

THE WILSON BULLETIN

A QUARTERLY MAGAZINE OF ORNITHOLOGY

Published by the Wilson Ornithological Society

VOL. 98, No. 3

SEPTEMBER 1986

PAGES 337-504

Wilson Bull., 98(3), 1986, pp. 337-352

A NEW SPECIES OF ANTWRN (FORMICARIIDAE: *HERPSILOCHMUS*) FROM PERU, WITH COMMENTS ON THE SYSTEMATICS OF OTHER MEMBERS OF THE GENUS

TRISTAN J. DAVIS AND JOHN P. O'NEILL¹

ABSTRACT.—In northern Peru during 1983 we collected specimens of an undescribed taxon of antwren of the poorly known genus *Herpsilochmus* that is best described as a new species, which we call *H. parkeri*, the Ash-throated Antwren. The new species may replace *H. axillaris* ecologically at similar elevations in the eastern Andes of northern Peru. Based on plumage patterns, the genus *Herpsilochmus* can be divided into four or five groups: *H. parkeri* appears to belong to the group consisting of all of the taxa that have previously been considered conspecific with *H. pileatus* (nominate *pileatus*, *atricapillus*, and *motacilloides*). These taxa, including *parkeri*, have allopatric distributions except for the complete overlap of the range of nominate *pileatus* within the range of *atricapillus*. Habitat differences apparently exist among the taxa: *parkeri* and *motacilloides* inhabit humid upper tropical and subtropical forest in the Andes, *pileatus* inhabits caatinga, and *atricapillus* prefers dry forest in southern South America. Plumage differences between the taxa are as great as are those between other species pairs within the genus *Herpsilochmus* whose ranges apparently overlap with no evidence of interbreeding. Owing to the lack of evidence of intergradation between *pileatus* and *atricapillus* where their ranges overlap, these taxa should be considered separate species. Upon consideration of the differences in habitat, plumage, and vocalizations that exist between *atricapillus*, *motacilloides*, and *parkeri*, it seems best to treat each of these taxa as separate species until further data are available. *Received 3 June 1985, accepted 11 Jan. 1986.*

The genus *Herpsilochmus* (Formicariidae), as currently recognized (Peters 1951; Meyer de Schauensee 1966, 1970), consists of nine species of antwrens, many of which are little known in the field and poorly repre-

¹ Museum of Zoology and Dept. Zoology and Physiology, Louisiana State Univ., 119 Foster Hall, Baton Rouge, Louisiana 70803-3216.



The *Herpsilochmus pileatus* complex, including the Ash-throated Antwren, *H. parkeri*, sp. nov. (upper pair) and (left to right) the White-browed Antwren, *H. pileatus*, the Black-capped Antwren, *H. atricapillus*, and the Yellow-bellied Antwren, *H. motacilloides*. Males are above, females below.
From a mixed-media painting by John P. O'Neill.

sented in most collections. In fall 1983, while on an expedition for the Louisiana State University Museum of Zoology (hereafter LSUMZ) in northern Peru, we obtained a series of an undescribed taxon of *Herpsilochmus* antwren. Our investigations of the relationships of this new form led us to review the species limits and taxonomy of the *H. pileatus* complex (*H. "p." pileatus*, *H. "p." atricapillus*, and *H. "p." motacilloides*). In this paper we propose that each of these taxa is best considered a full species.

The new antwren is most closely related to the taxa included in *H. pileatus* but represents a distinct new species that we propose to call

***Herpsilochmus parkeri* sp. nov.**

ASH-THROATED ANTWREN

HOLOTYPE.—Louisiana State University Museum of Zoology No. 116908; adult male from ca 15 km by trail northeast of Jirillo on the trail to Balsapuerto, 06°03'S, 76°44'W, 1350 m, Department of San Martín, Peru, 20 November 1983; collected by Tristan J. Davis, original no. 3051.

DIAGNOSIS.—A relatively large (ca 11.5–13 cm total length), sexually dimorphic antwren, the males of which most closely resemble the males of *H. "pileatus" atricapillus* of southern South America by their size, unspotted rectrices (throughout this paper, a spotted tail refers to one that has the inner webs of the innermost rectrices marked along their edge with black and white alternating, instead of having the white along the edge continuous [=“unspotted”]; when observed from above, the former appears as a row of spots along the center of the tail), unmarked chest, and gray and white underparts. Males distinguished from *atricapillus* by having a black loreal spot instead of a thin grayish black eyeline between eye and bill, an ash-gray instead of white throat, and darker gray sides, flanks and chest (Frontispiece, Fig. 2). Distinguished from *H. "p." motacilloides* by lack of yellowish wash on breast and belly, more black and white in the interscapulars, darker gray breast, sides and flanks, and ash-gray as opposed to whitish throat. Females like females of *H. "p." atricapillus* but differ in having a darker buff throat, a bright buff instead of whitish eyebrow, a clear white instead of a buffy abdomen, buffy gray instead of buff flanks, and midback gray only slightly tinged buff, lacking the strong olive-buff tones present on the backs of *atricapillus*. Females also similar to females of *H. dorsimaculatus* but differ in having a long, unspotted instead of a rather short, spotted tail and an unmarked, grayish back instead of a grayish back broadly striped with black and white.

DISTRIBUTION.—So far, known only from the type locality east-southeast of Moyobamba in the Department of San Martín, northern Peru (Fig. 1).

