

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3270, 22 pp., 9 figures, 5 tables August 10, 1999

Speciation in African Forest Robins (*Stiphornis*): Species Limits, Phylogenetic Relationships, and Molecular Biogeography

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ABSTRACT

The monotypic genus *Stiphornis* (Aves: Turdidae) is revised under a phylogenetic species concept to include four species, one of which, from the southwest Central African Republic, is new. Mitochondrial DNA sequence data are analyzed to explore the phylogenetic relationships within *Stiphornis*. These data indicate relatively high levels of sequence divergence among the species and corroborate their recognition as diagnosable taxa, a conclusion also supported by morphological evidence. These findings, along with the allopatric distributions of the species, compel attention to their phylogenetic and spatial history, which was not explored when this group was ascribed to a single "biological" species.

Data reviewed here also suggest that the northwest Congo Basin forest, where the new species was discovered, is more zoogeographically complex than has been previously suspected. In addition, application of a phylogenetic species concept emphasizes the narrow endemism of *S. gabonensis* and *S. sanghensis*, along with its implications for conserving their threatened habitats.

The findings of this paper also reinforce the notion that patterns of geographic variation in the lowland forests of West and Central Africa are still incompletely understood and that the impact of environmental and geological history on the diversification of the forest avifauna has not yet been fully explored.

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INTRODUCTION

During an expedition in 1996 to southwestern Central African Republic (CAR) to collect materials for the Hall of Biodiversity in the American Museum of Natural History, specimens of the African Forest Robin (“*Stiphronis xanthogaster*”) were obtained. Upon studying the material, it became apparent that specimens from the Dzanga-Sangha Dense Forest Reserve represented an undescribed population. An examination of species limits within the genus was undertaken based on comparisons of museum collections in North America and Europe, and taxic interrelationships were investigated by cladistic analysis of mitochondrial DNA (mtDNA) sequence variation. Additional specimens were obtained from the Reserve in June 1998.

Biological collections from the center of the Guineo-Congolian forest block (sensu White, 1983)—from southwestern CAR south to northern Congo Republic, and across northwestern Democratic Republic of Congo (DRC; formerly Zaire)—are underrepresented in museums, and elements of the forest avifauna have not been subject to intensive systematic analysis. Although workers have proposed that CAR encompasses a zoogeographic transitional area for other vertebrates (Fay, 1988; Joger, 1990), little is known about the patterns of variation in birds within the Congo Basin forest (see also Louette, 1992). For example, there is insufficient data at present to clarify the limits of geographic variation across the region of eastern Cameroon and eastern DRC.

Based on patterns of species richness and distribution, Diamond and Hamilton (1980) described areas of endemism for lowland African passerine birds that were later corroborated for both passerine and nonpasserine birds by Crowe and Crowe (1982). These descriptions, however, relied on maps in the British Museum atlases of distributions (Hall and Moreau, 1970; Snow, 1978), which reflect a geographic bias because Hall and Moreau (1970) consulted only British and southern African museum collections. Thus, species that Diamond and Hamilton (1980) characterized as disjunct across the Congo Basin are now known to occur within it, either be-

cause specimens were represented in other museums (see Louette, 1984) or have been shown to have more extensive ranges due to further collecting and fieldwork (data in Green and Carroll, 1991; Keith et al., 1992; Dowsett and Dowsett-Lemaire, 1997). As a consequence, patterns of species richness and endemism cannot be considered to be well known, especially for taxa in the Congo Basin forest region.

At this time, no hypotheses of historical interrelationships among the areas of endemism have been proposed based on phylogenetic analyses; instead, biogeographic investigations have largely focused on intermontane areas and their relationships or on montane-lowland affinities (e.g., Bruhl, 1997; Fjeldså and Lovett, 1997; Roy, 1997).

While it is to be expected that the expansion of a collections-based data set and increased fieldwork will clarify distributional information, broadly inclusive “biological” species concepts have also led to an under-resolution of patterns of geographic variation. This is true for the *Stiphronis* group in which some treatments identify patterns of variation in terms of a single taxonomic entity (e.g., Map 145 in Hall and Moreau, 1970), thus effectively obscuring the evolutionary diversity within the genus, and obviating the need to search for patterns of endemism and clarify historical area-relationships when they do, in fact, exist.

ACKNOWLEDGMENTS

We are grateful to R.W. Dickerman (University of New Mexico; AMNH) who collected specimens and offered his advice and insight during the study. We would like to thank the following individuals for access to the collections at their museums or for loans of material: C. Erard and E. Pasquet, Muséum National d’Histoire Naturelle de Paris; M. Louette, Musée Royale de l’Afrique Centrale; R. Prys-Jones, Natural History Museum (London), Department of Ornithology (Tring); J. Bates and D. Willard, Field Museum of Natural History (Chicago); David Allan, Durban Natural Science Museum; and K. Garrett, Natural History Museum of Los Angeles County. R. Dekker, Nationaal Natuurhistorisch Museum (Leiden) provided in-

formation about *Stiphornis* in that museum's collection. M. LeCroy (AMNH), R. Prys-Jones, and E. Warr (Natural History Museum) provided assistance with literature. In the CAR and in New York, the AMNH Exhibition Department provided support. The Ministère des Eaux, Forêts, Chasses, Pêches et du Tourisme gave us permission to collect in the CAR. Richard Carroll, Allard Blom, Tony Mokombo, and Bernard Difara of the World Wildlife Fund U.S. and Urbain Ngatoua, National Director of the Dzanga-Sangha Conservation Project, greatly facilitated our work in the CAR as did many local residents of Bayanga. D. Lunde, P. Sweet, and A. Porzecanski (AMNH) provided invaluable assistance in the field. J. Feinstein and J. Groth (AMNH) provided primers and advice on the molecular analysis. We would like to thank Dennis Finnin for photography. The manuscript benefitted from discussions with G. Barrowclough, S. Keith, and the comments of two anonymous reviewers. The 1996 expedition to the CAR was financed by the AMNH Biodiversity Hall project and by a grant from the National Science Foundation (ESI-9453023). The June 1998 expedition was sponsored by a grant from the Center for Biodiversity and Conservation at the AMNH, and we are grateful to Dr. Francesca Grifo, Director of the Center, for her advice and support. Molecular work was funded in part by grants from the City College (City University of New York) Dissertation Grant Program, and the Frank M. Chapman Memorial Fund (to PB). This work was also supported in part by the Leonard J. Sanford Fund in the Department of Ornithology. The molecular research reported in this paper is a contribution from the Lewis B. and Dorothy Cullman Research Facility at the American Museum of Natural History and has received generous support from the Lewis B. and Dorothy Cullman Program for Molecular Systematics Studies, a joint initiative of the New York Botanical Garden and the American Museum of Natural History.

MATERIALS AND METHODS

Museum study skins were examined for evidence of variation and diagnosability in features of external morphology. Mitochon-

drial DNA (mtDNA) sequence data for the entire cytochrome-*b* gene (1143 base pairs) were obtained for 13 *Stiphornis* individuals plus two individuals from an outgroup taxon, *Sheppardia cyornithopsis*. Vocalizations were analyzed with Canary 1.2 (Charif et al., 1995).

MATERIALS EXAMINED

We examined 290 specimens from collections at the AMNH, the Field Museum of Natural History (FMNH), the Natural History Museum of Los Angeles County (LACM), the Natural History Museum (BMNH), the Muséum National d'Histoire Naturelle de Paris (MNHN), the Musée Royale de l'Afrique Centrale (MRAC), and the Durban Museum. Specimens examined from each of the four taxa included (δ = male, ♀ = female, ? = sex undetermined): *S. erythrorhox* (AMNH 12 δ , 8 ♀ ; MRAC 8 δ , 2 ♀ , 2?; MNHN 1 ♀ ; BMNH 3 δ 3 ♀ 1?), *S. gabonensis* (AMNH 16 δ , 10 ♀ ; DM 3 δ , 2 ♀ ; MRAC 1 δ , 1 ♀ , 2?; MNHN 4 δ , 5 ♀ , 3?; BMNH 8 δ , 6 ♀ , 6?), *S. xanthogaster* (AMNH 37 δ , 21 ♀ , 4?; DM 5 δ , 2 ♀ ; LACM 8 δ , 4 ♀ ; FMNH 10 δ , 4 ♀ ; MRAC 38 δ , 12 ♀ , 5?; MNHN 3 δ , 2 ♀ , 1?; BMNH 19 δ , 8 ♀), and *S. sanghensis* (AMNH 5 δ , 10 ♀ , 8?). These specimens represented 99 localities across the range of *Stiphornis* in the forests of Africa, including Liberia, Sierra Leone, Ghana, Nigeria, Cameroon, Gabon, Equatorial Guinea, the Republic of Congo, the Congo Democratic Republic, Sudan, Uganda, and Kenya; localities with unambiguous coordinates are presented in the appendix.

