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A

MOLECULAR SYSTEMATICS AND BIOGEOGRAPHY OF CERTAIN GUINEO-CONGOLIAN PASSERINES

by

PAMELA BERESFORD

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York.

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Abstract

MOLECULAR SYSTEMATICS AND BIOGEOGRAPHY OF CERTAIN GUINEO-CONGOLIAN PASSERINES

by

PAMELA BERESFORD

Adviser: Professor Joel Cracraft

This research was designed to provided the first detailed phylogenetic and biogeographic analyses of passerine birds endemic to the Guineo-Congolian biome. The phylogenetic species concept was used to delineate basal evolutionary units in each of five genera (*Stiphrornis, Bleda, Criniger, Alethe* and *Sheppardia*), and their interspecific relationships and phylogeographic pattern were explored with DNA sequence data.

Each of the phylogenetic species recognized by external morphological characters (revealed by a survey of museum specimens) was corroborated by the mitochondrial DNA sequence data, which also showed relatively high levels of sequence divergence among the species. Certain biogeographic elements of the systematic patterns of *Stiphrornis*, *Bleda* and *Criniger* were shared and together allowed for a preliminary identification of areas of endemism and a hierarchy of vicariant events. These findings clarified phylogenetic and spatial patterns otherwise obscured when the taxa in these groups are classified as more inclusive (e.g. "biological") species, and they highlight the need for critical taxonomic revision of parts of the African avifauna. Phylogenetic relationships between species of akalats (*Sheppardia*, Aves: Turdidae) and alethes (*Alethe*, Aves: Turdidae) were also explored in order to clarify the historical biogeography of the two groups, which also have species occurring outside the lowland rainforest biome. While the composition of some species groups recognized in prior revisions of these genera were corroborated with the molecular data, these data gave little support for the monophyly of either *Alethe* or *Sheppardia* as those genera are currently circumscribed and show that many "*Cossypha*" allied to *Sheppardia*.

Phylogeographic pattern was also investigated in four species widespread in the Guineo-Congolian biome (*Bleda syndactyla, Criniger calurus, Sheppardia cyornithopsis* and *Alethe poliocephala*), and for *Alethe castanea* in the Congolian region. Within widespread species, some phylogeographic elements were shared, such as distinct lineages between Upper and Lower Guinea populations, and between eastern and western Congolian populations. This study revealed previously unknown mitochondrial diversity among closely related species and within widespread populations; in most cases strong geographic structure was evident in the gene trees and indicates the need for future studies to clarify the processes responsible for that phylogeograpic structure.

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I am primarily grateful to Joel Cracraft for acknowledging my twin interests in systematics and African faunas and facilitating every element of my progress through graduate school, in field ornithology, molecular systematics, research development and epistemology.

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I thank my aunt Florence, my brother Denis and my uncle Bill for helping me live comfortably in New York. Finally, I am grateful to both of my recently departed parents, David and Gloria, for taking me to Kinshasa. *Et lux perpetua.*

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Introduction

This study was designed to bring systematic hypotheses to bear upon considerations of the evolution of the African lowland forest biome. This region, characterized phytogeographically by White (1983) as the Guineo-Congolian biome, is also a valid biogeographic region for birds, as cluster analyses have shown (Crowe and Crowe 1982, Williams et al. 1999). Although distributional data have been studied to reveal restricted areas of high diversity (Diamond and Hamilton, 1980; Stattersfield et al., 1998) or to establish broad continent-wide faunal zones (Chapin, 1923; Crowe and Crowe, 1982; Williams et al., 1999), areas of endemism as conceived by historical biogeographers have not been described within the biome. Furthermore, modern systematic analyses of groups of African birds have only considered the lowland forest biome as a singular entity, and none have explored the distribution of genetic lineages within the region (e.g. Bloomer and Crowe, 1998; Roy, 1997; Roy et al. 2000, Veron, 1999). Therefore, neither distributional nor systematic data are available with which to investigate the assemblage of the biota, and these elements are critical components in efforts to explore spatiotemporal aspects of species diversity (Cracraft, 1994).

Notwithstanding the absence of rigorous systematic hypotheses for groups of related species, several hypotheses about speciation in the Guineo-Congolian biome have been offered; these are discussed below along with a brief characterization of their predictions for systematic relationships. For decades, diversity in this region has been attributed to Pleistocene climate-induced allopatric speciation (Moreau 1966, Diamond and Hamilton 1980), with species differentiation said to have occurred in refuges — patches hygrophilious forest that persisted during drier and/or cooler climate regimes (Maley 1996). The location of those refuges has been hypothesized using patterns of species richness by (Diamond and Hamilton 1980), based on distributional data that were geographically incomplete and taxonomically inaccurate, and these refuges, in turn, have been used to interpret palynological data in support of the location of those refuges (e.g. Maley 1996, Jahns et al. 1998). However, my own assessment of patterns of endemism does not strongly support a refugial scenario since no related group of species has endemics in each purported refuge. Furthermore, given the linear, east-to-west array of the refuges, the cyclical and possibly differential persistence of refuges, no particular relationship among species that may have differentiated in each or several refuges can be expected. Meadows (1996:166) remarked that "the Pleistocene refuge hypothesis so far seems to have stood the test of time in Africa, although it has been much more critically debated for South America." The absence of any critical debate on the Pleistocene refuge hypothesis, or the historical biogeography of the lowland avifauna generally, is undoubtedly due to the lack of systematic hypotheses and inadequate pattern analysis for the African fauna.

Recently, Fjeldsaa (1995; see also Fjeldsaa and Lovett, 1997) suggested an alternative to the Pleistocene refuge hypothesis. Fjeldsaa (1995) heuristically mapped the distributions of the few African passerines included in Sibley and Ahlquist's (1990) DNA hybridization study, and found that the youngest species were endemic to areas of topographic complexity, termed 'speciation centers.' Lowland forest biotas were predominately made up of taxa estimated to be of Miocene or Pliocene age, and were characterized as areas where species accumulate. Fjeldsaa and Lovett (1997:340) suggested that the assemblage of the lowland forest biota has been due to the adaptive redistribution of species which "originated elsewhere" and that detailed phylogenetic studies would be required to separate speciation events from patterns resulting from species redistribution. Fjeldsaa and Lovett (1997) surmised that current patterns of species richness, from which refuges were perceived, are simply individual species' responses to local ecological conditions and can be explained by current carrying capacity. Roy (1997) formulated the prediction from this "museum" model that montane species should be the most derived in a phylogenetic analysis, and Fjeldsaa (1995) suggested that if refuges, rather than carrying capacity, were causes of diversity, that non-refugial, or dispersed, populations should similarly be distal in a population phylogeny. Fjeldsaa (1995) also posited that lowland taxa could disperse to and differentiate in montane habitat, which appears to predict a sister relationship between lowland and montane species in which the montane species would also be derived in a phylogenetic analysis.