DESCRIPTION OF HOLOTYPE.—Crown, extending from bill to upper midback, Jet Black (capitalized color names from Smithe 1975). Eyebrow, extending from the side of the base of the bill passing just over the eye and extending to the side of the back of the crown, pale grayish white. Feathers just below eye pale grayish white finely edged with gray, near Medium Neutral Gray. Loes and line extending from behind eye, below eyebrow as far as the hind-crown, Jet Black. Auriculars pale grayish white, darkening slightly towards sides of neck. Chin pale grayish white. Throat and breast near Pale Neutral Gray, slightly intermixed with whitish. Sides of breast, sides, and flanks very close to Light Neutral Gray (slightly paler). Center of abdomen clear white. Undertail coverts grayish white. Back closest to Dark Neutral Gray, interscapulars along midback variously intermixed with Jet Black and white; Jet Black found on outer one-third to one-fourth of feathers, white usually found as a spot

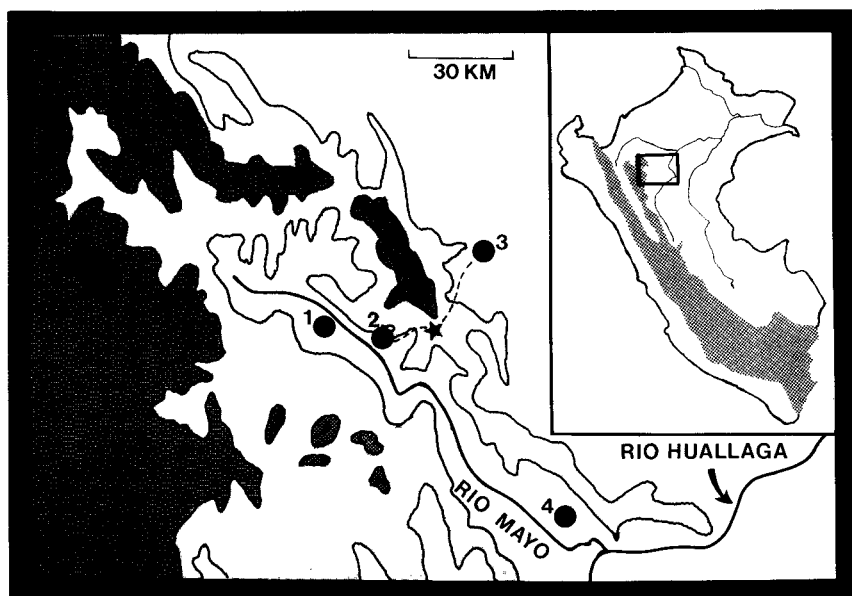


FIG. 1. Andes of northern Peru showing localities in the Río Mayo and Río Huallaga. 1. Moyobamba; 2. Jirillo; 3. Balsapuerto; 4. Tarapoto; star, type locality; dotted line, Jirillo-Balsapuerto trail (light stippling above 1000 m; dark stippling above 2000 m).

located on only one web about halfway down the length of the feather; a few of the feathers having some Jet Black lack any trace of white. Scapulars Blackish Neutral Gray to Jet Black broadly edged white on outer webs. Rump near Medium Neutral Gray. Upper tail coverts blackish Neutral Gray. Tail with rectrix numbers (numbering from the inside out on each side) 1, 4, and 5 (right), and 1, 5, and 6 (left); remaining rectrices missing. Rectrices white towards tips, black towards bases. Outermost rectrix with the most white (distal half white); each successive rectrix thereafter has relatively less white than the previous one. Central rectrices (no. 1 left and right) black, narrowly tipped white: inner webs narrowly fringed white on basal three-fourths of feather. Wings Jet Black, browner towards tips of remiges. Remiges edged white on outer webs except at their bases; inner webs edged with white but edging wider than on the outer webs. Upper wing coverts Jet Black broadly tipped white forming three distinct wing bars, the uppermost quite small. Soft part colors in life: iris brown; tarsi and feet bluish gray; maxilla black; mandible medium gray, lighter at edges.

MEASUREMENTS OF HOLOTYPE.—Wing (chord) 55.6 mm; tail 56.6 mm; culmen from base 16.5 mm; tarsus 17.5 mm; weight 11.5 g.

DESCRIPTION OF FEMALE.—Forehead orangish Cinnamon. Crown, extending from just above eyes to upper midback, between Sepia and Jet Black; some feathers with patch of white on one web forming elongated streaks on crown; a few feathers of forecrown with orangish Cinnamon shafts. Eyebrow extending from side of base of bill passing just over the eye and extending to the side of the back of the crown, lores, auriculars, and area just below eye between Clay Color and Yellow Ocher (feathers in area just below eye lightly edged Medium Neutral Gray). Line extending from behind eye beneath eyebrow between Sepia and Jet Black. Chin, throat, and breast close to Yellow Ocher (slightly grayish), throat



FIG. 2. A. Hand-held adult male *H. parkeri*. B. Tall forest understory at type locality.

slightly paler. Flanks and undertail coverts Pale Neutral Gray with a slight buffy wash. Abdomen white. Sides of breast and neck dull grayish Clay Color extending dorsally onto upper back forming an almost complete nuchal collar, broken in the middle by the thin black extension of the crown. Back Medium Neutral Gray, upper back lightly washed with ochraceous; a few feathers of the midback have their webs with black spots on them and some have very pale grayish white shafts with the same color on the nearby vanes; this pattern is reminiscent, although much reduced, of the coloration of the back in the males of the species. Inner webs of scapulars Dark Neutral Gray, outer webs Jet Black, the latter broadly edged white. Rump and upper tail coverts Medium Neutral Gray. Tail and wings similar to males.

