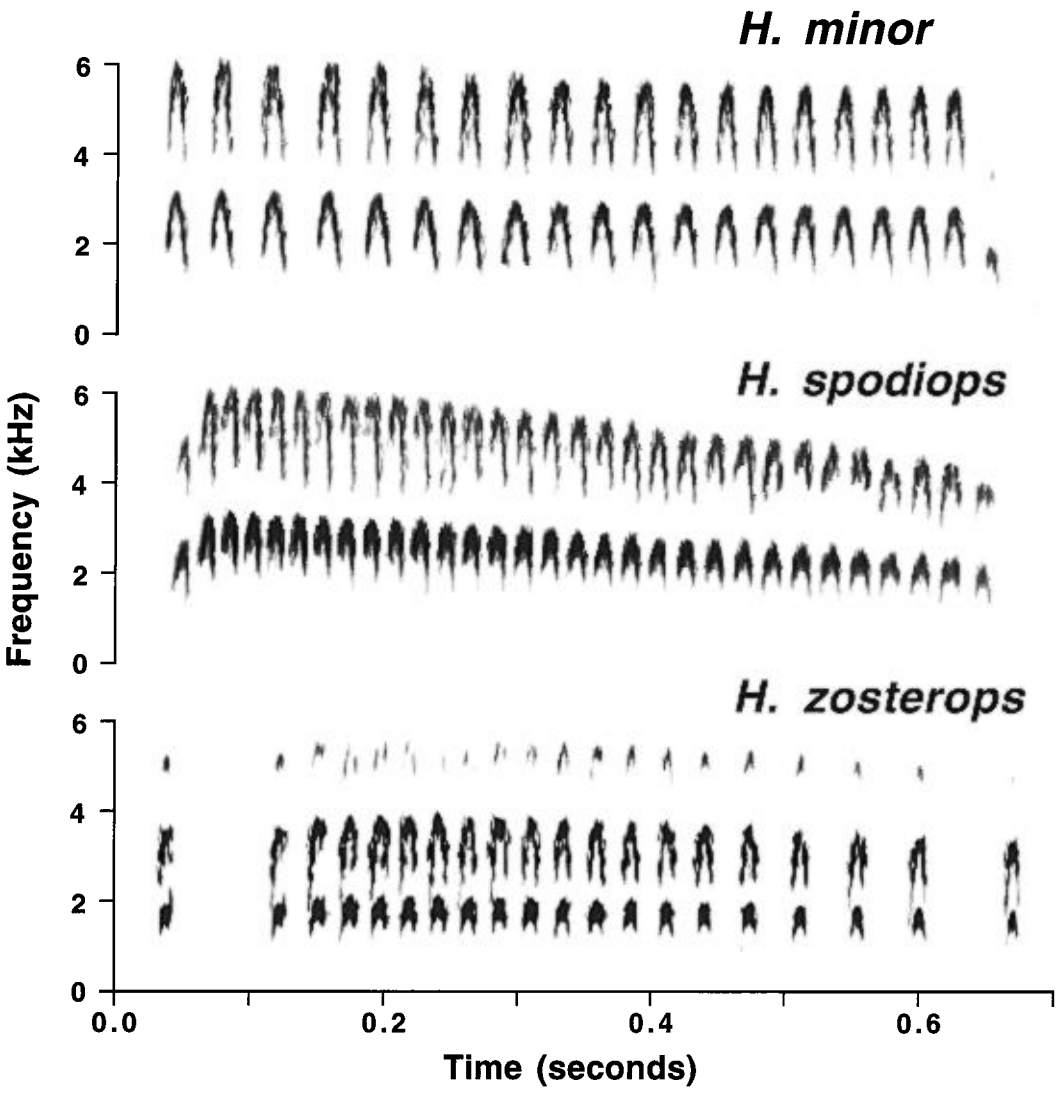

Fig. 2. Song of three *Hemitriccus* species: *H. minor* (Arquipélago Anavilhanas, Amazonas, Brazil; recorded by M. Cohn-Haft), *H. spodiops* (Villa Tunari, depto. Cochabamba, Bolivia; recorded by T. Parker; LNS 33708), and *H. zosterops* (ca. 80 km N Manaus, Amazonas, Brazil; recorded by M. Cohn-Haft). Spectrograms were produced on a Macintosh computer using Canary software (Cornell Laboratory of Ornithology Bioacoustics Department, Ithaca, New York) at following settings: frame size 128 points, FFT size 256 points, 85% overlap, Hamming window function.