Finally, Smith et al. (1997) suggested that species diversity may also be a product of selection across ecotones, based on genetic and morphological differences observed within one species. As articulated by Moritz et al. (2000), this model predicts that sister taxa should occupy different and adjacent habitats. However, this model seems not to be strictly applicable to clades wholly endemic to one biome. Furthermore, Moritz et al. (2000) recognize that a conceptual difficulty results from this model, to wit, why there are not many new species.

It should be noted that, in terms of species assemblage, the temporal domain of all of these hypotheses is primarily the Plio-Pleistocene. Also, the Ecotone Gradient Hypothesis of Moritz et al. (2000) does not provide any prediction of spatial pattern *within* the Guineo-Congolian biome; the 'museum' model of Fjeldsaa and Lovett (1997:340) ascribes richness and endemism to localized places with "intrinsic ecoclimatic properties . . . not yet elucidated in detail."

The aim of this research was to provide detailed phylogenetic analyses of patterns of speciation within the Guineo-Congolian avifauna in order for a historical biogeographic inquiry to proceed. Such an investigation needs a series of taxon cladograms that may be read as area cladograms for interpretation in terms of earth history events (Nelson and Platnick, 1981; Cracraft, 1986). Once broad patterns of endemism were established, groups of related species that have radiated within the lowland forest, and are therefore especially suitable for phylogenetic analysis, were identified. These included three genera co-distributed in the Guineo-Congolian biome with different degrees of allopatric and sympatric ranges (*Stiphrornis*, Turdidae; *Bleda* and *Criniger*, Pycnonotidae) and two genera that included taxa in the lowland forest as well as those outside of it (*Alethe* and *Sheppardia*: Turdidae). Each of the species studied in these clades occupies the lower strata of continuous-cover forest and together are not expected *a priori* to have responded differently to abiotic events. Phylogenetic species were used as the terminals in the systematic analyses, and museum specimens were reviewed to establish the distribution of morphological characters delimiting species. Multiple exemplars of specimens sampled for DNA sequence characters were used to explore the monophyly of those species. Finally, multiple exemplars of widespread taxa were sampled to explore the nature and geographic dispersion of intraspecific lineages.

The following three chapters are papers prepared for submission to scientific journals. The first chapter was published in 1999. Each paper is in the style required by the journal to which they have or will be submitted; literature citations follow each chapter.

The primary significance of this research is the new data provided by the systematic revisions of the focal genera, along with the resultant clarification of distributional and phylogenetic patterns. These results will facilitate rigorous approaches to a variety of questions about modes of speciation, rates of molecular evolution, and relative or absolute age of vicariant events.

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CHAPTER 1

SPECIATION IN AFRICAN FOREST ROBINS (STIPHRORNIS): SPECIES LIMITS, PHYLOGENETIC RELATIONSHIPS, AND MOLECULAR BIOGEOGRAPHY

PAMELA BERESFORD AND JOEL CRACRAFT

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ABSTRACT

The monotypic genus Stiphrornis (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 Stiphrornis. 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.

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 ("Stiphrornis 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 because 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 underresolution of patterns of geographic variation. This is true for the Stiphrornis 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.

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MATERIALS AND METHODS

Museum study skins were examined for evidence of variation and diagnosability in features of external morphology. Mitochondrial DNA (mtDNA) sequence data for the entire cytochrome-b gene (1143 base pairs) were obtained for 13 Stiphrornis 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 (M = male, F = female, ?=sex undetermined): S. erythrothorax (AMNH 12M, 8F; MRAC 8M, 2F, 2?; MNHN 1F; BMNH 3M 3F 1?), S. gabonensis (AMNH 16M, 10F; DM 3M, 2F; MRAC 1M, 1F, 2?; MNHN 4M, 5F, 3?; BMNH 8M, 6F, 6?), S. xanthogaster (AMNH 37M, 21F, 4?; DM 5M, 2F; LACM 8M, 4F; FMNH 10M, 4F; MRAC 38M, 12F, 5?; MNHN 3M, 2F, 1?; BMNH 19M, 8F), and S. sanghensis (AMNH 5M, 10F, 8?). These specimens represented 99 localities across the range of Stiphrornis 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 Table 6.

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 dDNTPs, 0.15 μL Taq polymerase [Promega, Madison, WI] and 2 μL buffer), placed in an Idaho Technologies air thermocycler at the following 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 H_20 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 dDNTPs, 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 18μL H_2O. 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% 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 loral 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.

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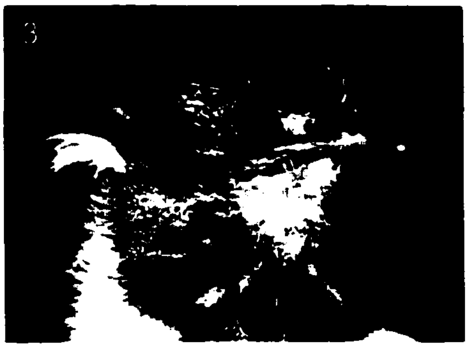

Fig. 1. Ventral and dorsal views of *Stiphrornis* taxa. Left to right, top: *S. erythrothorax*, AMNH 825486 (Liberia) and AMNH 827586 (Liberia); *S. gabonensis*, AMNH 297701 (Bioko, Equatorial Guinea) and AMNH 800617 (Cameroon); bottom: *S. xanthogaster*, AMNH 161024 (DRC) and AMNH 164023 (DRC); *S.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

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

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

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: *Stiphrornis 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).

Stiphrornis 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 *Stiphrornis* 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."

Stiphrornis 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 *Stiphromis* 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 (AMNH 599798) south through northeastern Gabon (MNHN 517, Bélinga) to Lukolela, DRC (AMNH 2696983) east through northeastern CAR (LACM 84941), Sudan, the Ituri forest, and Uganda to western Kenya (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* 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.

Stiphromis 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-Mbaéré 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, subadult (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 loral 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

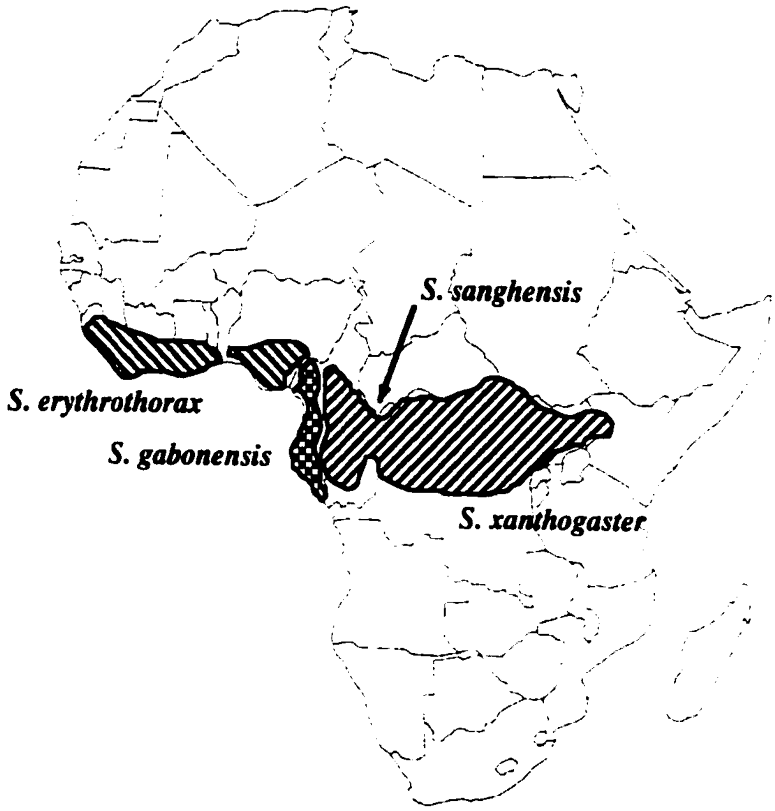

Fig. 4. Distributions of species of *Stiphrornis* (after Keith et al. (1992) and material examined in this study). Range limits of taxa in the western Congo Basin are poorly known at present, therefore it is uncertain whether parapatry exists between *S. gabonensis* and *S. erythrothorax*.