SPECIMENS EXAMINED.—*H. parkeri*: Peru: San Martín, 4 ♂♂ and 4 ♀♀ (LSUMZ), 1 ♂ skeleton (LSUMZ), 1 ♂ in alcohol (LSUMZ). *H. "pileatus" pileatus*: Brazil: Bahia, 1 ♂ ([AMNH=] American Museum of Natural History), 2 ♀♀ (AMNH), 1 sex ? (♂ by plumage) ([BM=] British Museum). *H. "pileatus" atricapillus*: Brazil: Bahia, 1 ♂ (AMNH); Pernambuco, 1 ♂ (AMNH), 1 ♀ (AMNH); Goiás, 1 ♂ (LSUMZ), 1 ♀ (LSUMZ); "Pianky" (probably Piauí), 1 ♀ (AMNH); Bolivia: Chuquisaca, 1 ♂ ([ANSP=] Academy of Natural Sciences of Philadelphia); "Chiquitos," 1 ♀ (LSUMZ); Santa Cruz, 8 ♂♂ ([FMNH=] Field Museum of Natural History, LSUMZ), 4 ♀♀ (FMNH, LSUMZ); Tarija, 1 ♂ (AMNH), 2 ♀♀ (ANSP). *H. "pileatus" motacilloides*: Peru: Junín: Utcuyacu, 1 ♂, 1 ♀ (AMNH); Pasco: Pichis Trail (formerly in Junín), 2 ♂♂, 1 ♀ (ANSP), Santa Cruz, 1 ♂, 1 ♀ (LSUMZ), Cushi, 1 ♂, 1 ♀ (LSUMZ). *H. sticturus* (excluding *dugandi*): British Guiana, 2 ♂♂, 1 ♀ (AMNH); Venezuela, 1 ♀ (AMNH). *H. "sticturus" dugandi*: Peru, 1 ♂, 1 ♀ (LSUMZ). *H. stictocephalus*: Guyana, 1 ♂, 2 ♀♀ (AMNH). *H. dorsimaculatus*: Brazil, 2 ♂♂, 2 ♀♀ (AMNH). *H. roraimae*: Venezuela, 2 ♂♂, 1 ♀ (AMNH); "Roraima," 1 ♀ (AMNH). *H. pectoralis*: Brazil, 2 ♂♂, 1 ♀ (LSUMZ). *H. longirostris*: Brazil, 4 ♂♂, 2 ♀♀ (LSUMZ, AMNH); Bolivia: Dept. Beni, Río Iténez, 1 ♂ (AMNH);

first report of the species in Bolivia). *H. axillaris*: Peru, 1 ♂, 1 ♀ (LSUMZ). *H. rufimarginatus*: Panama, 1 ♂, 1 ♀ (LSUMZ); Venezuela, 1 ♂, 1 ♀ (LSUMZ); Brazil, 1 ♂ (LSUMZ); Peru, 2 ♂♂, 3 ♀♀ (LSUMZ); Bolivia, 1 ♂, 2 ♀♀ (LSUMZ); Paraguay, 1 ♂ (LSUMZ).

ETYMOLOGY.—We are pleased to name this species after our good friend Theodore A. Parker III, who, after more than a decade of studying neotropical birds in both the field and the museum, is unrivaled in his knowledge of the natural history of South American avifauna. He eagerly shares his vast knowledge, and in this way he influences many of those interested in neotropical birds, both professionals and lay-people alike.

The proposed English name, Ash-throated Antwren, refers to the light grayish throat of the males of the new species; this is one of the characteristics that distinguishes it from closely related congeners.

REMARKS

Variation in the type series.—Only slight variation in plumage coloration is apparent within the series. Males vary in the amount of black and white mixed in the interscapulars. White is usually more predominant than the black; black on the interscapulars varies from a few centrally located blotches to rather extensive markings over much of the midback. The holotype has slightly more black in the interscapulars than the other three males. This individual variation in the amount of black and white in the interscapulars seems to be typical in those species of *Herpsilochmus* in which such interscapular markings occur. Perhaps this variability is age related (see below). Almost no variation in female plumage coloration is apparent except for one adult female (LSUMZ, skull 100% pneumatized), which has the throat and breast a slightly paler shade of buff. Females also vary in the amount of white spotting on the crown. The two females with 100% ossified skulls have very little white on the crown, while the other two females have more extensive white spotting (these latter two have their skulls 10% and 90% ossified). There seems to be considerable variation in the extent of white spotting on the crowns of females with this trait in the genus *Herpsilochmus* as a whole. Some specimens show only a trace of the spotting while others show extensive white spotting. This variation may be age related, but more specimens with gonad and skull data are needed to confirm this. Descriptions of soft part colors vary only slightly in the new species. The color of the lower mandible is apparently darker in the males; the color in all four males was recorded as gray (one with a black tip and another lighter along cutting edge), whereas in all four females it was recorded as light gray (one lighter at edges). Descriptions of the color of the tarsi and feet (=toes) of the birds of both sexes were light gray, gray, dark gray, and blue-gray.

Two males and one female of the new species show what may be age-related plumage variations. A male collected by O'Neill on 27 October has its skull only 5% pneumatized. This bird's plumage is exactly as in the other 3 males (two with fully pneumatized skulls and one with the

skull 50% pneumatized) except in the following ways: the black and white in the interscapulars is reduced to a few small spots, the gray of the underparts is a lighter shade than in the other males, and the black loreal spot is smaller. The male specimen with the 50% pneumatized skull (LSUMZ) also has a smaller loreal spot and less black in the interscapulars than the two birds with skulls 100% pneumatized, but it is otherwise similar to them. Both of these specimens appear to have adult rectrices (rounded as opposed to slightly pointed in juvenal rectrices); the former specimen, however, was in the process of molting almost its entire tail, and only three rectrices are fully grown, and with at least one of these three appearing fresh. The latter specimen also lacks several of its rectrices, but there is no apparent sign of molt. These two specimens probably had already lost most, if not all, of their juvenal rectrices and had begun to grow the rounded rectrices of the adult plumage. A female collected on 1 November by Davis has its skull 10% pneumatized, and its ovary was only 3×1 mm and smooth. This individual's plumage is as in the three other female specimens (two with fully pneumatized skulls and one with its skull 90% pneumatized) except as follows: the rectrices are pointed as opposed to rounded, and the white of the belly is not as pure as in the other females, being slightly intermixed with pale buff towards the breast.