the problem of paraphyly in *Hemitriccus*. Correcting that problem will inevitably require taxonomic changes at the generic level for several species that were not the focus of this study. To avoid unnecessary name changes, I suggest maintaining the widely used classification of Traylor (1979), in which *Snethlagea* is treated as a subgenus within *Hemitriccus*, until the phylogeny of all tody-tyrants is re-evaluated. Following this classification, *spodiops* should be removed from its position after *nidipendulus* in subgenus *Hemitriccus*, and placed after *minor* in subgenus *Snethlagea*.

The seemingly trivial taxonomic realignment suggested here, changing the subgeneric classification of *H. spodiops*, nevertheless has important biogeographic implications. A sister relationship between *spodiops* and *nidipendulus*, as suggested by Hellmayr (1927) and perpetuated by current classifications, suggests a biogeographic link between the Andes and southeastern Brazil. This is a well-documented pattern (e.g. Fitzpatrick and O'Neill 1979, Sick 1985, Willis 1992) but appears not to apply to the present case. By recognizing *spodiops* and *minor* as sister taxa, a novel link

TABLE 1. Some putative sister-species pairs in which one species inhabits the *yungas* belt of the Andean foothills and the other inhabits lowland Amazonia. References for sister relationships are provided for genera containing more than two species.

Yungas	Amazonia	Reference
Simoxenops striatus	*S. ucayalae*	
Myrmotherula longicauda	*M. klagesi*	Gyldenstolpe 1930
Myrmotherula spodionota	*M. haematonota*	Hackett and Rosenberg 1990, Whitney 1994
Hemitriccus spodiops	*H. minor*	This study
Chiroxiphia boliviana	*C. pareola*	Parker and Remsen 1987
Odontorchilus branickii	*O. cinereus*	

is proposed between the Andean foothills, home to *spodiops* and a variety of endemic taxa, and lowland Amazonia, where *minor* occurs. Most Amazonian taxa are thought to be most closely related to other lowland forms, either from elsewhere in Amazonia, from southeastern Brazil, or from across the Andes (e.g. Haffer 1969, 1974). Widespread lowland ancestors are presumed to have differentiated in response to vicariance events, such as formation of forest refugia by climatic change (e.g. Haffer 1969), or uplift of the Andes and the formation of large rivers (e.g. Capparella 1988). The mechanism for speciation between the Amazon lowlands and adjacent foothills, if this is indeed a significant pattern, remains to be explored.

Whatever the mechanism, a number of probable sister-taxon pairs show a similar pattern of distribution, with one form occupying the narrow *yungas* belt of the Andean foothills and the other occurring in southern Amazonia or more widespread in the Amazonian lowlands (Table 1). Also, several primarily lowland species contain recognized Andean foothill subspecies and Amazonian forms (e.g. *Crypturellus obsoletus, Xiphocolaptes promeropirhynchus, Philydor erythrocercus, Pyriglena leuconota*). Future phylogenetic work remains to determine the systematic affinities of foothill forms and other *yungas* endemics, such as *Thamnophilus aroyae, Myrmotherula grisea* (see Hackett and Rosenberg 1990, Parker et al. 1992, Whitney 1994), *Terenura sharpei,* and *Cyphorhinus thoracicus.* Although two-taxon statements (Table 1) cannot reveal the direction of evolution, larger clades containing lowland and foothill taxa should help to reveal whether lowland forms tend to originate in the Andean foothills or to evolve from lowlands into the Andes, as suggested for *Leptopogon* flycatchers (Bates and Zink 1994).