MOLECULAR METHODS

Collecting locales and other information pertaining to the 15 individuals sampled for the molecular analysis are presented in table 1. Genomic DNA was extracted from small pieces of tissue by boiling in 5% (w/v) Chelex (Bio-Rad, Hercules, CA) solution. Target regions (see table 2 for primers) of the cytochrome *b* gene were first obtained with 10 μL PCR reactions (1 μL DNA, 1 μL each of 10 μM L/H primers, 1 μL of 2mM dNTPs, 0.15 μL *Taq* polymerase [Promega, Madison, WI] and 2 μL buffer), placed in an Idaho Technologies air thermocycler at the fol-

TABLE 1
Information on Specimens Used in Molecular Analysis

Name	Museum	Locality	Genbank accession no.
<i>Stiphornis erythrothorax</i> 1	AMNH 827588	near Ziggida, Lofa County, Liberia	AF136724
<i>S. erythrothorax</i> 2	AMNH 827589	near Ziggida, Lofa County, Liberia	AF136725
<i>S. gabonensis</i> 1	MNHN 1998-786	Nditam, Cameroon (5°21'N, 11°14'E)	AF136726
<i>S. gabonensis</i> 2	MNHN EP1-50	Nditam, Cameroon	AF136727
<i>S. gabonensis</i> 3	MNHN EP1-64	Nditam, Cameroon	AF136728
<i>S. sanghensis</i> 1	AMNH 831845	Dzanga-Sangha Reserve, CAR	AF136729
<i>S. sanghensis</i> 2	AMNH 831847	Dzanga-Sangha Reserve, CAR	AF136730
<i>S. sanghensis</i> 3	AMNH 10836	Dzanga-Sangha Reserve, CAR	AF136731
<i>S. sanghensis</i> 4	AMNH 24731	Dzanga-Sangha Reserve, CAR	AF136732
<i>S. sanghensis</i> 5	AMNH 831846	Dzanga-Sangha Reserve, CAR	AF136733
<i>S. xanthogaster</i> 1	FMNH 357243	Ituri Forest, DRC	AF136734
<i>S. xanthogaster</i> 2	FMNH 357245	Ituri Forest, DRC	AF136735
<i>S. xanthogaster</i> 3	FMNH 357244	Ituri Forest, DRC	AF136736
<i>Sheppardia cyornithopsis</i> 1	AMNH 827632	near Ziggida, Lofa County, Liberia	AF136722
<i>S. cyornithopsis</i> 2	AMNH 827650	near Ziggida, Lofa County, Liberia	AF136723

lowing reaction conditions: denaturation at 94°C for 5 min, annealing at 50°C for 2 min, and extension at 71°C for 20 sec, all for 40 cycles. 5 µL of these PCR products were run out in 2% low-melting-point agarose gels, visualized with ethidium bromide and ultraviolet light, and the relevant sized bands excised, diluted in 190µL H₂O and melted at 72°C for 25 min. 40 µL PCR reactions were prepared with 1.5 µL of the gel-purified products, 2 µL each of the 10 µM L/H primers, 4 µL 2mM dNTPs, 8 µL buffer and 0.2 µL *Taq* polymerase and cycled in the air thermocycler under the following conditions: denaturation at 94°C for 8 min, annealing at 55°C for 8 min, and extension at 70°C for 22 sec. These products were purified with the

Gene Clean II system (BIO 101, Inc., San Diego, CA) resulting in a final suspension of DNA in 18 µL H₂O. 2.5 µL of this purified DNA was prepared for asymmetric cycle sequencing with 1.5 µL 10mM primer and 3 µL of dRhod Terminator RR Mix (Perkin Elmer) and cycled in a Perkin Elmer 9600 at the following reaction conditions: initial denaturation at 96°C for 1 min, followed by 32 cycles of denaturation at 96°C for 10 sec, annealing at 50°C for 5 sec, and extension at 60°C for 3 min. These products were filtered through sephadex columns (Princeton Separations), dried for 30 min in a Speed-Vac (Savant, Hicksville, NY), and suspended in a Blue Dextran-150 mM EDTA:formamide loading buffer. Samples were run out on 5%

TABLE 2
Primer Information

Primer numbers follow those of the *Gallus* sequence (Desjardins and Morais, 1990). Primers are arranged according to their paired use in initial amplifications; L and H refer to light and heavy strands, respectively.

L14578 (ND5)	5-ctaggaatcatcctagccctaga-3
H15104	5-tgtgtcagccatattggacgtctcggc-3
L15068	5-actagcaatacactacacagcaga-3
H15505	5-tgcatgaattcctattgggttgtttgatcc-3
L15236	5-ttcctatacaagaaacctgaaa-3
H15710	5-atagcgtaggcgaataggaagtatc-3
L15656	5-ccagacctcctaggagaccaga-3
H16065	5-aacgcagtcctctccggtttacaagac-3

Long Ranger (FMC, Philadelphia, PA) gels in TBE buffer in an Applied Biosystems, Inc. (Foster City, CA) 377 automated sequencer. Sequences have been deposited in GENBANK with accession numbers AF136722-AF136736.

SYSTEMATIC METHODS

Sequences were assembled and aligned with Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, MI) and verified by eye. Because the sequences are from coding genes, alignment was straight-forward. For phylogenetic analysis, most-parsimonious trees were obtained through a branch-and-bound search using PAUP* (Swofford, 1998). Sequences from two individuals of *Sheppardia cyornithopsis* were used to root trees. Sequence divergence measures were estimated for all pairwise comparisons both as uncorrected (p) distances and under the HKY85 model as implemented in PAUP*, with base frequencies and transition/transversion substitution rates based on observed values.

SYSTEMATICS OF *STIPHRORNIS*

Although there are no phylogenetic hypotheses at present about the relationships of *Stiphrornis* to other Turdidae, taxonomists have broadly concurred in placing *Stiphrornis* in a group of "African Robins" (White, 1962) or "African forest-dwelling robins" (Irwin and Clancey, 1974) along with *Sheppardia*, *Pogonocichla*, *Swynnertonia*, *Cossypha*, and *Alethe*; the exact membership of this assemblage varies, and some authors assign certain genera to the chats within the Muscicapidae (e.g., Jensen, 1989; Sibley and Monroe, 1990).

Sharpe (1903) recognized *Stiphrornis* as a polytypic taxon, but within a few decades W. L. Sclater's *Systema Avium Aethiopicarum* (1930) ranked all *Stiphrornis* species as subspecies within a single species. Although the compilers of "Peters' Checklist" (Mayr and Paynter, 1964) placed *Stiphrornis* within *Erithacus*, most ornithologists continued to maintain *Stiphrornis* (White, 1962; Hall and Moreau, 1970), and Irwin and Clancey (1974: 7) explicitly objected to the expansion of *Erithacus* to include African forms "in

view of the manifest differences between the African forest-dwelling robins [and] the type of the genus *Erithacus*."

White (1962) recognized three subspecies: *Stiphrornis erythrothorax erythrothorax*, *S.e. gabonensis*, and *S.e. xanthogaster*. Whereas geographic variation in *Stiphrornis* has historically been recognized at some taxonomic level, Hall and Moreau (1970) mapped *Stiphrornis* as a monotypic taxon in their distributional atlas. In the following revision we recognize four phylogenetic species within *Stiphrornis*.

Genus *Stiphrornis* Hartlaub 1855

TYPE SPECIES: *Stiphrornis erythrothorax* Dabocrom, Ghana (Nationaal Natuurhistorisch Museum [Leiden], not accessioned).

DIAGNOSIS: The genus is characterized by a narrow, lateromedially compressed bill, short legs and tail, and a white loreal spot. Compared to other African forest turdines, *Stiphrornis* differs in the color pattern of the chin, throat, and breast, which is not distributed further down onto the sides of the belly and flanks as in other taxa, but is instead markedly demarcated between the breast and belly plumage. Within the genus, plumage and color patterns provide diagnostic characters for each species (Table 3).

INCLUDED SPECIES: *Stiphrornis erythrothorax*, *S. gabonensis*, *S. xanthogaster*, *S. sanghensis* n. sp.

DISCUSSION: In the original description of the genus, Hartlaub's (1855) discussion of the type species *S. erythrothorax* was followed by one for "*S. superciliaris*," a form that had been named *Sylvia prasina* and has been recognized as *Hylia prasina* (Sylviidae) since 1859 (Sharpe, 1883). In 1874, Reichenow described "*Stiphrornis alboterminata*," a taxon already described as a nectariniid, *Nectarinia gabonica*, and since 1930 has been named *Anthreptes gabonicus* (Chapin, 1954).

Stiphrornis erythrothorax Hartlaub, 1855

Figure 1

HOLOTYPE: Male from Dabocrom, Ghana; type in Nationaal Natuurhistorisch Museum (Leiden), not accessioned.

DIAGNOSIS: The only species of the genus



with an olive-green wash on all upper surfaces. *S. erythrothorax* shares with *S. gabonensis* a russet throat and chin, and white feathers on the belly.

DISCUSSION: *Stiphornis erythrothorax* ranges from Sierra Leone to the Niger Delta (e.g., Degema, Nigeria: AMNH 599790; see fig. 4), primarily in lowland forest but also in riverine and savanna habitats within the Upper Guinea region (Keith et al., 1992).

Stiphornis gabonensis Sharpe, 1883

Figure 1

HOLOTYPE: An adult (indeterminate sex) collected in "Gaboon," BMNH 1876.5.23.206.

DIAGNOSIS: Chin and throat russet and belly white, like *S. erythrothorax*, but differs in having dorsal plumage dark or slaty gray with a faint olive wash, not as green as in *S. erythrothorax*.

DISCUSSION: *S. gabonensis* is limited to evergreen coastal forest, ranging from just east of the Niger River delta (records from Kumba and Mamfe, Nigeria) south to Gabon (and possibly limited by the Ogooué River; e.g., Kango, Gabon: AMNH 345033) east to Malen, Cameroon (e.g., AMNH 800617). This species is also found on the island of Bioko, Equatorial Guinea.

Sharpe (1883) named this species upon comparing specimens of *Stiphornis* while compiling volume 7 of the British Museum Catalogue. The new taxon was described as "very similar" to *S. erythrothorax* but distinguished by the dorsal plumage being "dark slaty grey with a faint olive tinge."

Stiphornis xanthogaster Sharpe, 1903

Figure 1

HOLOTYPE: Adult (indeterminate sex) from the River "Ja" (Dja), Cameroon, BMNH 1903.7.16.100. An immature syntype (indeterminate sex) is also in the collection.

DIAGNOSIS: Differs from other *Stiphornis* in having chin and throat tawny and abdominal feathers pale cream. The dorsal plumage is gray-brown lightly washed olive, not as dark gray as in *gabonensis* and not green as in *erythrothorax*.

DISCUSSION: *S. xanthogaster* is the most widespread member of the genus, ranging from the River Dja in Cameroon (e.g., AMNH 599798) south through northeastern Gabon (e.g., MNHN 517, Bélinga) to Lukolela, DRC (e.g., AMNH 2696983) east through northeastern CAR (e.g., LACM 84941), Sudan, the Ituri forest, and Uganda to western Kenya (e.g., Kipkabus, AMNH 788638) (fig. 4). Although mainly restricted to lowland primary forest, in eastern DRC *S. xanthogaster* occurs in transitional forest up to 1400 m (Keith et al., 1992).