Breeding and molt.—None of the specimens was in breeding condition. The largest testis of any of the males was 3×1.5 mm, and the largest ovary of any of the females 6×3 mm, with the ova and the oviduct minute. Because all the specimens were collected from the end of October to late November, it may be that most breeding takes place during the drier part of the year (the dry season in the area is from about May to September or October), although much singing was heard throughout our stay. Two birds were in light to moderate body molt. Although no body molt was recorded in the remaining specimens, the rectrices of almost all of the specimens varied from lightly worn to heavily worn at the tips, especially in the females. The condition of the feathers leads one to suspect that the main part of the breeding season had just been completed, and the birds had not yet gone through a postbreeding molt. Six of the nine specimens obtained were apparently paired when collected; the three that were not known to be paired when collected include the female with the 10% pneumatized skull, the male with the 5% pneumatized skull, and a male that was netted.

Habitat and ecology.—Habitats at the only known locality for the new species are very heterogeneous. The Moyobamba Valley directly to the west of the mountain ridge is moderately xeric, owing to a partial rain-shadow effect. Our camp was situated at what appeared to be the upper elevational limit of the savanna-like habitat that characterizes much of that valley. This habitat was distributed only in scattered patches at 1350

m. There was also a distinct habitat, located mostly on ridges in the area, that resulted from the outcropping of sandy, poor-quality soils where vegetation was usually short (ca 4 m), extremely dense, and of low floristic diversity. A semistunted, more-diverse forest was also present and seemed to form a transition between the savanna-like vegetation and the tall cloud forest that was present in areas with good soil. The semistunted forest had a canopy height of ca 12 m, whereas the tall forest averaged 30–35 m in height. For more information on this locality and its avifauna, see Davis (1986).

H. parkeri was noted most commonly in the canopy and midlevels of the tallest forest. The undergrowth in this habitat was moderately open, the canopy was mostly closed, and epiphytes were common (Fig. 2B). The antwren was only slightly less common in the semistunted forest and was also found there from the midlevels of the forest to the canopy. The undergrowth in this latter habitat was extremely dense, and the canopy was only slightly closed; epiphytes there were extremely abundant. *H. parkeri* was recorded only once from the savanna-like habitat, where one male was netted in some low bushes at the surprisingly abrupt border between this habitat and the semistunted forest (the abrupt transition may be fire-maintained). The species was usually seen traveling in pairs in association with a mixed-species flock, and its song was heard quite often. Other species of birds noted in the same flocks with *H. parkeri* included, most commonly, *Myrmotherula schisticolor*, *Automolus ochrolaemus*, *Xiphorhynchus ocellatus*, *Xenops rutilans*, and *Hemitriccus rufigularis*.

Although the avifauna at this locality was very similar to the avifauna at another LSUMZ collecting locality almost directly across the Moyobamba Valley (Parker and Parker 1982), the only species of *Herpsilochmus* recorded at the latter site was *H. axillaris*. At a similar locality in the Department of Amazonas (east of La Peca) at a slightly higher elevation ca 180 km northwest of the type locality of the new species, an LSUMZ party also recorded only *H. axillaris*. At both of these localities *H. axillaris* was uncommon to rare. It is possible that *H. parkeri* is indeed truly restricted to the low mountain range east of Moyobamba, an isolated area with poor soil and low plant diversity, and is ecologically replaced elsewhere in northern Peru at similar elevations by *H. axillaris*. Of course it is possible that we overlooked the latter species at the locality where *H. parkeri* was common, but we doubt this because we spent a month there studying the avifauna.

Stomach contents of five individuals of *H. parkeri* were examined (LSUMZ Stomach Contents Collection). These stomachs contained a variety of insects, primarily Coleoptera (including Curculionidae and Coccinellidae, at least one of which was identified as a probable *Brachiacantha* sp. of the tribe Hyperaspini) and Hemiptera (both of which were present

in five stomachs), and Hymenoptera (present in four stomachs). Other insects identified in the stomachs but in lower frequencies than the previously mentioned taxa included Homoptera (including at least one Fulgoroidea), Formicidae, Orthoptera, Dermaptera, and one spider of the Araneae (probably Salticidae).

Voice.—The song of *H. parkeri* began with a series of 3–4 well-spaced notes followed by an accelerating and slightly descending rapid succession of notes that ran together towards the end and stopped abruptly; an entire song phrase lasted 3–4 sec. Songs of closely related *motacilloides* and *atricapillus* seem to differ in lacking the introductory component (pers. obs.; tape recordings in Library of Natural Sounds, Cornell University). The song of *atricapillus* differs additionally by becoming slower towards the end so that the terminal sequence is somewhat protracted. Songs of *pileatus* remain unknown.