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-Mbaéré 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 "Sangha 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

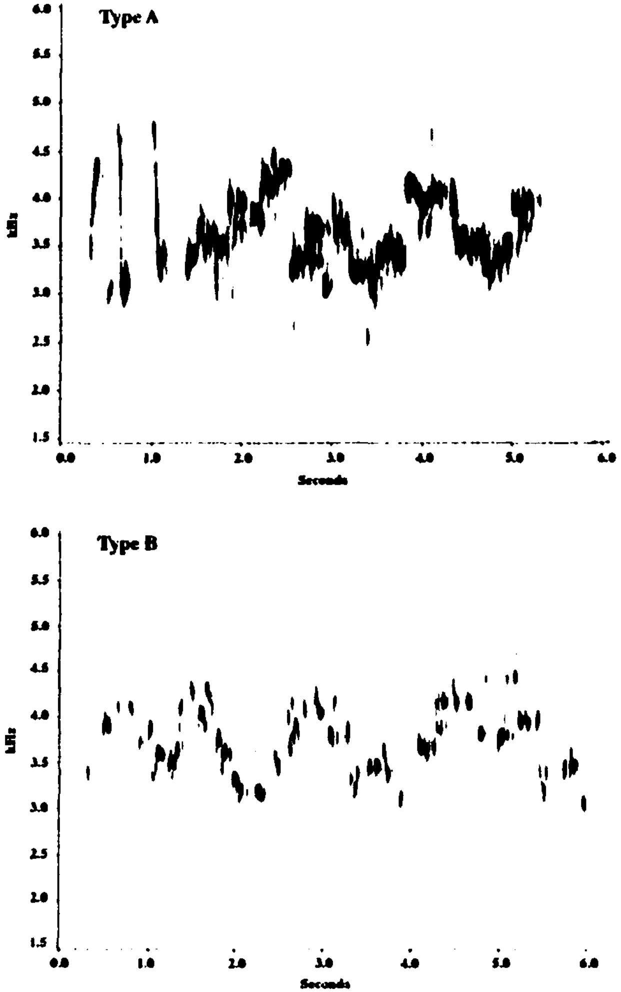

Fig 5. Spectrograms of two types of *Stiphrornis sanghensis* calls, recorded in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998.

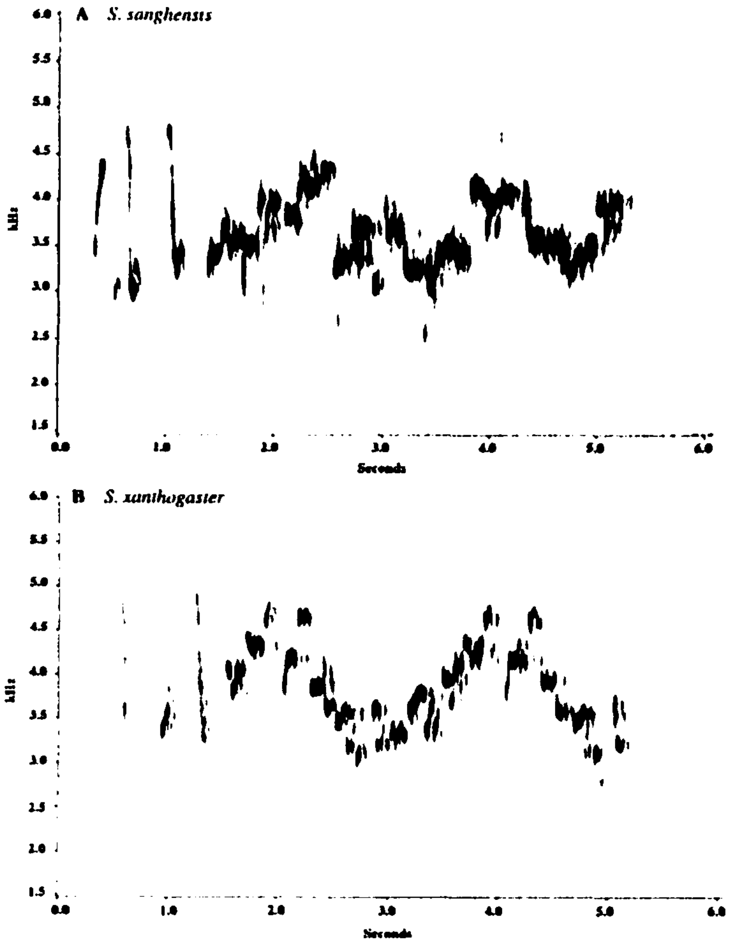

Fig 6. Spectrograms of two Type A *Stiphrornis* calls. (A) *S. sanghensis*, recorded in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998; (B) *S. xanthogaster*, recorded near Mt. Hoyo, DRC, Cornell Library of Natural Sounds Catalogue Number LNS01456.

of the Sangha River. Future collecting of Stiphrornis 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 x 5 mm and 10 x 5 mm, compared to testes sizes of 1.5 x 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 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