S. mabirae was described by Jackson (1910) based on specimens collected in the Mabira Forest, Uganda, and diagnosed by the chin being as dark as the rest of the throat region and by the upperparts being "more olive." Chapin (1953) did not find it "easy to distinguish specimens of *xanthogaster* . . . from those of *mabirae*" and White (1962) subsumed *mabirae* into *xanthogaster*. The distribution of the relative intensity of chin and throat pigmentation and the saturation of the dorsal olive wash varies among individuals, not geographically, thus precluding the use of these characters to delineate *mabirae*

←

Fig. 1. Ventral and dorsal views of *Stiphornis* taxa. Left to right, top: *S. erythrothorax*, AMNH 825486 (Liberia) and AMNH 827586 (Liberia); *S. gabonensis*, AMNH 297701 (Bioko, Equatorial Guinea) and AMNH 800617 (Cameroon); bottom: *S. xanthogaster*, AMNH 161024 (DRC) and AMNH 164023 (DRC); *S. sanghensis*, AMNH 832117 (CAR) and AMNH 832121 (CAR). Photograph by D. Finnin.

Fig. 2. Adult male *Stiphornis sanghensis*, photographed in in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998. Photograph by J. Cracraft.

Fig. 3. Juvenile male *Stiphornis sanghensis*, photographed in in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998. Photograph by J. Cracraft.

as a distinct taxon. Specimens of *S. xanthogaster* from the Kivu region in DRC at Musée Royale de l'Afrique Centrale and the Durban Museum have a more pale yellow wash to the belly feathers than do specimens from other parts of the range.

Stiphornis sanghensis, new species

Figures 1–3

HOLOTYPE: Adult male, AMNH 832121, collected in the Dzanga-Sangha Dense Forest Reserve (2°55'N, 16°15'E, ca. 1 km north of Bayanga, Sangha-Mbaèrè Prefecture), Central African Republic, on 13 June 1998, by P. Beresford.

PARATYPES: AMNH 832123, adult female, 6 June 1998; AMNH 832126, adult female, 13 June 1998; AMNH 832120, adult male, 14 June 1998; AMNH 832124, adult female, 17 June 1998; AMNH 832128, juvenile (indeterminate sex), 19 June 1998; AMNH 832127, immature female, 2 July 1998. The following were collected on the west bank of the Sangha River, across from the previous locality: AMNH 832125, adult female, 24 June 1998; AMNH 832116, adult female, 24 June 1998; AMNH 832117, adult (indeterminate sex), 24 June 1998; AMNH 832122, adult female, 24 June 1998; AMNH 832118, adult male, 24 June 1998; and AMNH 832119, adult female, 25 June 1998 (prepared as flat skin and partial skeleton). The following were collected at the confluence of the Babongo and Sangha Rivers (2°59'N, 16°14'E, ca. 8 km north of Bayanga): AMNH 831845, adult (indeterminate sex), 16 November 1996; AMNH 831846, sub-adult (with ossified skull, indeterminate sex), 17 November 1996; AMNH 831847, adult male, 24 November 1996; AMNH 831848, adult (indeterminate sex), 3 December 1996. Skeletons: AMNH 24732, sex undetermined; AMNH 24731, male; AMNH 24871, female; AMNH 24869, male; AMNH 24870, adult female (prepared as flat skin and partial skeleton). Fluid preserved: AMNH 10836, AMNH 10863.

DIAGNOSIS: Distinguished from its congeners by a deep orange-yellow chin, throat, and upper breast, and a yellow wash to the belly feathers.

DESCRIPTION OF HOLOTYPE: Crown and

forehead dark slate, lightly tinged olive; nape and upper back basally gray, feathers tipped dark olive green; lower back and upper tail coverts basally gray, tipped with lighter olive green; white loreal spot, black malar feathers, auriculars dark blue-gray; chin, throat, and breast bright orange-yellow, appearing iridescent at certain angles; feathers at sides of breast edged dark gray; upper and lower belly feathers basally dark gray becoming cream and tipped yellow; feathers of flanks and sides more gray; remiges brown with leading edge washed olive; rump, upper tail coverts, and rectrices gray-brown with yellow-green wash on dorsal surface. See Table 4 for measurements of the type series.

DESCRIPTION OF PARATYPES: Two immature individuals were collected. On the younger bird (AMNH 832128), the chin, throat, upper breast, crown, and dorsal feathers all bear subterminal dull orange spots, with the belly feathers basally gray and tipped white, producing a mottled effect. The primaries are gray-brown edged olive. The immature tail feathers are pure russet, and a set of emerging rectrices are gray-brown. The other immature bird, a male (AMNH 832127, fig. 3), bears a plumage intermediate between the younger and adult plumages: only the upper breast and a few dorsal feathers bear the dull orange subterminal spot, while both the chin and most of the belly (except for a thin, central line of mottled gray and white feathers) are lemon yellow. The primaries are gray-brown edged olive, and the rectrices are gray brown with an olive wash on the dorsal surfaces. A subadult paratype (AMNH 831846), which is molting to adult plumage, shows more extensive basal gray on the (paler) belly and flank feathers and bears rufous-edged primaries. An adult male not in breeding condition (AMNH 832120) has the crown and nape not as dark, with feathers tipped paler olive green.

ETYMOLOGY: The name refers to the type locality, the Dzanga-Sangha Dense Forest Reserve in the Sangha-Mbaèrè Prefecture of the Central African Republic. The reserve lies at the northern edge of the Guineo-Congolian forest block of White (1983) and is dominated by mixed semi-deciduous evergreen rainforest (see Green and Carroll, 1991). We propose the English name "San-

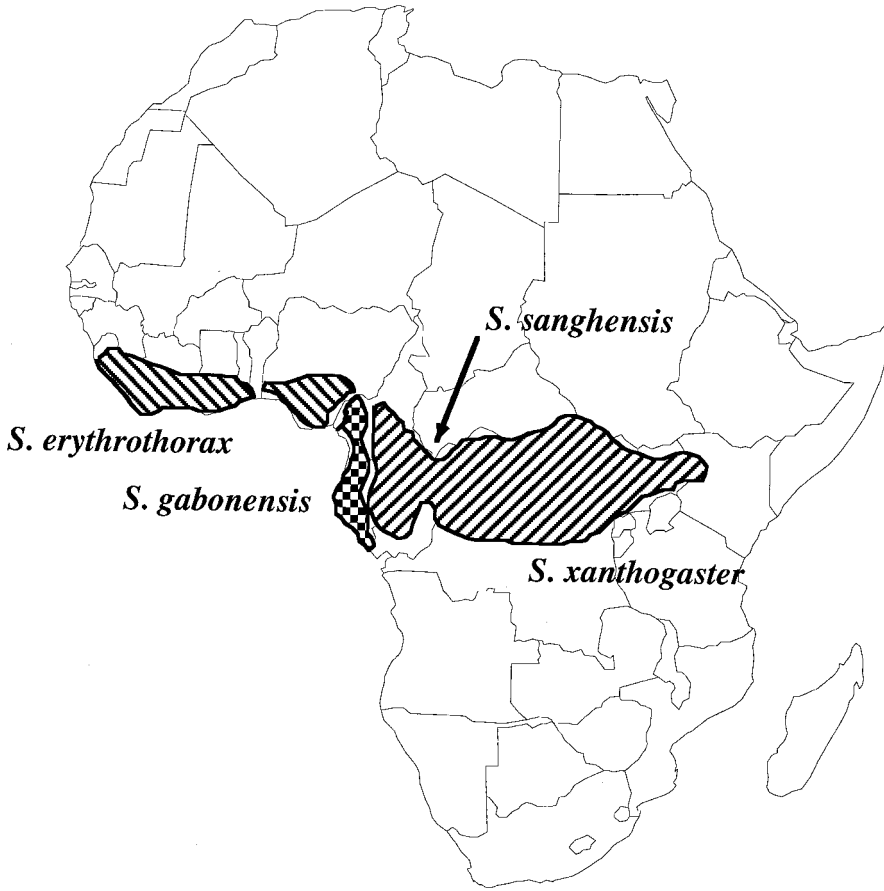


Fig. 4. Distributions of species of *Stiphornis* (after Keith et al. (1992) and material examined in this study). Range limits of taxa in the western Congo Basin are poorly known at present, therefore it is uncertain whether parapatry exists between *S. gabonensis* and *S. erythrothorax*.

gha Forest Robin” in reference to the type locality.

DISCUSSION: To date, *S. sanghensis* is known only from the Dzanga-Sangha Dense Forest Reserve, where it was commonly observed and captured in the lower strata of primary forest, old second-growth forest, and moderately inundated forest along both sides of the Sangha River. Future collecting of *Stiphornis* from eastern Cameroon, northern Congo Republic, and northwestern DRC should clarify the range limits of *S. sanghensis*, *S. xanthogaster*, and *S. gabonensis*.

Birds collected in June 1998 were in breeding condition. Two females had yolking eggs low in their oviducts, another an enlarged oviduct. Three males had large testes,

measuring between 7×5 mm and 10×5 mm, compared to testes sizes of 1.5×2 mm in the nonbreeding male collected in November 1996.