Systematic relationships.—Four to five groups in the genus *Herpsilochmus* can be distinguished based on shared plumage patterns. The most differentiated taxa in the genus, *H. axillaris* and *H. rufimarginatus* (possibly two different “groups”), are both bright yellow below (unlike all other members of the genus) and have unspotted tails. The former inhabits cool upper tropical and subtropical forests in the Andes, whereas the latter inhabits mostly forested lowlands from Central America to Bolivia and Paraguay. Another group consists of *H. longirostris* and *H. pectoralis*; we consider these two species closely related because both male and female plumages are extremely similar and their ranges almost abut. A third group consists of those species in the genus that possess a tail that is spotted along the inner webs of the central rectrices. This group includes the following species: *H. sticturus* (including *dugandi*), *H. stictocephalus*, *H. dorsimaculatus*, and *H. roraimae*. The first two in this group are probably more closely related to one another than either is to any other member of the group. *H. roraimae* differs from all other members of this group in having a longer tail, consequently with more spots, and in having spots on both webs of the central rectrices instead of just on the inner webs. Some individuals of the other species in this group do show a hint of spots on the outer webs also. The last group includes the taxa that have been included in the species *H. pileatus*. For reasons discussed later, all three taxa within that species are best treated as distinct species. This last group can be distinguished as having a tail that lacks spots, with the central rectrices edged with white on their inner webs for most of their length; as lacking any distinct dark markings across the chest, and as having their underparts basically gray and white (1 taxon with a yellowish wash below). All except nominate *pileatus* can also be distinguished as having a relatively longer tail than do most other members of the genus (Table 1).

TABLE 1
SELECTED MEASUREMENTS (MM) OF THE SPECIES OF *HERPSILOCHMUS*

Species	Culmen (from base)		Wing chord		Tail		Tarsi	
	N	\bar{x} (range)	N	\bar{x} (range)	N	\bar{x} (range)	N	\bar{x} (range)
<i>parkeri</i>	8	17.2 (16.5-17.6)	8	54.7 (52.4-57.9)	6	57.0 (55.7-58.3)	8	18.2 (16.8-19.1)
<i>pileatus</i>	4	15.5 (14.3-17.3)	4	46.7 (43.0-49.8)	3	44.1 (43.0-45.1)	4	16.8 (15.6-17.2)
<i>atricapillus</i>	21	16.15 (15.1-16.7)	23	52.3 (49.0-56.0)	20	52.5 (48.2-55.7)	22	18.1 (16.5-18.9)
<i>motacilloides</i>	10	16.0 (15.5-16.5)	10	52.5 (50.5-54.5)	10	53.6 (49.8-56.4)	9	17.2 (16.4-18.1)
<i>sticturus</i>	4	16.2 (15.9-16.4)	4	46.7 (45.2-47.5)	4	34.2 (33.6-35.3)	4	15.8 (15.5-16.0)
"s." <i>dugandi</i>	2	16.2 (15.9-16.4)	2	47.8 (46.5-49.1)	2	34.5 (34.4-34.6)	2	16.3 (15.7-16.8)
<i>stictocephalus</i>	3	16.1 (15.9-16.3)	3	46.8 (45.0-48.1)	3	35.1 (34.7-35.4)	3	15.6 (14.8-16.4)
<i>dorsimaculatus</i>	4	16.7 (16.4-17.1)	4	48.1 (46.6-51.3)	4	39.9 (38.2-40.2)	3	17.0 (16.5-17.4)
<i>roraimae</i>	4	17.3 (16.8-17.9)	4	53.3 (52.5-54.2)	4	52.6 (51.6-54.7)	4	18.4 (17.9-19.3)
<i>pectoralis</i>	3	16.8 (16.1-17.3)	3	51.2 (50.7-51.8)	3	38.3 (38.1-38.6)	3	19.6 (19.2-19.9)
<i>longirostris</i>	21	19.0 (18.1-19.9)	21	60.2 (57.9-62.6)	20	54.2 (49.1-57.4)	20	19.5 (18.8-21.2)
<i>axillaris</i>	2	15.9 (15.3-16.5)	2	51.8 (50.1-53.5)	2	45.8 (45.5-46.1)	2	16.7 (16.3-17.0)
<i>rufimarginatus</i>	13	16.7 (15.7-17.4)	13	50.0 (47.8-53.2)	12	43.3 (37.4-48.5)	13	18.1 (17.1-18.9)

H. parkeri, based on plumage alone, best fits into the last group. The tail pattern in the new species is exactly as in the other members of the group. The plumage of the males in the new species closely resembles the male plumage of both *H. "pileatus" atricapillus* and *H. "pileatus" motacilloides*. The females of *H. parkeri* resemble the females of *H. dorsimaculatus* in that they both have a bright buff throat and breast contrasting with a white belly and grayish flanks, an ochraceous forehead, and a black crown with white spots. *H. dorsimaculatus* and *H. parkeri* are the only species in the genus that possess this particular color pattern, although there is a hint of this pattern (e.g., a pale buffy wash across the breast) in several other members of the genus. Otherwise, *H. dorsimaculatus* and *H. parkeri* are very different. *H. parkeri* females, with their long, unspotted tails and unmarked grayish backs, lack the spotted and relatively short tail of *H. dorsimaculatus*, and also lack the boldly striped back characteristic of the latter species. Additionally, the females of *H. parkeri* share similarities with the females in the *H. pileatus* group including similarly patterned, relatively long tails, and unmarked grayish backs, in addition to a similar overall body size and shape. For the above reasons, we believe that *H. parkeri* is most closely related to the taxa previously included in *H. pileatus*.