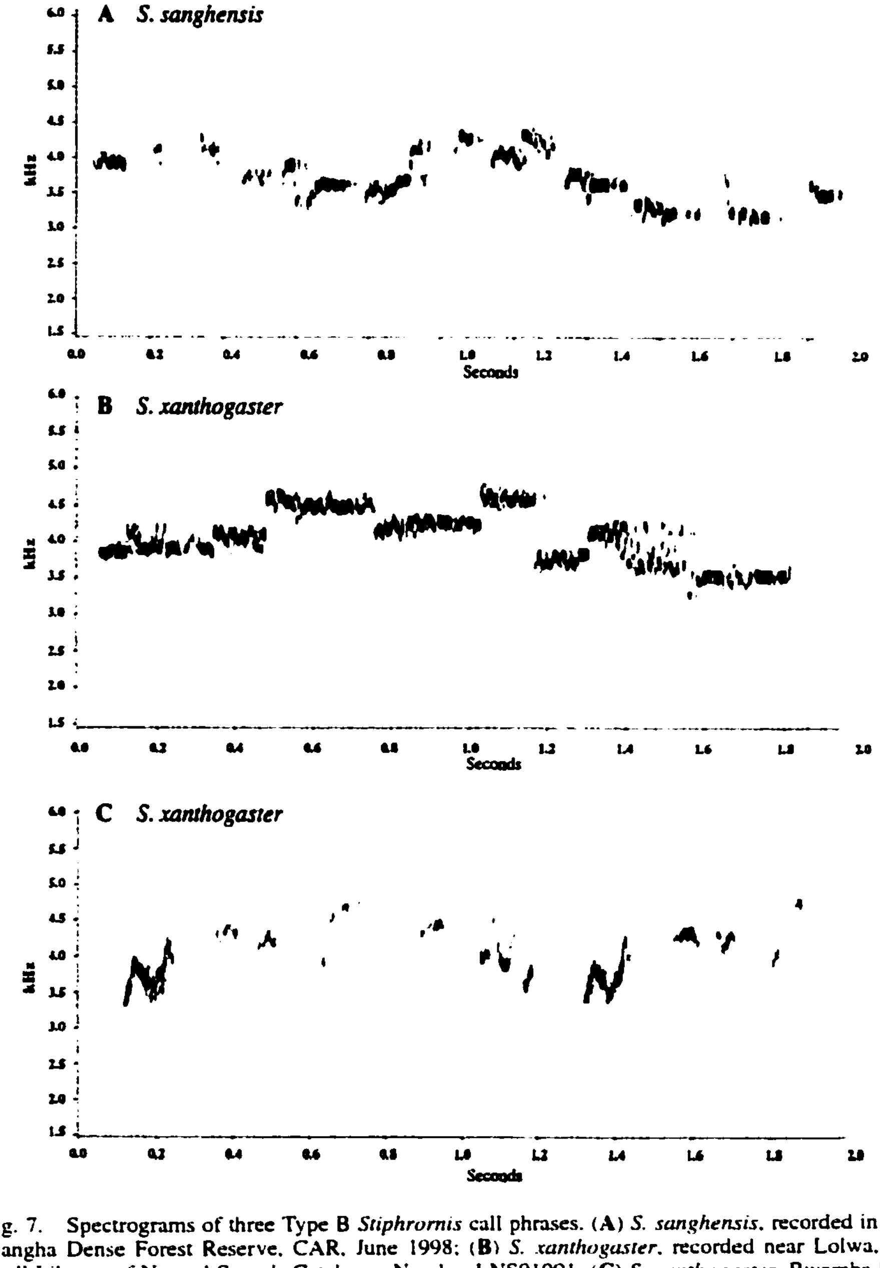

Fig. 7. Spectrograms of three Type B *Stiphrornis* call phrases. (A) *S. sanghensis*, recorded in Dzanga-Sangha Dense Forest Reserve, CAR, June 1998; (B) *S. xanthogaster*, recorded near Lolwa, DRC, Cornell Library of Natural Sounds Catalogue Number LNS01091; (C) *S. xanthogaster*, Bwamba Forest, Uganda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

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 Stiphrornis 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 Stiphrornis 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 Stiphrornis. The other species, S. erythrothorax and S. gabonensis, are themselves united and form the sister group of S. sanghensis and S. xanthogaster.

Within Stiphrornis, 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 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); less clear are 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 Stiphromis 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 Stiphromis 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 Stiphromis 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

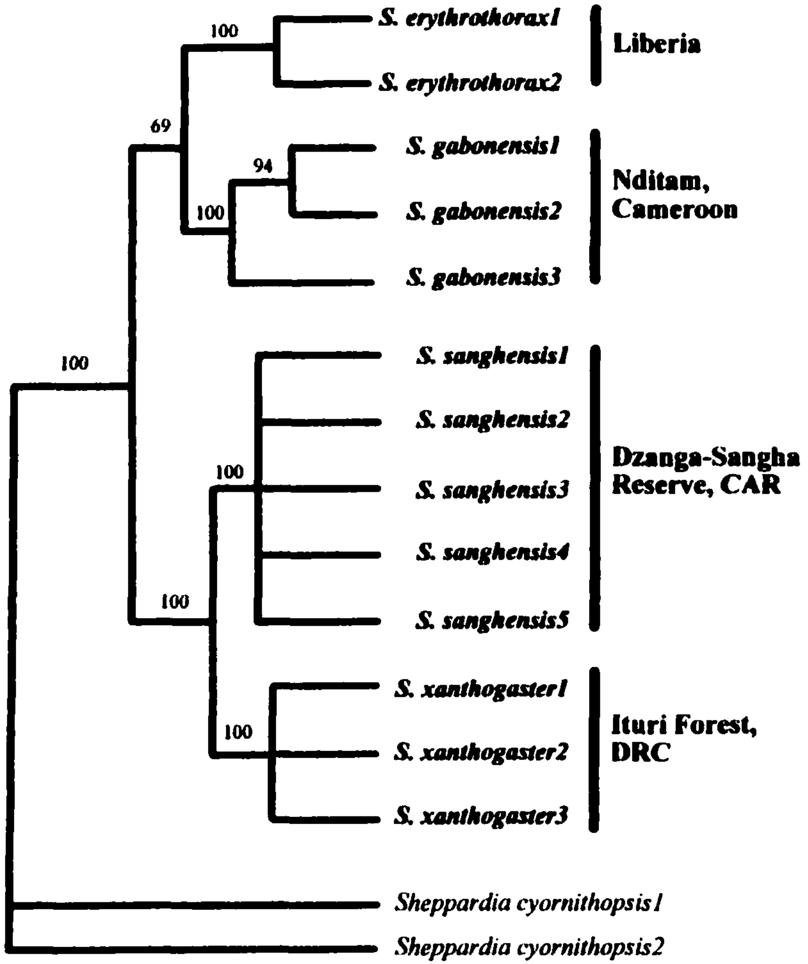

Fig 8. Strict consensus of five most-parsimonious trees (243 steps, CI = 0.868) derived from a branch-and-bound search on cytochrome-*b* sequence data for 13 *Stiphrornis* haplotypes and two outgroup haplotypes. Bootstrap values based on 500 replicates.