Vocalizations were heard throughout the day during June and July 1998. Two types of calls were heard (fig. 5) and verified by playback; both calls were recorded in the field in 1998 on three days from at least two individuals. “Type A” begins with a few high chirps and continues with a series of modulated notes; several of these phrases may be given consecutively for several minutes in an unbroken stream. The Type A call was also heard as single or paired phrases, especially when answered by another Type A call from a different individual. The “Type B” call is

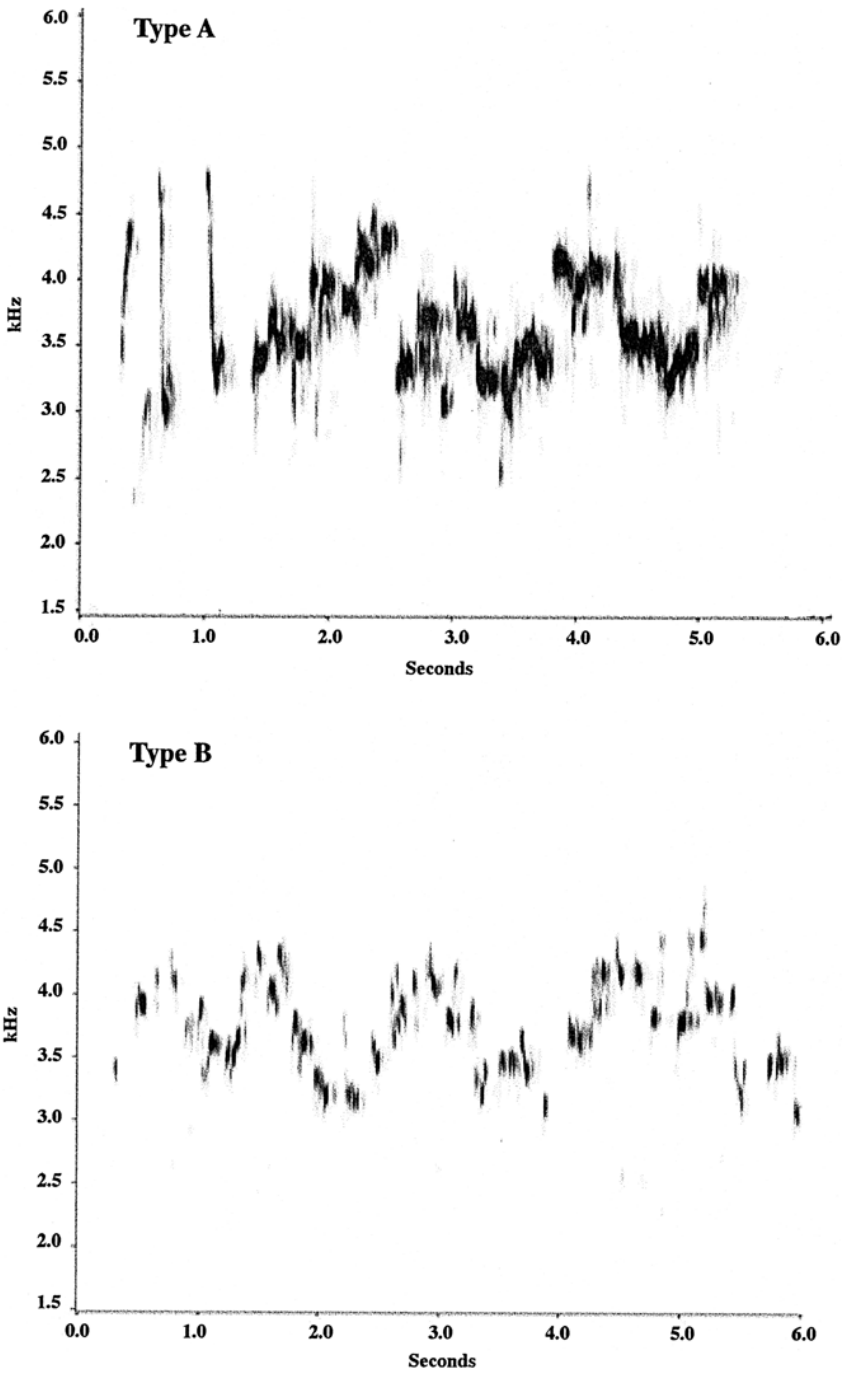


Fig. 5. Spectrogram of two types of *Stiphornis sanghensis* calls, recorded in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998.

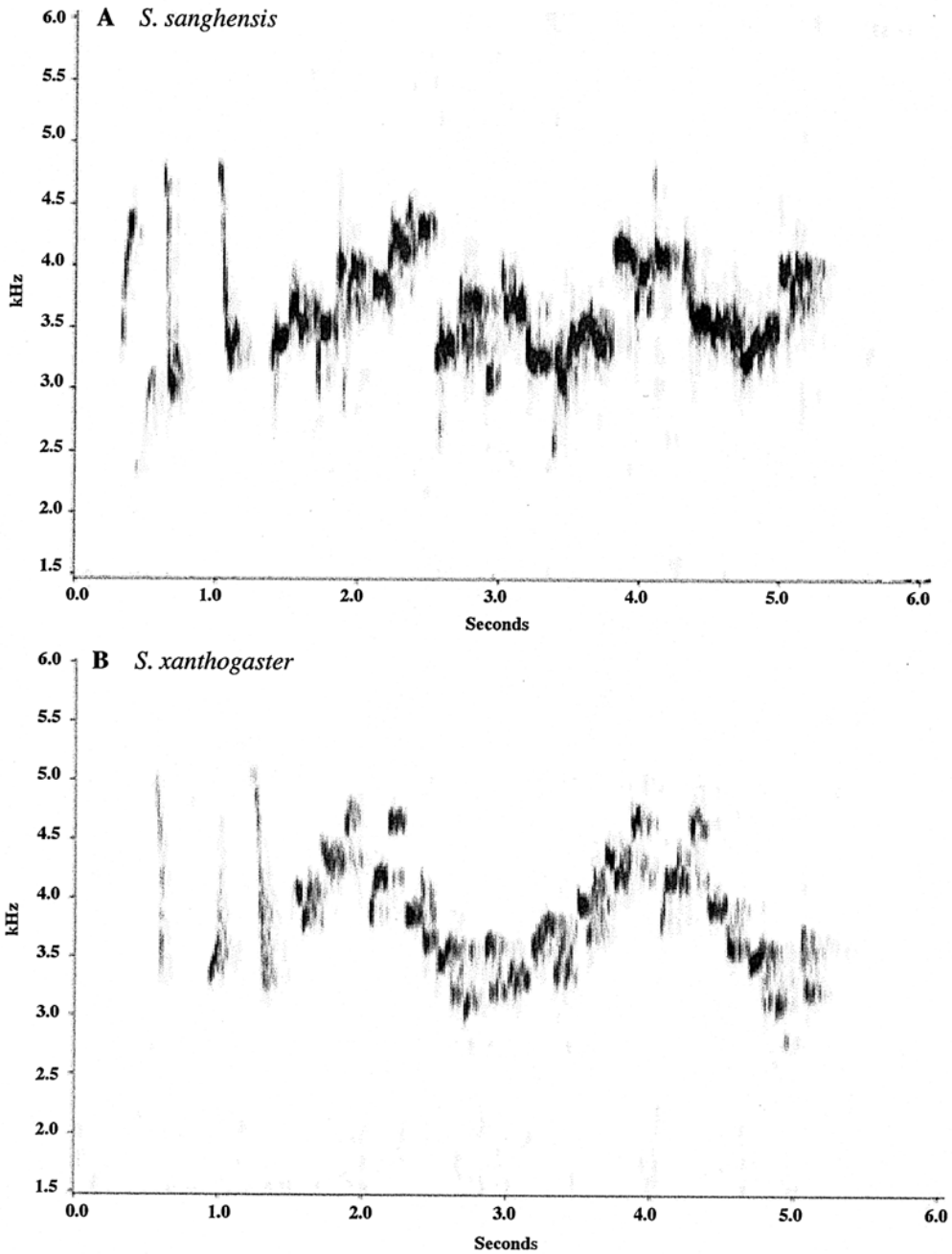


Fig. 6. Spectrograms of two Type A *Stiphornis* calls. (A) *S. sanghensis*, recorded in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998; (B) *S. xanthogaster*, recorded near Mt. Hoyo, DRC, Cornell Library of Natural Sounds Catalogue Number LNS01456.

best described as a rolling trill, with no clear demarcation of units or phrases, and was also given for continuous bouts of up to several minutes' duration. The duetting behavior described by Brosset and Erard (1986) was not heard in CAR.

One Type A call from *S. xanthogaster* (Mt. Hoyo, 1°20'N, 29°46'E; Cornell Library of Natural Sounds catalogue number LNS01456) was compared to that of *S. sanghensis* (fig. 6). The three opening notes are structurally different, and the remaining parts of the phrases are modulated differently between the two individuals. Three Type B calls are compared in figure 7, although the homology of these calls has not been established. The spectrogram of the call from the individual from eastern DRC (Lolwa, 1°23'N, 29°30'E; Cornell Library of Natural Sounds catalog number LNS01091) represents a phrase that is repeated continuously; by contrast, the call of *S. sanghensis* seems to have no distinct phrase markings. Similarly, the call from the individual from Uganda (Keith and Gunn, 1971) has distinct phrases, of which two are shown in the spectrogram. The calls of the two *S. xanthogaster* individuals are as different from each other as each of them are from *S. sanghensis*. Until more well-documented vocalizations are studied, it is impossible to determine which of these differences reflect variation among individuals, populations, or species. At present, it appears that more field recordings, made at various times of the year and in various behavioral contexts, will be required in order to describe the vocal repertoire of *Stiphornis* species. Although vocalizations of *S. erythrothorax* and *S. gabonensis* were not analyzed in this study, they are onomatopoeically described as different in Keith et al. (1992), and C. Chappuis (personal commun.) finds them to differ markedly from each other and from those of *S. xanthogaster*.

As noted by Keith et al. (1992), adult females of *S. erythrothorax* have duller throats than do adult males, and adult females of *S. gabonensis* have a slight olive wash on the dorsal feathers. Males of *S. sanghensis* show more intense pigmentation on the throat and upper breast, and the crown and face are of a deeper black than in females. No sexual dimorphism was reported for *S. xanthogaster*

by Keith et al. (1992). The dichromatism in *S. gabonensis* may explain the "greener back" (Louette, 1981: 128) of unsexed *S. gabonensis* specimens from Ngoumé, Cameroon (5°30'N, 11°26'E) as well as the apparent "intergradation" in western Cameroon mentioned by Hall and Moreau (1970: 123). Since immature specimens of *S. sanghensis* have paler chins and may thus resemble *S. xanthogaster* specimens, comparative analyses must account for differences among individuals of different age and breeding condition. Similarly, the yellow wash on the belly feathers that is one of the diagnostic features for mature *S. sanghensis* is more sulphurous than the cream to pale yellow tint on the bellies of some specimens of *S. xanthogaster*, a condition also seen on the belly of a subadult *S. sanghensis* (AMNH 831846).