SYSTEMATICS OF THE *HERPSILOCHMUS PILEATUS* COMPLEX

The three taxa that have been included in *Herpsilochmus pileatus* (nominate *pileatus*, *motacilloides*, and *atricapillus*) are quite distinct from one another (Frontispiece), but, along with *H. parkeri*, appear to form a "natural" group. The distinguishing and shared plumage characteristics of these four taxa are listed in Table 2. The males show fewer differences in plumage coloration between taxa than do the females, but this is typical among many closely related taxa of Formicariidae. Selected measurements of these four taxa and the remaining species in the genus *Herpsilochmus* are given in Table 1. Of the four taxa involved in the *H. pileatus* complex, *atricapillus* and *pileatus* appear to be the most similar in plumage coloration, while *atricapillus*, *motacilloides*, and *parkeri* are more similar to each other in size and proportions than any of these is to *pileatus* (although *parkeri* averages larger in all characters measured) (Table 1). In both sexes tail length seems to be the best distinguishing character and can serve to distinguish *pileatus* from similarly plumaged *atricapillus*, as well as *motacilloides* and *parkeri*, with no apparent overlap (Naumberg 1939) (Table 1).

These three taxa and *H. parkeri* are all essentially allopatric: *pileatus* inhabits a small portion of eastern Brazil; *atricapillus* occurs from eastern Bolivia east, south of Amazonia, to eastern Brazil; *motacilloides* inhabits

TABLE 2
SELECTED CHARACTERS OF MEMBERS OF THE *HERPSILOCHMUS PILEATUS* SPECIES COMPLEX

Species	Sex	Lores	Throat	Midbreast	Belly	Forehead	Crown	Back	Neck
<i>pileatus</i>	♂	Whitish	White	White	White	Black	Black	Gray mixed black and white	Gray
	♀	Whitish	White	White (rarely with buff tinge)	White tinged buff near vent and flanks	Blackish (tinged buff in some specimens)	Blackish with pale edges (scalloped effect)	Gray tinged brownish-olive	Gray
<i>atricapillus</i>	♂	Whitish	White	White-pale gray	White	Black	Black	Gray mixed black and white	Gray
	♀	Whitish	Buff-very pale buff	Buff	Buff-very pale buff	Ochraceous	Black with white elongated spots	Gray tinged olive-buff	Gray tinged buff near breast
<i>motacilloides</i>	♂	Black	White	White washed yellow	White washed yellow	Black	Black	Gray mixed black and white	Gray
	♀	Black	White	White washed yellow	White washed yellow	Ochraceous	Black with white elongated spots	Gray tinged olive-buff	Gray
<i>parkeri</i>	♂	Black	Pale gray	Pale gray	White	Black	Black	Gray mixed black and white	Gray
	♀	Buffy-white	Buff	Buff	White	Ochraceous	Black with white elongated spots	Gray	Gray tinged dull buff encircling neck

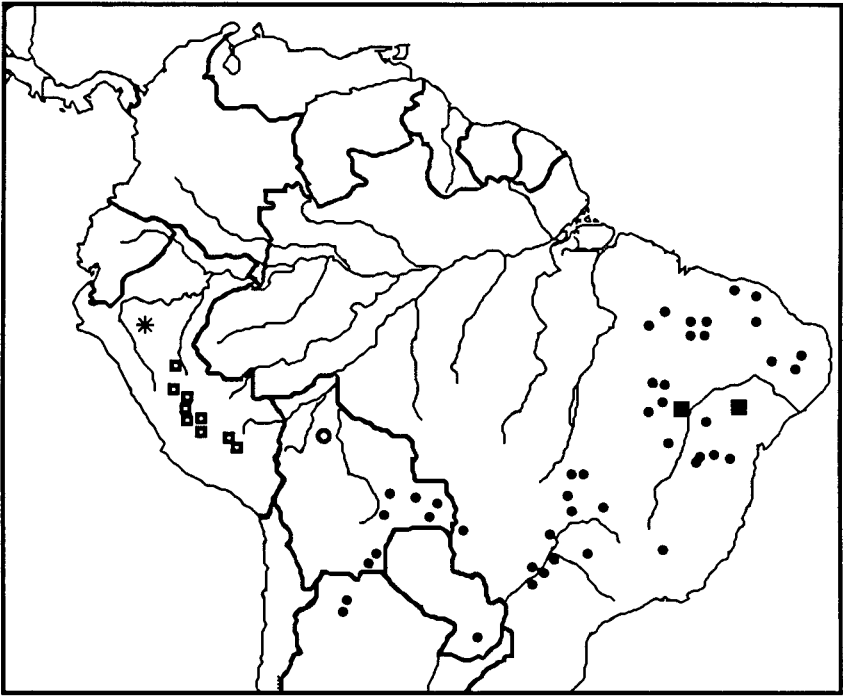


FIG. 3. Map of the distribution of members of the *Herpsilochmus pileatus* species complex. Large, solid squares: *pileatus*; small squares with open dot: *motacilloides*; asterisk: *parkeri*; small solid circles: *atricapillus*; large open circle: sight record of *atricapillus* by Remsen (in press).