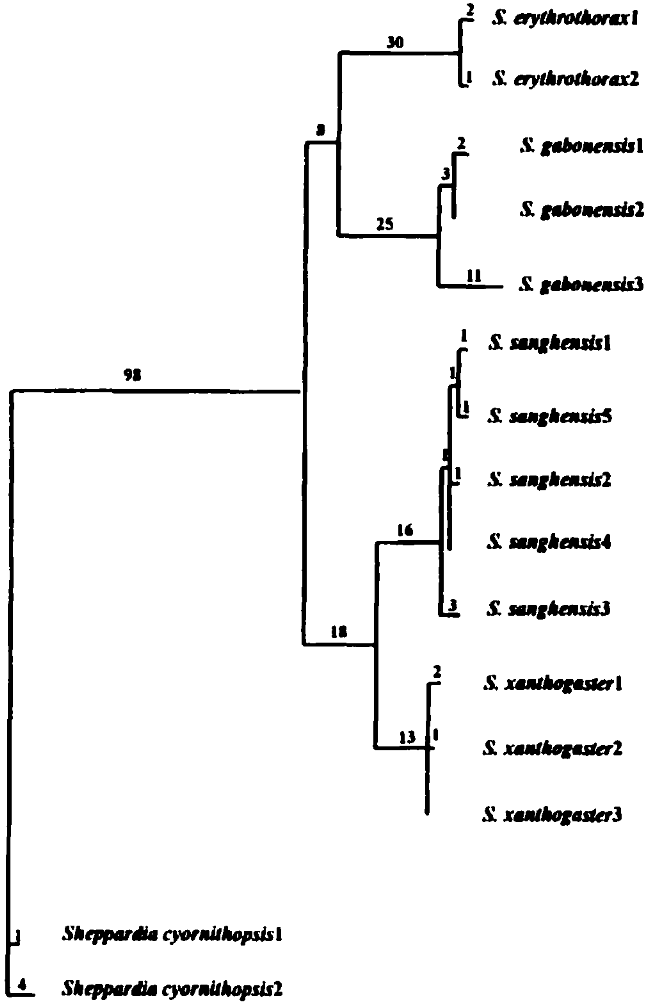

Fig. 9. One of five most-parsimonious trees obtained from the analysis of Figure 8 (branch-and-bound search, DELTRAN optimization), derived from parsimony analysis of cytochrome-*b* sequence data for 13 *Stiphrornis* haplotypes and two outgroup haplotypes, chosed to illustrate relative branch lengths.

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 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 "Stiphrornis 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 Stiphrornis 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 Stiphrornis through the recognition of three subspecies, Hall and Moreau (1970) chose to map Stiphrornis 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, Chappuis 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 lead 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 Stiphrornis 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 Mount 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.

Fjeldsa° 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) (Fjeldsa° 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.

TABLE 1
Information on Specimens Used in Molecular Analysis

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

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-ttcctatacaaagaaacctgaaa-3
H15710	5-atagcgtaggcgaataggaagtatc-3
L15656	5-ccagacctcctaggagacccaga-3
H16065	5-aacgcagtcatctccggtttacaagac-3

TABLE 3
Summary of Plumage Variation in *Stiphrornis*

Plumage/body part	*sanghensis*	*xanthogaster*	*gabonensis*	*erythrothorax*
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 Stiphrornis sanghensis Type Series. 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. Weight is given in grams.

AMNH	Weight (g)	Wing (mm)	Tail (mm)	Culmen (mm.)	Tarsus (mm)
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

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 *Sheppardia cyornithopsis* 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 *S. cyornithopsis* 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 *Stiphrornis erythrothorax* 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 *S. erythrothorax* 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 *S. gabonensis* 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 *S. gabonensis* 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 *S. gabnonensis* 3	128	125	68	67	16	14	–	0.066	0.065	0.064	0.064	0.066	0.061	0.06	0.059
8 *S. sanghensis* 1	130	129	68	68	70	68	75	–	0.003	0.003	0.002	0.002	0.030	0.029	0.028
9 *S. sanghensis* 2	131	130	69	69	69	67	74	3	-	0.004	0.001	0.003	0.029	0.028	0.027
10 *S. sanghensis* 3	130	129	68	68	68	66	73	4	5	–	0.003	0.003	0.030	0.029	0.028
11 *S. sanghensis* 4	130	129	68	68	68	66	73	2	1	4	–	0.002	0.028	0.027	0.026
12 *S. sanghensis* 5	132	131	70	70	70	68	75	2	3	4	2	–	0.030	0.029	0.028
13 *S. xanthogaster* 1	127	124	69	71	65	65	70	34	33	34	32	34	–	0.003	0.002
14 *S. xanthogaster* 2	126	123	70	70	64	64	69	33	32	33	31	33	3	–	0.001
15 *S. xanthogaster* 3	125	122	69	69	63	63	68	32	31	32	30	32	2	1	–

TABLE 6
Gazetteer of *Stiphrornis* 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
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
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°07E
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
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
Sudan	
Bangangai Forest	4°51'N 27°45'E
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

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CHAPTER 2

PHYLOGENETIC SPECIES OF THE GUINEO-CONGOLIAN AVIFAUNA: MOLECULAR SYSTEMATICS OF *BLEDA* AND *CRINIGER* (AVES: PYCNONOTIDAE)

INTRODUCTION

Previous evolutionary studies on the biota of the tropical lowland forests have contributed valuable insights into our understanding of the origins of tropical diversity, yet patterns of genetic diversity and phylogenetic relationships within the endemic avifauna of the African Guineo-Congolian region have not been investigated using contemporary systematic methods. One of the benefits of molecular systematics is that it allows characterization of the geographic attributes of genetic and taxonomic diversity, and this study endeavors to clarify such patterns among the species of codistributed genera in the African lowland rainforest biome.

Refuge concepts of one kind or another continue to play a significant role in explanations of African lowland forest bird diversity. Earth scientists, for example, have relied strongly on notions of refuges as defined by ornithologists (e.g., Diamond and Hamilton 1980, Prigogine 1988) to explain discontinuous forest coverage suggested by palynological data (Maley 1996; Dupont et al. 2000); one authority even suggested that "the Pleistocene refuge hypothesis so far seems to have stood the test of time in Africa" (Meadows 1996:166). Similarly, in a recent analysis of forest tree distribution and pollen evidence, Hamilton (2001:66) stated that "For Uganda at least, the refugium theory of the origin of hotspots in African forests is well supported." Similar explanations had been applied to the biotas of other continents, but the general belief that Pleistocene isolation in forest refuges has driven much of the diversification we see today is being replaced by more refined, area-specific explanatory hypothesis (Bush, 1990; Hewitt, 1996), partly as a result of new evolutionary studies. Thus, various workers (Fjeldsaa 1994, Klicka and Zink 1997) have inferred dates derived from molecular clocks, suggesting that the ages of putative refuge species are much older than the Pleistocene. Fjeldsaa (1994, Fjeldsaa and Lovett 1997) proposed an alternative to the Pleistocene refuge hypothesis for the lowland forest, suggesting that the avifauna was composed of old and relict species, the biogeographical signal of which has been "erased", and younger species that have accumulated in the forests as a result of speciation processes in topographically complex areas with some degree of ecoclimatological stability. This hypothesis, however, has not yet been explored for endemic lowland birds.

The existence of an avian area of endemism that is broadly congruent with the Guineo-Congolian phytogeographic region of White (1983) has long been recognized by zoogeographers (Chapin 1923, Moreau, 1966) and has also been revealed by methods of discriminant and classification analyses (Diamond and Hamilton 1980, Crowe and Crowe 1982, Williams et al. 1999). However, to date no areas of endemism (in the sense of cladistic biogeography; Nelson and Platnick, 1981; Humphries and Parenti, 1999) have been described or considered from the perspective of phylogenetic biogeography. Recent reviews of the complicated ranges of the endemic passerines (Louette,1992; Dowsett-Lemaire and Dowsett, 2001) discuss the nature of the barriers partitioning the avifauna into regions of varying geography and composition.