RELATIONSHIPS AND BIOGEOGRAPHIC PATTERNS OF *STIPHRORNIS*

CLADISTIC ANALYSIS

Sequence analysis and comparison of complete cytochrome *b* sequences for individuals of 13 *Stiphornis* and 2 *Sheppardia* demonstrated that each represented a separate mitochondrial haplotype: thus they were all included in a cladistic analysis. Five equally parsimonious trees of 243 steps were found using 183 parsimony-informative characters, and the strict consensus of these trees is shown in figure 8. The individual haplotypes assigned to each species are seen to cluster together, each cluster having a bootstrap value of 100%. The new species, *S. sanghensis*, is postulated to be the sister species of *S. xanthogaster* and the two form one lineage within *Stiphornis*. The other species, *S. erythrothorax* and *S. gabonensis*, are themselves united and form the sister group of *S. sanghensis* and *S. xanthogaster*.

Within *Stiphornis*, 125 sites were variable (10.9%); changes at third positions comprised most of this variation (104 sites), followed by changes at first positions (18) and then 3 changes at second positions. The transition: transversion ratio was 7:1.

A phylogram in figure 9, representing one of the five equally parsimonious trees, is used to illustrate the relative branch lengths

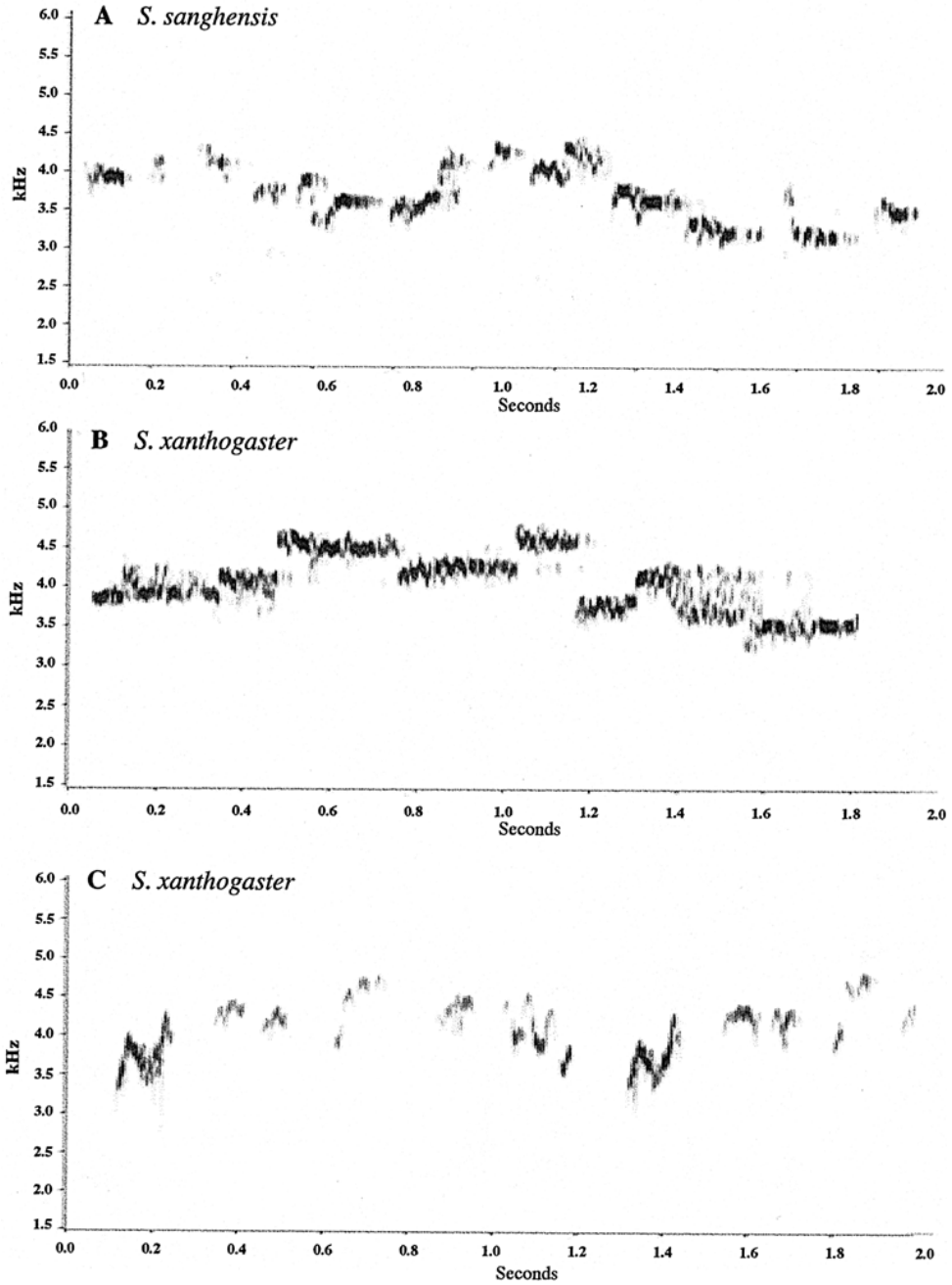


Fig. 7. Spectrograms of three Type B *Stiphornis* call phrases. (A) *S. sanghensis*, recorded in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998; (B) *S. xanthogaster*, recorded near Lolwa, DRC, Cornell Library of Natural Sounds Catalogue Number LNS01091; (C) *S. xanthogaster*, Bwamba Forest, Uganda (Keith and Gunn (1971)).

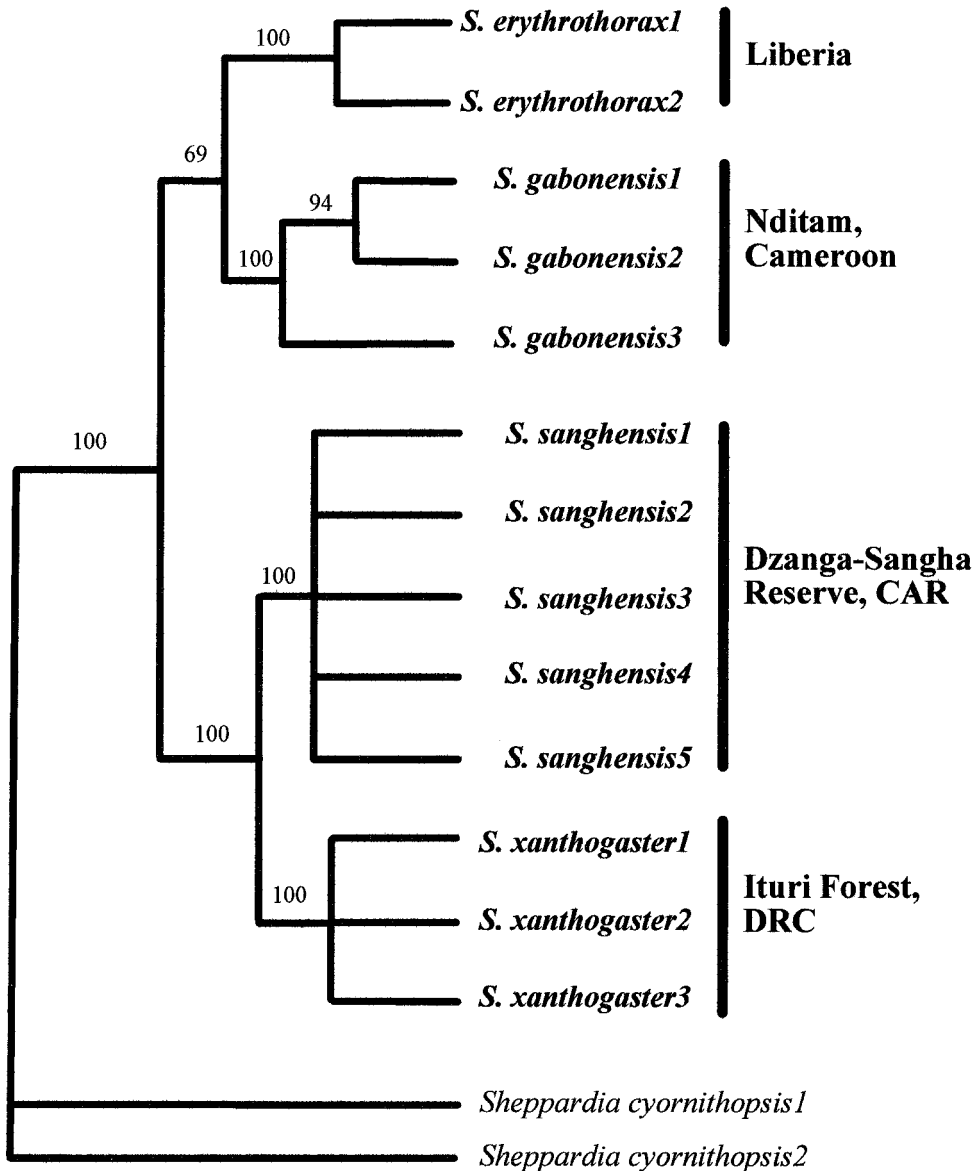


Fig. 8. Strict consensus of five most-parsimonious trees (243 steps, CI=0.868) derived from a branch-and-bound search on cytochrome-*b* sequence data for 13 *Stiphromis* haplotypes and two outgroup haplotypes. Bootstrap values based on 500 replicates.

→

Fig. 9. One of five most-parsimonious trees obtained from the analysis of figure 8 (branch-and-bound search (DELTRAN optimization), derived from parsimony analysis of cytochrome-*b* sequence data for 13 *Stiphromis* haplotypes and two outgroup haplotypes, chosen to illustrate relative branch lengths.