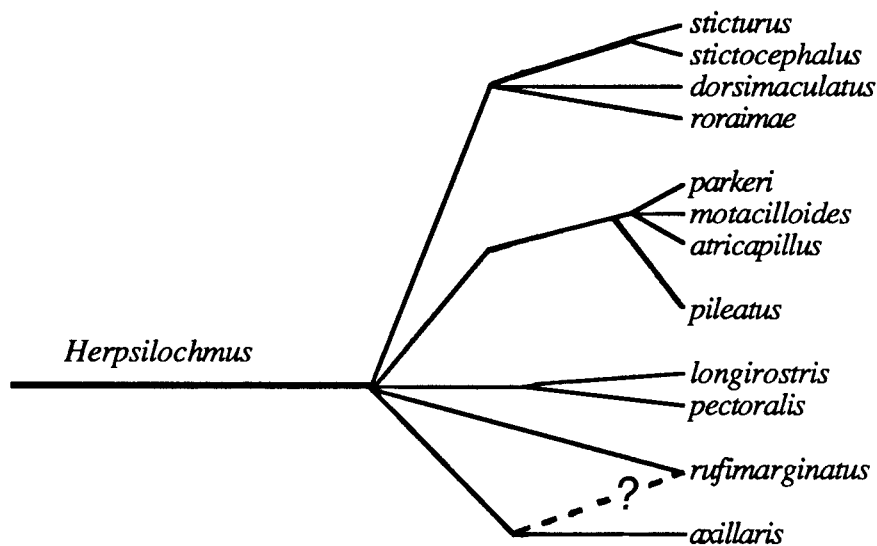
central and southern Peru; and *H. parkeri* appears to be restricted to a small portion of northern Peru. Although nominate *pileatus* and *atricapillus* are essentially allopatric in that they have not been collected at the same locality, they are known to occur within 50 km of each other (Naumberg 1935, 1939), and localities of *atricapillus* are known that essentially surround the two known localities of *pileatus*. Thus, it actually appears that their ranges may overlap (Fig. 3).

In addition to the morphological and plumage differences that these four taxa exhibit, apparent differences exist in their preferred habitats. Nominate *pileatus* and *atricapillus* both are found in eastern Brazil where *pileatus* was said to inhabit caatinga forest (Naumberg 1939), a specialized forest type found in northeast Brazil from Rio Grande do Norte to southern Bahia, characterized by deciduous, thorny scrubland with many cacti and other succulents with the ground more or less open (Meyer de Schauensee 1970). In this region of Brazil, *atricapillus* was said to inhabit a habitat with dense underbrush and very little high forest (Naumberg

1939). J. V. Remsen (field notes, LSUMZ) found *atricapillus* to be fairly common in fairly tall deciduous forest in the Department of Santa Cruz, Bolivia, especially along a river where the trees tended to have more leaves, the canopy was variable, the undergrowth was dense with many ferns, there was no moss on the trees (only dried lichens), and epiphytes were virtually nonexistent. Although it appears that *pileatus* and *atricapillus* have ranges that essentially overlap, these two taxa may replace each other by habitat. Both known localities of *pileatus* are in caatinga, whereas the closest localities of *atricapillus* are in more humid deciduous forest; however, a few localities of *atricapillus* more distantly located from the localities of *pileatus* are also in caatinga (Naumberg 1935, 1939). In contrast to these habitat types, the habitat of both *motacilloides* and *parkeri* is dense, tall, evergreen cloud forest with heavy moss and epiphytic growth along the humid slopes of the Peruvian Andes in the Upper Tropical and Subtropical "zones." *H. parkeri* was found only at 1350 m even though elevations down to 750 m were studied intensively in the same range of foothills. Southeast Peruvian *motacilloides* has been recently collected at elevations of over 2000 m in the Andes (LSUMZ), but a few older specimens have localities of less than 1000 m. Both *pileatus* and *atricapillus* are more typical of elevations below 1000 m (Naumberg 1935, 1939; LSUMZ).

Vocalizations of different species within this genus are similarly structured. Nonetheless, the song of *parkeri* differs distinctively from the song of *motacilloides*, one of the taxa most closely related to *parkeri* and the one nearest to it geographically. The song of *atricapillus* differs from both *motacilloides* and *parkeri*. At present, however, lack of sufficient data on the vocalizations of the members of the genus precludes emphasizing vocalizations in determining the specific status of the taxa in question. Such an analysis must wait at least until vocalizations of *parkeri* are available and playback experiments between the taxa can be performed.

Due to the equivocal distribution of *pileatus* with respect to that of *atricapillus* and the lack of evidence of intergradation, these two taxa should be considered separate species. The classification of the remaining two taxa (*motacilloides* and *parkeri*) with respect to *atricapillus* is more difficult. Although Zimmer (1932) felt that *pileatus* and *atricapillus* were more closely related to each other than either was to *motacilloides*, we perceive that the latter two are almost equally differentiated from the nominate *pileatus*. Since *atricapillus*, *motacilloides*, and *parkeri* are completely allopatric, they could well be considered to be conspecific. Direct application of the biological species concept is difficult with allopatric populations (Mayr 1963), and degrees of morphological, biochemical, or behavioral differentiation must be used to determine specific status of such isolated taxa. Even so, such classifications remain tentative pending



DEGREE OF SIMILARITY

FIG. 4. Hypothetical relationships within the genus *Herpsilochmus*; dotted line indicates possible closer relationship between *rufimarginatus* and *axillaris*.

further knowledge of the natural histories of the taxa. Differences in plumage are as great between these taxa as are differences between other species pairs within the genus *Herpsilochmus* (i.e., *H. sticturus* and *H. stictocephalus*, and *H. longirostris* and *pectoralis*; as well as *atricapillus* and *pileatus* as already discussed). At least two of these pairs consist of species that are known to occur in the same general areas with no apparent interbreeding. In addition to differences in plumage, habitat preferences and vocal differences between *atricapillus* and *motacilloides-parkeri* also exist, as mentioned above. We perceive that given the above differences, *atricapillus* should also be considered specifically distinct from *motacilloides* and *parkeri*.