These regions include Upper Guinea for the westernmost forests, which are currently highly fragmented and bounded on the east by the Togo or Dahomey Gap, a biogeographic barrier recognized for birds since at least R. B. Sharpe in 1893 (Chapin, 1932) and continues to be described for other vertebrates and plants (White, 2001). Farther east from the Dahomey Gap, the forests of southern Nigeria form an area of hybrid nature, being at once the eastern limit of some taxa and the western limit of others (Rand, 1951; Marchant, 1954). Moreau (1966:159) wanted to recognize this complexity by naming it separately from Upper or Lower Guinea in zoogeographic discussions; today the forests in southern Nigeria are included by ornithologists in Lower Guinea forests in the Victoria Basin. Some avian ranges appear to be delimited by the Cameroon Highlands, and still further some ranges are limited east of the Atlantic coastal forests of Cameroon and Gabon. Although distributional data have been analyzed to show a band of relatively high avian species replacement here (Williams et al., 1999:468), the geographic or ecological correlates of this turnover are not easily identified and a boundary cannot be precisely delineated at present (Louette, 1990; Beresford and Cracraft, 1999; Dowsett-Lemaire and Dowsett, 2001).

The congruent elements of richness and endemism have given rise to refuge hypotheses and ornithologists have sought to describe the historical causes of these patterns largely in terms of such hypotheses. Thus, the "area" of interest has often been the smallest discrete areas with high species richness. Notably, under current taxonomic schemes, no group of birds has endemics in each of the four (Diamond and Hamilton 1980) or five (Prigogine 1988) areas purported to have been refuges. Fjeldsaa and Lovett (1997) directed focus away from the Pleistocene refuge hypothesis by suggesting that the discontinuities in patterns of species richness and endemism evidenced in current distributions might be explained in terms of ecological features of the Guineo-Congolian biome, although Crowe and Crowe (1982) found that environmental factors did not account for a significant amount of variation in continental avian distribution patterns.

Whether African forest refuges can be explained by discontinuities in forest cover or by the persistence of landscape features, the functional equivalence of such "islands" in promoting allopatric speciation is the same. However, there are several major impediments to understanding patterns and mechanisms of speciation for this biome. First, phylogenetic analyses of groups of related species, both within and outside the forest region, have not formed the basis for descriptions of diversification patterns. Second, in recent systematic analyses of African avian clades, the lowland forest as a whole was considered to be a single terminal area (Roy 1997, Veron 1998, Bloomer and Crowe 1998), thus precluding analysis of patterns within the forest region itself. Other studies, in addition, have focused on microevolutionary processes within forest-dwelling species (e.g. Smith et al 1997) and therefore have not addressed patterns of speciation which take place at a larger scale. Finally, pattern analysis has been frustrated by imprecise taxonomy, both in the sense of historical contingency (that is, the biased effects of colonial sampling effort and the ongoing shortage of trained zoologists in Africa), and in terms of the overly inclusive nature of the biological species concept —specifically, the failure of that concept to reflect the complexities of geographic pattern as revealed by diagnosable taxa.

This study was designed to investigate patterns of speciation and historical biogeography of the African forest biome using African forest songbirds in which basal taxonomic units are resolved (phylogenetic species; Cracraft 1983, Nixon and Wheeler 1990; Beresford and Cracraft 1999), their interrelationships are investigated, and their area relationships are then inferred. Two co-distributed genera of forest-dwelling bulbuls (family Pycnonotidae) were chosen because their monophyly is well supported, they have species broadly restricted to the lowland forest biome, and their shared understory habitat preference makes it likely that their history was influenced by similar abiotic factors. In addition, pycnonotids are a large component of forest avifaunas; in Gabon, for example, they had the highest avian biomass in one long-term study (Brosset 1990).

Few polytypic genera of forest-dwelling African birds have species whose monophyly can be assumed or whose species limits are considered to be well understood. For example, the more widely occurring bulbul genera *Andropadus* and *Phyllastrephus* cannot be rigorously diagnosed at present nor are their species interrelationships likely to be resolved easily by molecular phylogenetics (Roy 1997). Other genera, like the weavers *Malimbus*, either have not been subjected to recent systematic revision or have forest representatives within the clade with complicated biogeographic patterns outside the lowland biome. Therefore, the bristlebills (*Bleda* Bonaparte 1857) and the bearded bulbuls (*Criniger* Temminck 1820) are ideal candidates for an historical analysis as each has widespread species across the forest biome as well as species of limited distribution that together reveal nested patterns of endemism.

The taxonomic history of *Bleda*, in particular, exemplifies the limitations inherent in the biological species concept and its failure to bring a critical perspective to individuating basal taxonomic units within the African avifauna. That was not the case when these taxa were first described. Although Fjeldsaa (2000:69) has correctly maligned the "typological 'oversplitting' of morphospecies" of the 19th century, it is argued here that the extreme lumping that followed in avian taxonomy in the early 20th century also led to inaccurate results. For example, when Cassin (1856:159) described *Bleda notata*, he recognized the affinity of *B. notata* to the previously described *B. canicapilla*, but commented that *notata* "does not, however, closely resemble that species, nor any other known to us, and is strongly marked by the bright yellow spot in front of the eye, which character distinguishes it at once from *T. eximius* [*Bleda eximia*]." Today this feature might be recognized as an apomorphy that renders *Bleda notata* diagnosibly distinct from its congeners, but Sclater (1930), followed by Rand (1958), Hall and Moreau (1970), and subsequent compendia, treated *notata* as a subspecies of *Bleda eximia* which together with the eastern form *ugandae* have been considered to form a polytypic biological species. As a consequence, *Bleda notata* has not been recognized by two widely used avifaunal lists (Sibley and Monroe 1990, Dowsett and Forbes-Watson 1993.

A more critical approach to the taxonomy of *Bleda* was provided by Chappuis and Erard (1993), who were initially inspired by variation in vocalizations encountered in the field. Those data, as well as morphometric measurements, led them to suggest that *Bleda eximia notata* and *B. e. ugandae* are more closely related to *Bleda canicapilla* than either is to *Bleda eximia eximia* (see Results). Following this revision, the taxon *Bleda notata* has begun to be recognized, in the conservation literature by Stattersfield et al. (1998) and in a regional avifaunal review by Dowsett-Lemaire and Dowsett (2001). The status of the taxon "*ugandae*," the interrelationships proposed by Chappuis and Erard (1993), and the area relationships among phylogenetic species were all explored further in this study. The history of *Bleda* taxonomy demonstrates, however, that much remains to be learned and clarified about the basal evolutionary units of this largely unrevised avifauna, as systematic work for birds from other parts of Africa is beginning to show (e.g. Dowsett-Lemaire and Dowsett, 1988; Roy, 1997; Ryan et al., 1998).