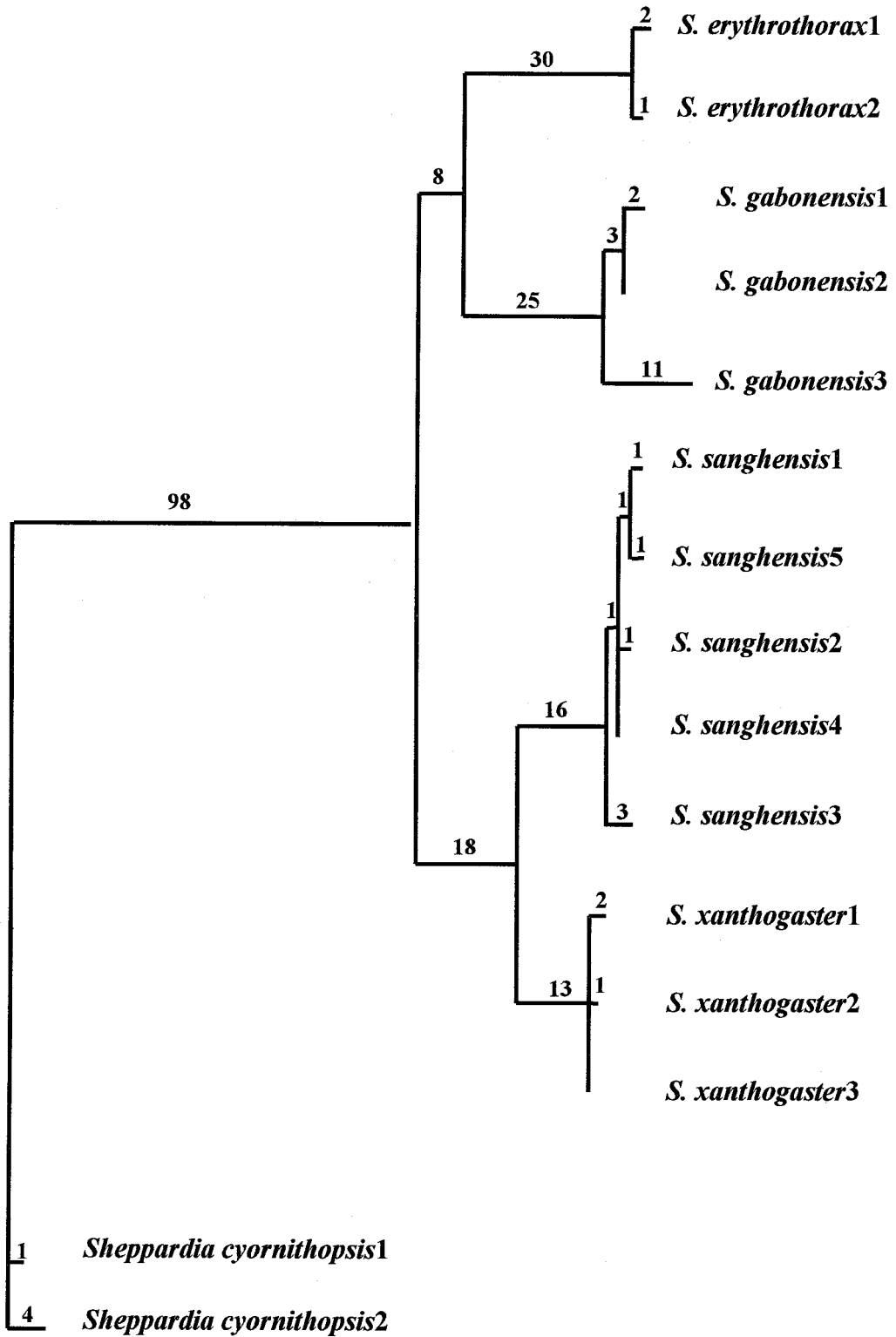


TABLE 3
Summary of Plumage Variation in *Stiphornis*

Plumage/body part	<i>sanghensis</i>	<i>xanthogaster</i>	<i>gabonensis</i>	<i>erythrothorax</i>
Forehead, forecrown, and crown	Gray to dark gray with olive wash	Gray to dark gray with olive wash	Darker gray with faint olive wash	Gray with green wash
Nape, mantle, and back	Gray with olive wash	Gray with olive wash	Slaty gray, only faintly tinged olive	Gray with green wash
Chin, throat and breast	Bright yellow-orange	Tawny; varies to pale beige at chin and throat	Russet	Russet
Upper and lower belly	Yellow	Cream	White	White
Upper wing coverts	Dark brown	Dark brown	Dark brown to slaty gray	Dark brown edged olive
Rump, upper tail coverts and dorsal surface of rectrices	Gray washed yellow-green	Gray with olive wash generally brighter than on dorsals	Gray with olive wash generally brighter than on dorsals	Gray with green wash, not distinct from dorsals
Lesser underwing coverts	Gray tipped pale yellow	Gray tipped cream	Gray tipped white	Gray tipped white
Flank and tibiotarsus	Light gray tipped yellow	Light gray tipped cream	Light gray tipped white	Light gray tipped white

TABLE 4
Measurements of *Stiphornis sanghensis* Type Series

Weight is given in grams. Measurements (in millimeters) were taken as follows: wing from carpal to tip of longest primary (chord); tail from pygostyle to tip of longest rectrix; and culmen from tip to base of skull.

AMNH	Weight	Wing	Tail	Culmen	Tarsus
831845	17.1	64	37	14.4	21.2
831846	18.1	56	32	12.9	21.6
831847	18.0	62	35	14.3	23.2
831848	18.0	67	39	15.3	22.3
832116	15.5	60	31	14.8	20.2
832117	17.0	62	36	12.6	22.6
832118	16.5	66	37	14.6	22.6
832120	17.5	65	37	13.9	19.1
832121	17.5	64	38	15.2	21.4
832122	15.0	59	32	12.9	21.4
832123	22.5	61	34	14.4	19.8
832124	16.0	59	30	13.9	21.9
832125	15.5	57	33	14.5	21.4
832126	17.0	60	36	14.1	22.9
832127	16.0	62	31	11.6	20.6
832128	15.5	53	16	14.0	20.8

among the haplotypes and the five taxa. The mean uncorrected pairwise divergence values (table 5) between *erythrothorax* and either *xanthogaster* or *sanghensis* is 5.8%, whereas *gabonensis* differs from the other two by 6.0% sequence divergence. Although rate homogeneity within cytochrome *b* has not been demonstrated for passerine birds, these values are comparable to distances seen among species in other groups (e.g., Hackett, 1996; Klicka and Zink, 1997; Avise and Walker, 1998). These data are also consistent with the hypothesis that *S. xanthogaster* and *S. sanghensis* have diverged relatively more recently from each other, with a mean pairwise divergence value of 2.8% between them, than have *S. gabonensis* and *S. erythrothorax* which exhibit 5.4% divergence between them.

Based on the distribution of plumage features among African turdines, the russet chin, throat, and breast of *S. erythrothorax* and *S. gabonensis* appears to be the primitive condition, whereas the lighter condition shown

by *S. xanthogaster* and *S. sanghensis* is probably a shared derived character. This interpretation is congruent with the phylogenetic hypothesis implied by the molecular data.

MOLECULAR BIOGEOGRAPHY

The distributional information, summarized under each species description above, delineates specific ranges for *S. erythrothorax* (referred to here as the Upper Guinea lowland forest region, limited in the east by the Cameroon highlands) and *S. gabonensis* (coastal evergreen forests of the Cameroon-Gabon region); the ranges of *S. sanghensis* and *S. xanthogaster* are less clear. Both species occur in the Congo Basin, but further research is required to describe their distributions with more precision. Current distributional information for *S. gabonensis* shows it to be more habitat-specific—restricted to the coastal evergreen forests of the Cameroon-Gabon region by drier habitats—than are the other *Stiphornis* taxa that appear to frequent several habitat types. *S. erythrothorax* appears to tolerate a wide range of forest types in the lowlands of the Upper Guinea region and ranges east to Mt. Cameroon and the highlands of the Adamawa Plateau.

The area relationships revealed by the phylogenetic results indicate that the Upper Guinea and Cameroon-Gabon regions are more closely related to each other than either is to areas in the Congo Basin. Assuming the history of *Stiphornis* mirrors that of the areas, the relative branch lengths on the phylogram (fig. 9) suggest that these areas have been isolated from each other longer than have the areas within the Congo Basin forest.

DISCUSSION

Phylogenetic relationships based on nucleotide characters among the *Stiphornis* haplotypes corroborate the recognition of four distinct phylogenetic species. The branch lengths (fig. 9) suggest that each clade has been isolated for a relatively long time (see below). Thus, the historical independence of these taxa indicated by this analysis combined with their apparently allopatric distributions may also imply some ecological distinctness as well, differences that might not