Even with the separation of *atricapillus* as a distinct species, there remains the possibility of treating *motacilloides* and *parkeri* as conspecific. These two taxa are separated from each other by ca 500 km of apparently suitable habitat for both species. Although there are few localities that have been collected at the appropriate elevations between the known ranges of these two taxa, only *H. axillaris*, an unrelated taxon, has been

found at such localities (e.g., Afluente, Department of San Martín [Parker and Parker 1982]). The known range of *motacilloides* extends from the Department of Huánuco to the central portion of the Department of Cuzco, a span of about 450 km. Specimens of *motacilloides* from the nearest localities to the known locality of *parkeri* show no trends toward characteristics of the latter taxon and are essentially identical to specimens of *motacilloides* from the southernmost localities. A single specimen of *motacilloides* from the Cordillera Vilcabamba, Department of Cuzco, does show less of a yellowish wash below than any of the other specimens of *motacilloides* we have examined, but it is otherwise identical to the rest of the series. Therefore, until additional information is available from geographically intermediate populations (if there are any), it seems best to consider *motacilloides* and *parkeri* as separate species. The resulting classification, recognizing *H. pileatus*, *H. atricapillus*, *H. motacilloides*, and *H. parkeri*, is consistent with respect to the species limits within the rest of the genus (Fig. 4). Although these four species are obviously closely related, we hesitate to classify them formally in a single superspecies until the ranges of *H. pileatus* and *H. atricapillus* are better known. The type of distribution that these four species show may be the result of withdrawal of a widespread ancestral form into isolated pockets of suitable habitat during the climatic changes of the Plio-Pleistocene, whereupon several disjunct populations differentiated from the others. Such a model has been hypothesized by Haffer (1974) for numerous taxa in lowland South America and has received support from studies of several groups of birds, especially tyrannids (Short 1975; Fitzpatrick 1976, 1980; Fitzpatrick and O'Neill 1979).

ACKNOWLEDGMENTS

We are extremely grateful to M. Sánchez S., M. Chávez de Sánchez, and A. Urbay T. whose hard work helped make our stays in the field successful. M. and I. Plenge, A. and H. Koenig, and G. del Solar provided valuable assistance in Peru. We appreciate the helpful comments on various drafts of this manuscript by J. W. Fitzpatrick, K. C. Parkes, J. V. Remsen, Jr., and T. S. Schulenberg. Schulenberg also kindly examined and measured specimens unavailable to the authors. T. A. Parker III assisted with descriptions of vocalizations and provided the authors access to tape recordings at the Library of Natural Sounds at Cornell University; to this Library we also extend our thanks. We especially thank C. B. Barr (Dept. Entomology, Louisiana Agricultural Experiment Station, Louisiana State Univ. Agricultural Center) for identifying the stomach contents of the new species. We thank M. M. Swan for preparing Figures 3 and 4. We are grateful to the following people for loan of, or permission to examine, comparative material: L. L. Short and M. LeCroy (AMNH); F. B. Gill and M. B. Robbins (ANSP); D. Snow (BM); and J. W. Fitzpatrick and D. Willard (FMNH). We thank the staff of the Dirección General Forestal y de Fauna of the Ministerio de Agricultura, Lima, Peru, for their help and for issuing the necessary permits. We continue to be grateful for the generous financial support of LSUMZ field studies given by J. S. McIlhenny, H. I. and L. R. Schweppe, and the late B. M. Odom.

LITERATURE CITED

- DAVIS, T. J. 1986. Distribution and natural history of some birds from the departments of San Martín and Amazonas, Northern Peru. *Condor* 88:50-56.
- FITZPATRICK, J. W. 1976. Systematics and biogeography of the Tyrannid genus *Todirostrum* and related genera (Aves). *Bull. Mus. Comp. Zool.* 147:435-463.
- . 1980. Some aspects of speciation in South American Flycatchers. *Acta XVII Congressus Internationalis Ornithologici*, Band II:1273-1279.
- AND J. P. O'NEILL. 1979. A new species of tody-tyrant from northern Peru. *Auk* 96:443-447.
- HAFFER, J. 1974. Avian speciation in tropical South America. *Publ. Nuttall Ornithol. Club* 14.
- MAYR, E. 1963. *Animal species and evolution*. Harvard Univ. Press, Cambridge, Massachusetts.
- MEYER DE SCHAUENSEE, R. 1966. *The species of birds of South America and their distribution*. Livingston, Narberth, Pennsylvania.
- . 1970. *A guide to the birds of South America*. Livingston, Wynnewood, Pennsylvania.
- NAUMBERG, E. M. B. 1935. Gazetteer and maps showing stations visited by Emil Kaempfer in eastern Brazil and Paraguay. *Bull. Am. Mus. Nat. Hist.* 68:449-470.
- . 1939. Studies of birds from eastern Brazil and Paraguay, based on a collection made by Emil Kaempfer. *Bull. Am. Mus. Nat. Hist.* 76:231-276.
- PARKER, T. A., III AND PARKER, S. A. 1982. Behavioral and distributional notes on some unusual birds of a lower montane cloud forest in Peru. *Bull. Brit. Ornithol. Club* 102:63-70.
- PETERS, J. L. 1951. *Checklist of birds of the world*, Vol. VII. Harvard Univ. Press, Cambridge, Massachusetts.
- REMSEN, J. V., JR. Aves de una localidad en la sabana húmeda del norte de Bolivia. *Ecología en Bolivia*. In press.
- SHORT, L. 1975. A zoogeographic analysis of the South American chaco avifauna. *Bull. Am. Mus. Nat. Hist.* 154:163-352.
- SMITHE, F. B. 1975. *Naturalist's color guide*. Am. Mus. Nat. Hist., New York, New York.
- ZIMMER, J. T. 1932. Studies of Peruvian Birds. V. The genera *Herpsilochmus*, *Microrhopias*, *Formicivora*, *Hypocnemis*, *Hypocnemoides*, and *Myrmochanes*. *Am. Mus. Nat. Hist. Novit.* 538.

COLOR PLATE

The Frontispiece painting has been made possible by an endowment established by George Miksch Sutton. The painting is by J. P. O'Neill.