Hemitriccus is a large genus with the potential to reveal or support a variety of biogeographic patterns. Despite this, no phylogenetic hypothesis exists for species of *Hemitriccus,* and it probably is not possible to resolve entirely the phylogenetic relationships of tody-tyrants and related genera without biochemical techniques. External morphology is extremely conservative in the group and often is ambiguous as an indicator of relationships. With syringeal morphology, Lanyon (1988b) could place to genus several species for which external morphological characters had been equivocal, and he even suggested novel generic limits, but he could not achieve resolution below the level of genus. Nevertheless, my study demonstrates that the potential resolving power of morphological characters has not been exhausted in this group. Furthermore, vocalizations in tody-tyrants, although also highly conservative (e.g. Fig. 2), have not been applied before as phylogenetic characters. When voice is coupled with careful reanalysis of morphological characters in larger series of modern specimens, a new level of phylogenetic resolution should be attainable.

Acknowledgments.—My trip to Bolivia, where I encountered *H. spodiops* in the field, was made possible by a grant from the National Geographic Society to J. V. Remsen, Jr. My fieldwork in Brazil has been funded generously by the Biological Dynamics of Forest Fragments Project, administered jointly by the Smithsonian Institution and the Instituto Nacional de Pesquisas da Amazônia in Manaus, Brazil. Other financial support came from the Louisiana State University Museum of Natural Science and Board of Regents. The Library of Natural Sounds (LNS) of the Cornell University Laboratory of Ornithology provided tape recordings in its care and a tape recorder for use in the field. Special appreciation goes to the late T. A. Parker III for making his voluminous collection of tape recordings available for study through LNS, and to B. M. Whitney, K. J. Zimmer, T. S. Schulenberg, A. Whittaker, A. W. Kratter, J. F. Pacheco, P. C. Stouffer, and E. O. Willis for providing me with copies of their unarchived recordings. Donna Dittmann drew the bills, and Heiko Schoenfuss translated texts from German. Tom Schulenberg provided copies of hard-to-find references. Conversations and field work with Doug Stotz and Bret Whitney have stimulated and challenged my thinking about *Hemitriccus* relationships. Thoughtful comments by D. Stotz, S. Cardiff, T. Chesser, D. Dittmann, J. Fitzpatrick, J. Kirchman, A. Kratter, V. Remsen, and an anonymous reviewer improved the manuscript.

LITERATURE CITED

BATES, J. M., AND R. M. ZINK. 1994. Evolution into the Andes: Molecular evidence for species relationships in the genus *Leptopogon.* Auk 111:507–515.

BERLEPSCH, H. G. VON. 1901. Mitteilungen über die von den Gebrüdern G. und O. Garlepp in Bolivia gesammelten Vögel und Beschreibungen neuer Arten. Journal für Ornithologie 49: 81–99.

BERLEPSCH, H. G. VON. 1909. Über eine neue Gattung aus der Familie der Tyrannidae. Journal für Ornithologie 57:104–107.

CAPPARELLA, A. P. 1988. Genetic variation in Neotropical birds: Implications for the speciation process. Pages 1658–1664 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Science, Ottawa.

CRACRAFT, J., AND R. O. PRUM. 1988. Patterns and processes of diversification: Speciation and historical congruence in some Neotropical birds. Evolution 42:603–620.

FITZPATRICK, J. W. 1976. Systematics and biogeography of the tyrannid genus *Todirostrum* and related genera (Aves). Bulletin of the Museum of Comparative Zoology 147:435–463.

FITZPATRICK, J. W., AND J. P. O'NEILL. 1979. A new tody-tyrant from northern Peru. Auk 96: 443–447.

GYLDENSTOLPE, N. 1930. Notes on Ant Wrens allied to *Myrmotherula surinamensis* Gmelin, together with the descriptions of two new forms. Arkiv for Zoologi 21A, No. 26.

HACKETT, S. J. 1993. Phylogenetic and biogeographic relationships in the Neotropical genus *Gymnopithys* (Formicariidae). Wilson Bulletin 105:301–315.

HACKETT, S. J., AND K. V. ROSENBERG. 1990. Comparison of phenotypic and genetic differentiation in South American antwrens (Formicariidae). Auk 107:473–489.