TABLE 5
Pairwise Distances
Above diagonal, uncorrected pairwise distances; below diagonal, number of bases differing in pairwise comparisons.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 <i>Sheppardia cyornithopsis</i> 1	—	0.003	0.108	0.105	0.113	0.112	0.112	0.114	0.115	0.114	0.114	0.115	0.111	0.11	0.109
2 <i>S. cyornithopsis</i> 2	4	—	0.107	0.104	0.110	0.109	0.109	0.113	0.114	0.113	0.113	0.115	0.108	0.108	0.107
3 <i>Stiphornis erythrothorax</i> 1	123	122	—	0.003	0.052	0.052	0.059	0.059	0.060	0.059	0.059	0.061	0.060	0.061	0.06
4 <i>S. erythrothorax</i> 2	120	119	3	—	0.052	0.052	0.059	0.059	0.060	0.059	0.059	0.061	0.062	0.061	0.06
5 <i>S. gabonensis</i> 1	129	126	60	60	—	0.002	0.014	0.061	0.060	0.059	0.059	0.061	0.057	0.056	0.055
6 <i>S. gabonensis</i> 2	128	125	59	59	2	—	0.012	0.059	0.059	0.058	0.058	0.059	0.057	0.056	0.055
7 <i>S. gabonensis</i> 3	128	125	68	67	16	14	—	0.066	0.065	0.064	0.064	0.066	0.061	0.06	0.059
8 <i>S. sanghensis</i> 1	130	129	68	68	70	68	75	—	0.003	0.003	0.002	0.002	0.030	0.029	0.028
9 <i>S. sanghensis</i> 2	131	130	69	69	69	67	74	3	—	0.004	0.001	0.003	0.029	0.028	0.027
10 <i>S. sanghensis</i> 3	130	129	68	68	68	66	73	4	5	—	0.003	0.003	0.030	0.029	0.028
11 <i>S. sanghensis</i> 4	130	129	68	68	68	66	73	2	1	4	—	0.002	0.028	0.027	0.026
12 <i>S. sanghensis</i> 5	132	131	70	70	70	68	75	2	3	4	2	—	0.030	0.029	0.028
13 <i>S. xanthogaster</i> 1	127	124	69	71	65	65	70	34	33	34	32	34	—	0.003	0.002
14 <i>S. xanthogaster</i> 2	126	123	70	70	64	64	69	33	32	33	31	33	3	—	0.001
15 <i>S. xanthogaster</i> 3	125	122	69	69	63	63	68	32	31	32	30	32	2	1	—

have been evident, or even looked for, in a widely distributed "biological species." For example, distributional records show that *S. gabonensis* is narrowly endemic to the Cameroon-Gabon region's humid coastal lowland forest. The restricted nature of its range, and possibly its ecology, were not fully appreciated when it was ranked as a subspecies. Recognizing these taxa as phylogenetic species may consequently have relevance for their conservation. If conservation priorities are predicated on knowledge of species ecologies, and those ecologies are based on a biological species concept, then there may be a risk that ecologies of target populations are being misunderstood. For example, if conservation plans for a biological species called "*Stiphornis erythrothorax*" were based on information from populations distributed somewhere other than these coastal forests, then the genetic, morphological and ecological distinction displayed by *S. gabonensis* could be misunderstood. The same may be true for *S. sanghensis* or any other polytypic biological species.

The systematic perspective provided by *Stiphornis* has broad implications. Our results suggest that taxonomic variation may be underreported in maps in the *Atlas* of Hall and Moreau (1970) as a result of their application of the biological species concept. Thus, although the taxonomic schemes of Sclater (1930) and White (1962) allowed for geographic variation in *Stiphornis* through the recognition of three subspecies, Hall and Moreau (1970) chose to map *Stiphornis* as monotypic (although they discussed some variation in the accompanying text). Further systematic revisions of African lowland forest birds may reveal other groups in which geographic and taxonomic variation have been obscured. For example, in a reanalysis of the phylogenetic relationships among the species of *Bleda* (Pycnonotidae) using morphometric and vocalization characters, Chapuis and Erard (1993) found one subspecies to be more closely related to another biological species than to its purported conspecifics; these results, in conjunction with our own, indicate that phylogenetic and biogeographic patterns within the African forest biome cannot be recovered using the biological species concept.

These examples underscore the point that incomplete mapping of taxonomic variation has led to misunderstandings about African biogeography, and as a consequence, interpretations (e.g., Diamond and Hamilton, 1980; Endler, 1982; Mayr and O'Hara, 1986) based on the distributional data in Hall and Moreau (1970) may need to be reexamined. It could be argued, for example, that Endler's (1982) failure to find contact zones evenly distributed between three purported refuges (areas of endemism) might be interpreted not as evidence against the refuge theory per se but as an indication that taxonomic patterns of variation were insufficiently resolved to reveal areas of contact accurately.

Our poor knowledge about patterns of geographic variation also raises questions about the spatial units of biogeographic analysis (areas of endemism). Moreau (1966) recognized a "Lower Guinea" zoogeographic region that included the Congo Basin west to southern Nigeria, but the distributional patterns as well as area relationships described here for the sister taxa *Stiphornis erythrothorax* and *S. gabonensis* (Upper Guinea + Cameroon-Gabon) reinforce the composite nature of the southern Nigerian forest as noted by Marchant (1954). Similarly, Prigogine (1988) has suggested areas of endemism for birds in addition to those described by Diamond and Hamilton (1980). Additional phylogenetic analyses combined with better knowledge of taxon distributions should clarify the identity and composition of avifaunal areas of endemism.

Although no biogeographic hypotheses have been proposed about historic relationships among African lowland forest areas of endemism, descriptions of processes underlying African avifaunal diversity have usually relied on vicariance through changes in forest cover caused by Pleistocene climatic fluctuations (e.g., Diamond and Hamilton, 1980; Louette, 1981; Prigogine, 1988). Few of these explanations have involved phylogenetic analysis of relevant endemics. At the same time, little is presently known about the impact of climatic change on past forest dynamics within the Guineo-Congolian forest (Maley, 1996). The location of Pleistocene lowland forest refuges has instead been inferred from areas of endemism for birds and

mammals, although some Pleistocene forest contractions have recently been corroborated by paleoclimatic data in West Africa (e.g., Maley, 1996; Maley and Brenac, 1998).

Whether or not the location of putative Pleistocene forest refugia will be corroborated from paleobotanical data, the results of this analysis implicate Mt. Cameroon and its associated highlands as the zoogeographic barrier between *S. gabonensis* and *S. erythrothorax*. Although a "molecular clock," if in fact one exists, has not been calibrated for passerine birds, some workers accept a rate of 2.0% mitochondrial cytochrome *b* sequence divergence per million years (see Klicka and Zink, 1997; Avise and Walker, 1998); under this rate assumption, the divergence of *S. erythrothorax* and *S. gabonensis*, as well as the split between (*S. erythrothorax*, *S. gabonensis*) and (*S. sanghensis*, *S. xanthogaster*) may have occurred approximately 3 million years ago, during the Upper Pliocene. These results and interpretations are at least suggestive that geomorphological and hydrological factors should be studied in addition to paleoclimate for their possible role in vicariant events within the African lowland forests.

Fjeldså and Lovett (1997) proposed that most African lowland forest birds are phylogenetically "old" and predate the Pleistocene. In their model, based on relative branching rates derived from DNA-hybridization phylogenies, lowland areas of high species richness are the result of the carrying capacity of specific habitats, phyletic speciation, and the immigration of "younger" species from topographically complex areas (in which diversity is created according to a disturbance-regime model) (Fjeldså and Lovett, 1997). It is difficult to evaluate such complex causal models of speciation processes unless the patterns invoked are well understood, in terms of both geographic variation and phylogenetic relationships among the taxa involved (Cracraft, 1989; Bates et al., 1998).

At this time it is apparent that patterns of variation of birds within the Guineo-Congolian forest are poorly known. The zoogeographically complex nature of the northwestern part of the Congo Basin forest that is emerging through our discovery of *S.*

sanghensis as well as from surveys of other vertebrates (Fay, 1988; Joger, 1990) underscores the need for more careful analyses of the distribution of geographic variation in and around the Congo Basin. Although new species are being described by other vertebrate zoologists (e.g., Joger, 1990) including a new species of shrew from the CAR (Ray and Hutterer, 1996), since 1966 no new avian species has been described from the Congo Basin forest (Mayr and Vuilleumier, 1983; Vuilleumier and Mayr, 1987; Vuilleumier et al., 1992; Hockey, 1997). This study, however, suggests that this situation may be an artifact of viewing patterns of geographic variation and endemism through the lens of a particular species concept. Future work in African zoogeography, especially for lowland forest taxa, should focus on patterns of geographic variation within the framework of a phylogenetic species concept in order to discover differentiated taxa, their areas of endemism, and the barriers responsible for them, as well as to test process-oriented hypotheses relating to paleoclimatic and geological events affecting biotic history.

REFERENCES

- Avise, J. C., and D. Walker
1998. Pleistocene phylogeographic effects on avian populations and the speciation process. *Proc. R. Soc. London. B* 265: 457–463.
- Bates, J. M., S. J. Hackett, and J. Cracraft
1998. Area-relationships in the Neotropical lowlands: an hypothesis based on raw distributions of passerine birds. *J. Biogeogr.* 25: 783–793.
- Brosset, A., and C. Erard
1986. Les oiseaux des régions forestières du nord-est du gabon. Vol. 1. Ecologie et comportement des espèces. Paris: Soc. Natl. Prot. Nat.
- Bruhl, C. A.
1997. Flightless insects: a test case for historical relationships of African mountains. *J. Biogeogr.* 24: 233–250.
- Chapin, J. P.
1953. The birds of the Belgian Congo, Pt. 3. *Bull. Am. Mus. Nat. Hist.* 75A.
1954. The birds of the Belgian Congo, Pt. 4. *Ibid.* 75B.
- Chappuis, C., and C. Erard
1993. Species limits in the genus *Bleda* Bon-