The classification of species in the second genus considered here, *Criniger*, have generally been more stable than have those of *Bleda* (Table 1). Recent classifications (Sibley and Monroe, 1990; Keith et al. 1992, Dowsett and Forbes-Watson 1993) have traditionally treated *C. barbatus* and *chloronotus* as sister species, and *Criniger calurus* is considered a polytypic species with three subspecies (Keith et al. 1992). By contrast, the taxonomic status of *Criniger ndussumensis* has been plagued by two issues: its status as a form distinct from other subspecies of *Criniger calurus*, and its status as a subspecies of, or a full species sister to, *C. olivaceous*. In the mid-20th century ornithologists began struggling with *C. ndussumensis*, either acknowledging it to be a subspecies of *C. calurus* (Chapin, 1953, for whom differences in bill size and plumages with other *calurus* subspecies were not species-level characters), a subspecies of *C. olivaceous* (e.g., based on differences in vocalization from *calurus*, Dowsett and Dowsett-Lemaire 1991), or not a valid taxon at all (based on no perceived ecological differences, Brosset and Erard 1986). Characters (presence of grayish anteocular spot, color of plumage on various body parts) used by White (1956, 1962) to place *ndussumensis* as a subspecies of *Criniger olivaceous* were interpreted by Rand (1958) to indicate species status to *C. ndussumensis*. However, Dowsett and Forbes-Watson (1993) and Dowsett-Lemaire and Dowsett (2001) considered them conspecific but, as discussed further below, this application of a polytypic species concept has potential consequences for the endangered status of the apparently rare, Upper Guinea endemic *Criniger olivaceous* (Collar and Stuart 1985).

In this paper, species limits within *Bleda* and *Criniger* were tested under a phylogenetic species concept (e.g. Davis and Nixon, 1992) using specimen-based plumage character analysis and molecular sequence data; cladistic hypotheses about species interrelationships were then generated from the molecular data. These results, when interpreted phylogenetically and combined with the phylogeographic pattern derived for widespread species, provided a framework for inferring historical biogeographic patterns.

MATERIALS AND METHODS

Materials Examined

Morphological and distributional data for approximately 1400 specimens of species of *Bleda* and *Criniger* were obtained from collections at the American Museum of Natural

History, the Natural History Museum (Tring), the Muséum National d'Histoire Naturelle de Paris, the Musée Royale de l'Afrique Centrale (Tervuren), the National Museum of Natural History and the Philadelphia Academy of Natural Sciences (Table 1). Bills of *Criniger calurus* and *Criniger ndussumensis* were measured with digital calipers; reported here are upper mandible lengths (tip of bill to base of skull) and widths (distance across proximal end of nares). The collecting locality of each specimen examined was entered into a database along with other information available on specimen labels (e.g. collector, soft part data, breeding status). Geographic coordinates were obtained from online (www.br.fgov.be/RESEARCH/DATABASES/GEOGRAPHY, Liège University, courtesy of Alain Empain; NIMA), digital (the Digital Gazetteer of the Vertebrate Section, Royal Museum for Central Africa (D. Meirte and H. Schmitz), and published gazetteers. Coordinates were converted to decimal degrees and specimens for which localities could be determined were mapped in ArcView 3.2 (ESRI, 1999) with the WWF ecoregion shapefile (wwf_eco), and layouts were modified in Adobe Illustrator 8.

Other genera of bulbuls were widely sampled to resolve molecular trees as well as to search for sister taxa to *Bleda* and *Criniger*. Although most classifications have listed *Nicator* adjacent to *Bleda*, morphological and molecular data (Olson 1990, Dowsett et al. 1999) have been interpreted otherwise, and no specific sister taxon for *Criniger* has been identified; therefore many outgroup taxa were initially included.

Mitochondrial DNA sequence data for the entire cytochrome-*b* gene (mt cyt *b*, 1143 base pairs) were obtained for 96 individuals and nuclear data for beta-fibrinogen intron 5 of the beta-fibrinogen gene (nu *fibint*5, 543 bps) were obtained for 24 of those 96 individuals. Primers for the intron were designed by S. Hackett (Field Museum, Chicago; see also Weissbach et al. 1991, Chung et al. 1990). Collecting locales and voucher information pertaining to the 96 individuals sampled for the molecular analysis are presented in Table 2.

Molecular Methods

Tissue or blood genomic DNA was extracted from small pieces of tissue by boiling in 5% (w/v) Chelex (Bio-Rad, Hercules, CA) solution; museum study skin DNA was amplified according to the protocol in Mundy et al. (1997). PCR amplification for both loci followed standard protocols (e.g. Beresford and Cracraft 1999, Lee et al. 1997). For specimens of museum study skins, lab equipment and reagents were irradiated, and "hot-start" PCR reactions was performed exclusively with high annealing temperatures and fragments of approximately 260bp were amplified with primers designed using sequences from conspecific tissue samples (Table 3). Final products were suspended in a Blue Dextran-150 mM EDTA:formamide loading buffer. Samples were run out on 5% Long Ranger (FMC, Philadelphia, PA) gels in TBE buffer in an Applied Biosystems, Inc. (Foster City, CA) 377 automated sequencer.

Systematic Methods

Mitochondrial sequences were assembled and aligned with Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, MI) and verified by eye. The alignment of the cyt *b* sequences was straightforward; the acquisition of multiple overlapping fragments, the agreement between amplifications from multiple fragments and amplifications from entire cyt *b* genes (obtained for at least one exemplar per species) and the maintenance of a reading frame indicated that nuclear copies were not amplified. Although alignment programs (CLUSTAL W, MALIGN) were used to explore alignments for nu beta *fibint*5, the final alignment was assembled by eye to favor internal trailing gaps (see also Prytchiko and Moore 2000 for intron 7). Sequence divergence measures were estimated for pairwise comparisons for mt cyt *b* both as uncorrected (p) distances and under the K2P model as implemented in PAUP*, with base frequencies, transition/transversion substitution rates, and gamma correction value based on observed values. Substitutions patterns were reconstructed with MacClade v. 4.

For phylogenetic analysis, most-parsimonious trees were obtained through heuristic searches with PAUP* (version 4.06b; Swofford, 2001); characters were unordered and equally weighted, and searches were conducted with 20 replicates of random addition sequences with the TBR method. For the larger dataset (96 exemplars), branch support was determined using 10,000 fast-heuristic bootstrap replicates; for all other datasets, branch support was determined with 1,000 bootstrap replicates and decay indices. Command files for decay index calculation were generated in MacClade v. 4 (Maddison and Maddison, 2000). Outgroups were not defined *a priori*.

Alternative hypotheses about relationships among *Bleda* species were tested under MP and ML frameworks, using single exemplars for each taxon plus an outgroup. The Kishino-Hasegawa test was used for MP trees and, following the recommendations of Goldman et al. (2000), the Shimodaira-Hasegawa test for ML trees. ModelTest v3.0 (Posada and Crandall, 1998) was used to determined that the data were best analyzed with a GTR+I+G model. Parameter values from the shortest/most likely tree were fixed for full optimization approximations of the test statistic in the Shimodaira-Hasegawa test as implemented in PAUP* v.4.08b, and the optimization was also conducted by estimating new parameters for each tested topology.