HAFFER, J. 1969. Speciation in Amazonian forest birds. Science 165:131–137.

HAFFER, J. 1974. Avian speciation in tropical South America. Publications of the Nuttall Ornithological Club No. 14.

HAFFER, J. 1993. Time's cycle and time's arrow in the history of Amazonia. Biogeographica 96:15–45.

HELLMAYR, C. E. 1927. Catalogue of birds of the Americas and the adjacent islands. Part 5, Tyrannidae. Field Museum of Natural History Publication No. 242, Zoological Series, vol. 13.

LANYON, W. E. 1988a. A phylogeny of the thirty-two genera in the *Elaenia* assemblage of tyrant flycatchers. American Museum Novitates 2914: 1–57.

LANYON, W. E. 1988b. A phylogeny of the flatbill and tody-tyrant assemblage of tyrant flycatchers. American Museum Novitates 2923:1–41.

PARKER, T. A., III, J. M. BATES, G. COX. 1992. Rediscovery of the Bolivian Recurvebill with notes on other little-known species of the Bolivian Andes. Wilson Bulletin 104:173–178.

PARKER, T. A., III, A. CASTILLO U., M. GELL-MANN, AND O. ROCHA O. 1991. Records of new and unusual birds from northern Bolivia. Bulletin of the British Ornithologists' Club 111:120–138.

PARKER, T. A., III, AND J. V. REMSEN, JR. 1987. Fifty-two Amazonian bird species new to Bolivia. Bulletin of the British Ornithologists' Club 107:94–107.

REMSEN, J. V., JR. 1984. High incidence of "leapfrog" pattern of geographic variation in Andean birds: Implications for the speciation process. Science 224:171–173.

REMSEN, J. V., JR., T. A. PARKER, III, AND R. S. RIDGELY. 1982. Natural history notes on some poorly known Bolivian birds. Gerfaut 72:77–87.

REMSEN, J. V., JR., O. ROCHA O., C. G. SCHMITT, AND D. C. SCHMITT. 1991. Zoogeography and geographic variation of *Platyrinchus mystaceus* in Bolivia and Peru, and the circum-Amazonian distribution pattern. Ornitologia Neotropical 2:77–83.

SIBLEY, C. G., AND J. E. AHLQUIST. 1990. Phylogeny and classification of birds. Yale University Press, New Haven, Connecticut.

SIBLEY, C. G., AND B. L. MONROE, JR. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut.

SICK, H. 1985. Observations on the Andean-Patagonian component of southeastern Brazil's avifauna. Pages 233–237 *in* Neotropical ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely, and F. G. Buckley, Eds.). Ornithological Monographs No. 36.

SNETHLAGE, E. 1907. Neue Vogelarten aus Südamerika. Ornithologische Monatsberichte 15:193–196.

STOTZ, D. F. 1992. Specific status and nomenclature of *Hemitriccus minimus* and *Hemitriccus aenigma*. Auk 109:916–917.

TRAYLOR, M. A., JR. 1977. A classification of the tyrant flycatchers (Tyrannidae). Bulletin of the Museum of Comparative Zoology 148:129–184.

TRAYLOR, M. A., JR. 1979. Tyrannidae. Pages 1–240 *in* Check-list of birds of the world, vol. 8 (M. A. Traylor, Jr., Ed.). Harvard University Press, Cambridge, Massachusetts.

WHITNEY, B. M. 1994. Behavior, vocalizations, and possible relationships of four *Myrmotherula* antwrens (Formicariidae) from eastern Ecuador. Auk 111:469–475.

WILLIS, E. O. 1992. Zoogeographical origins of eastern Brazilian birds. Ornitologia Neotropical 3:1–15.

ZIMMER, J. T. 1940. Studies of Peruvian birds, No. 34. The genera *Todirostrum, Euscarthmornis, Snethlagea, Poecilotriccus, Lophotriccus, Myiornis, Pseudotriccus,* and *Hemitriccus*. American Museum Novitates 1066:1–23.

Received 7 July 1995, accepted 3 November 1995.