- aparte, 1857. *Z. zool. Syst. Evolutionsforsch.* 31: 280–299.
- Charif, R. A., S. Mitchell, and C. W. Clark
1995. *Canary 1.2 User's manual*. Ithaca, NY: Cornell Lab. Ornith.
- Cracraft, J.
1989. Speciation and its ontology: the empirical consequences of alternative species concepts for understanding patterns and processes of differentiation, pp. 28–59. *In* D. Otte and J. A. Endler (eds.), *Speciation and its consequences*. Sunderland, MA: Sinauer Assoc.
- Crowe, T. M., and A. A. Crowe
1982. Patterns of distribution, diversity and endemism in Afrotropical birds. *J. Zool. (London)* 198: 417–442.
- Desjardins, P., and R. Morais
1990. Sequence and gene organization of the chicken mitochondrial genome. *J. Mol. Biol.* 212: 599–634.
- Diamond, A. W., and A. C. Hamilton
1980. The distribution of forest passerine birds and Quaternary climatic change in tropical Africa. *J. Zool. (London)* 191: 379–402.
- Dowsett, R., and F. Dowsett-Lemaire (eds.)
1997. *Flore et faune du Parc National d'Odzala, Congo*. Turaco Res. Rep. 6.
- Endler, J. A.
1982. Pleistocene forest refuges: fact or fancy? *In* G. Prance (ed.) *Biological diversification in the tropics*: 641–656. New York: Columbia Univ. Press.
- Fay, J. M.
1988. Forest monkey populations in the Central African Republic: the northern limits. A census in Manovo-Gounda-St. Floris National Park. *Mammalia* 52(1): 57–74.
- Fjeldså, J., and J. Lovett
1997. Geographical patterns of old and young species in African forest biota: the significance of specific montane areas as evolutionary centres. *Biodivers. Conserv.* 6: 325–346.
- Green, A. A., and R. W. Carroll
1991. The avifauna of Dzanga-Ndoki National Park and Dzanga-Sangha Rainforest Reserve, Central African Republic. *Malimbus* 13: 49–66.
- Hackett, S. J.
1996. Molecular phylogenetics and biogeography of tanagers in the genus *Ramphocelus* (Aves). *Mol. Phylogenet. Evol.* 5(2): 368–382.
- Hall, B. P., and R. E. Moreau
1970. *An Atlas of Speciation in African Passerine Birds*. London: British Museum (Natural History).
- Hartlaub, G.
1855. Beschreibung einiger neuen, von Herrn H.S. Pel, holländischem residenten an der Goldküste, daselbst gesammelten vogelarten. *J. Ornithol.* 17: 344–360.
- Hockey, P.
1997. New birds in Africa. *Africa Birds and Birding* 2(1): 39–44.
- Irwin, M. P. S., and P. A. Clancey
1974. A re-appraisal of the generic relationships of some African forest-dwelling robins (Aves: Turdidae). *Arnoldia (Rhodesia)* 6(34): 1–19.
- Jackson, F.
1910. *Bull. Br. Ornithol. Club* 25: 85.
- Jensen, F. P.
1989. A review of some genera of African chats (Aves: Muscicapidae, Erithacini). *Steenstrupia* 15(6): 161–175.
- Joger, U.
1990. The herpetofauna of the Central African Republic, with a description of a new species of *Rhinotyphlops* (Serpentes: Typhlopidae). *In* G. Peters and R. Hutterer (eds.), *Vertebrates in the tropics*: 85–102. Bonn: Mus. Alexander Koenig.
- Keith, G. S., and W.W.H. Gunn
1971. Birds of the African rain forests. *Sounds of nature* 9. Fed. of Ontario Nat. and Am. Mus. Nat. Hist.
- Keith, S., E. K. Urban, and C. H. Fry
1992. *The birds of Africa*, vol. 4. London: Academic Press.
- Klicka, J., and R. Zink
1997. The importance of recent ice ages in speciation: a failed paradigm. *Science* 277: 1666–1669.
- Louette, M.
1981. The birds of Cameroon: an annotated checklist. *Klasse Wet.* (43) 163.
1984. Apparent range gaps in African forest birds. *Proc. Pan Afr. Ornithol. Congr.* 5: 275–286.
1992. Barriers, contact zones and subspeciation in central equatorial Africa. *Bull. Br. Ornithol. Club* 112A: 209–216.
- Maley, J.
1996. The African rain forest—main characteristics of changes in vegetation and climate from the Upper Cretaceous to the Quaternary. *Proc. R. Soc. Edinburgh B*: 104: 31–74.
- Maley, J., and P. Brenac
1998. Vegetation dynamics, palaeoenvironments and climatic changes in the for-

- ests of western Cameroon during the last 28,000 years B.P. *Rev. Palaeobot. Palynol.* 99: 157–187.
- Marchant, S.
1954. The relationship of the southern Nigerian avifauna to those of Upper and Lower Guinea. *Ibis* 96: 371–379.
- Mayr, E., and R. J. O'Hara
1986. The biogeographic evidence supporting the Pleistocene forest refuge hypothesis. *Evol.* 40(1): 55–67.
- Mayr, E., and R. A. Paynter, Jr. (eds.)
1964. Check-list of birds of the world, vol. 10. Cambridge, MA.: Mus. Comp. Zool.
- Mayr, E., and F. Vuilleumier
1983. New species of birds described from 1966 to 1975. *J. Ornithol.* 124: 217–232.
- Moreau, R. E.
1966. The bird faunas of Africa and its islands. London: Academic Press.
- Prigogine, A.
1988. Speciation patterns of birds in the central African forest refugia and their relationship with other refugia. *Acta XIX Congr. Int. Ornithol.* 2: 144–157. Ottawa: Univ. Ottawa Press.
- Ray, J. C., and R. Hutterer
1996. Structure of a shrew community in the Central African Republic based on the analysis of carnivore scats, with the description of a new *Sylvisorex* (Mammalia: Soricidae). *Ecotropica* 1: 85–97.
- Reichenow, A.
1874. *J. Ornithol.*:103.
- Roy, M. S.
1997. Recent diversification in African greenbuls (Pycnonotidae: *Andropadus*) supports a montane speciation model. *Proc. R. Soc. (London).* B 264: 1337–1344.
- Slater, W. L.
1930. *Systema Avium Aethiopicarum* Pt. 2. London: Br. Ornithol. Union.
- Sibley, C. G., and B. L. Monroe, Jr.
1990. *Distribution and Taxonomy of Birds of the World*. New Haven, CT: Yale University Press.
- Sharpe, R. B.
1883. *Catalogue of the Passeriformes in the British Museum: Cichlomorphae* Pt. 4. London: British Museum
1903. A hand-list of the genera and species of birds vol 4. London: British Museum (Natural History).
- Snow, D.
1978. *An Atlas of Speciation in African Non-passerine Birds*. London: British Museum (Natural History).
- Swofford, D. L.
1998. PAUP*. Phylogenetic analysis using parsimony (*and other methods). Version 4. Sunderland, MA: Sinauer Associates.
- Vuilleumier, F., and E. Mayr
1987. New species of birds described from 1976 to 1980. *J. Ornithol.*, 28: 137–150.
- Vuilleumier, F., M. LeCroy, and E. Mayr
1992. New species of birds described from 1981 to 1990. *Bull. Br. Ornithol. Club* 112A: 267–309.
- White, C.M.N.
1962. A revised check-list of African shrikes, orioles, drongos, starlings, crows, waxwings, cuckoo-shrikes, bulbuls, accentors, thrushes and babblers. Lusaka: Govt. Printer.
- White, F.
1983. *The vegetation of Africa*. Paris: UNESCO.

APPENDIX 1

Gazetteer of *Stiphornis* Specimens Examined***erythrothorax***

LIBERIA

Bong Co.	7°00'N 9°40'W
Cape Mount	6°45'N 11°23'W
Dugbe R.	4°51'N 8°46'W
Gbarnga	7°02'N 9°26'W
Grassfield	7°30'N 8°35'W
Mt. Nimba	7°35'N 8°28'W
Zigida	8°02'N 9°29'W

SIERRA LEONE

Sugar Loaf	8°25'N 13°14'W
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NIGERIA

Degema	4°48'N 6°45'E
Ede	7°40'N 4°30'E
Fadom Kagomi	9°30'N 8°00'E
Ilard	6°55'N 3°00'E
Lagos	6°28'N 3°25'E
Mamu Forest	6°10'N 7°10'E
Owerri	5°30'N 7°01'E

gabonensis

CAMEROON

Dume	4°18'N 13°28'E
Efulen	2°42'N 10°30'E
Eseka	3°39'N 10°46'E
Kribi	2°57'N 9°55'E
Kumba	4°38'N 9°25'E
Lolodorf	3°10'N 10°42'E
Mamfe	5°46'N 9°17'E
Mbonge	4°35'N 9°05'E
Melan	3°51'N 11°30'E
Nditam	5°21'N 11°14'E
Ndoi	4°55'N 9°30'E
Ngoumé	5°30'N 11°26'E
Victoria	4°00'N 9°12'E

GABON

Bassin D'Ivindo	0–2°N 12–14°E
Bélinga	0°36'N 13°08'E
Kango	0°10'N 10°09'E
Kribi	2°56'N 9°56'E
Oveng	2°25'N 12°16'E

EQ. GUINEA

Bioko	3°13'N 8°24'E to 3°48'N 8°58'E
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xanthogaster

DRC

Angumu	0°7'S 27°41'E
Avakubi	1°21'N 27°40'E

Babeyru	1°53'N 27°32'E
Basankusu	1°14'N 19°48'E
Bassin Lindi	0°33'S 28°40'E to 0°32'N 25°07'E
Beritee	3°25'N 24°32'E
Epulu	1°25'N 28°35'E
Gamangui	2°10'N 27°15'E
Ibanga	2°47'S/28°25'E
Ibembo	2°38'N 23°37'E
Ikela	1°11'S 23°16'E
Luhoho R.	4°30'S 35°08'E to 5°30'S 36°25'E
Kailo	2°38'S 26°07'E
Lukolela	1°07'S 17°11'E
Lusambo	4°58'S 23°27'E
Mauda	4°05'N 27°41'E
Medje	2°26'N 27°17'E
Moga	2°21'S 26°49'E
Ngayu	1°45'N 27°33'E
Panga	3°17'N 26°44'E
Poko	3°09'N 26°53'E

KENYA

Kipkabus	0°18'N 35°31'E
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UGANDA

Budongo Forest	1°40'N 31°25'E to 1°53'N 31°41'E
Katera	0°45'N 31°59'E
Luwala	0°27'N 33°07'E
Mabira Forest	0°23'N 32°54'E to 0°32'N 33°07'E
Mutwanga	0°20'N 29°45'E
Ntandi	0°48'N 31°59'E
Semliki Valley	0°08'S 29°36'E to 1°12'N 30°30'E
Lugalambo	0°24'N 33°03'E

CAR

Ouessi River	5°35'N 24°36'E
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SUDAN

Bangangai Forest	4°51'N 27°45'E
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CAMEROON

Assobam	3°17'N 14°04'E
Bitye	3°10'N 12°20'E
Mieri	4°14'N 13°58'E
Yokoudouma	3°25'N 15°03'E