RESULTS

Genetic Diversity Among Bulbuls

Total uncorrected pairwise nucleotide differences for mt cyt b ranged from 0 to 9.9% within *Bleda syndactyla* to 12.8% between *Criniger olivaceous* and *Criniger barbatus* (Table 4). Kimura 2-parameter distances followed the same pattern as the uncorrected values but are slightly higher. Total pairwise differences between species in the focal genera and outgroup taxa (not shown in Table 4) ranged from 18.0% between *Bleda syndactyla* and *Nicator* species, 16.0% between *Nicator* and *Criniger calurus* and between *Bleda* and *Phyllastrephus*, and 12.2% between *Criniger ndussumensis* and *Andropadus gracilis*.

Generic Monophyly and Relationships

Because this study was designed to explore relationships between phylogenetic species as well as geographic genetic structure within widespread species, multiple exemplars were used. However, PAUP* was unable to complete a single heuristic search for the entire data set including all 96 cyt b sequences (460 informative characters) because of the large number of nearly identical haplotypes within several species; therefore the number of rearrangements was limited to 3 million per each of the 20 replicates. The strict consensus of 1368 trees (length 2392, CI 0.323), rooted with species of *Nicator*, is shown in Figure 1 and is compared with the only other available branching diagram, Delacour's (1943) traditional conception of relationships among pycnonotid genera based on external morphology. An analysis with third positions treated as transversions resulted in two islands of identical length (935 steps) with less resolution (not shown) than the cladogram shown in Fig. 1. The monophyly of both *Bleda* and *Criniger* were supported with this larger dataset. However, it should be noted that there is no support for a close relationship between *Nicator* and *Bleda*, contra many classifications from Delacour (1943) through

Monroe and Sibley (1990). Indeed, no clear sister relationships among pycnonotids emerge for either *Bleda* or *Criniger*, and general implications of the cladogram in Fig. 1 for pycnonotid systematics is discussed further below.

Interspecific Relationships

From the 96 sequences, 53 exemplars were retained for species-level tree-searching routines using cyt *b* and 24 sequences were utilized for *fibint5*. In these two analyses, 379 (33%) cyt b characters were informative whereas 81(15%) of the *fibint5* were. Of the 379 informative sites in cyt b, 308 occurred at third positions, followed by 60 at first positions and 11 at third positions; the overall transition: transversion ratio was 3:1. The ts:tv ratio was more balanced for the nuclear intron, with 38 transitions and 34 transversions. As has been shown for other birds with intron 7 (Prytchiko and Moore, 2000), base compositions (Fig. 2) were biased for cyt *b* and were less biased for *fibint5* than for cyt *b* (Fig. 2). The differences in base compositions are reflected in the different frequencies of unambiguous nucleotide changes reported in MacClade v4.0 (Fig 2). The alignment for *fibint5* shows that the two *Pycnonotus* species (*P. barbatus* from Africa and *P. jocosus* from southeast Asia) share a 12 bp deletion and a 21 bp deletion with respect to the other taxa, that both *Nicator* species share a 3 bp insertion, and that *Pycnonotus* + *Nicator* share a 6bp insertion.

The reduced cyt b data set gave two most parsimonious (MP) networks (length 1546, CI 0.426), and *fibint5* gave six most parsimonious networks (length 182, CI 0.857); one phylogram from each dataset is shown on Figure 3 with bootstrap and decay index values. The alternate topologies for both loci simply involve rearrangements of terminal exemplars within clades. The monophyly of the genus *Bleda* is strongly supported at 100% bootstrap support (Fig. 3A). Although the monophyly of the genus *Criniger* is weakly recovered at 62% bootstrap support in the cyt *b* tree (Fig. 3A), this low support appears to be an effect of the large number of exemplars in the tree; and the monophyly of *Criniger* received 86% fast-heuristic bootstrap support with more distantly related exemplars in Figure 1. In an analysis not shown here, 21 unique datasets were constructed varying the representation and number (2 to 16 OTUs) of outgroup taxa listed in Table 2 and bootstrap searches were conducted (1000 replicates of 20 random-addition sequence heuristic MP searches); 20 of these datasets recovered the genus *Criniger* with support values between 100 and 80% (14 of those recovered monophyly between 100-90%) and one set recovered monophyly at 60%. For example, an analysis including all *Criniger* exemplars and *Andropadus gracilis*, *Thescelocichla leucopleura*, *Hypsipetes mcclellandii* and *Nicator chloris* recovers *Criniger* monophyly at 90% bootstrap support, while an analysis with the same taxa except *Nicator chloris* recovers it at only 60% support. No particular pattern of taxon inclusion and generic monophlyly was detected in the trials; as discussed above, there are at present no explicit hypotheses of relationships among species of bulbuls with which to guide the inclusion or exclusion of non-*Criniger* species. These results indicate that the lack of support for a monophyletic *Criniger* here is due to the combined effects of taxon sampling and resultant homoplasy in the mt sequence data. This implies that a more comprehensive, higher-level systematic analysis of the family Pycnonotidae should recover the monophyly of *Criniger* with more confidence.

The nuclear *fibint5* data set recovered the monophyly of *Bleda* and *Criniger*, with 92 and 72% bootstrap support, respectively (Fig.3B). A partition homogeneity test implemented in PAUP* indicated no significant conflict between the nuclear intron and the mitochondrial gene. The combined nuclear and mitochondrial data gave three MP trees (length 1697, CI 0.499). The three topologies differed only in the placement of the *Alophoixus* plus *Pycnonotus* clade, and their strict consensus is shown in Fig. 4 with *Nicator* species used as the root. As in the 96 specimen cyt *b* dataset, no support was evident for any close relationship between *Bleda* and *Nicator*, nor was there any clear signal for sister candidates for either *Criniger* or *Bleda*. With the combined data, the monophyly of *Bleda* received 100% bootstrap support, and monophyly of *Criniger* received 95% bootstrap support.

Species Limits, Distributional Patterns and Relationships within *Bleda*

Species limits and distributions. The phylogenetic species delineated by external morphological character variation are listed in Table 1 along with a brief description of the diagnostic characters used to distinguish each species; distributions of each are shown on Figure 5. Five phylogenetic species were delineated in *Bleda* (*syndactyla, eximia, ugandae, notata* and *canicapilla*), and the cyt *b* data (Fig. 3A) shows strong branch support for each of the five phylogenetic species circumscribed by morphological data: *syndactyla* 96%, *eximia* 100%, *ugandae* 100%, *notata* 100%, and *canicapilla* 100%). Chappuis (1991) described a subspecies of *Bleda canicapilla* from the Senegambia but the status of that taxon was not considered in this study due to a paucity of morphological and molecular exemplars.

Relationships. The relationships proposed by the revision of Chappuis and Erard (1993), based on morphometrics and vocalizations, are shown in Figure 6. The sister relationship between *B. notata* and *B. canicapilla* proposed by Chappuis and Erard (1993) is moderately well recovered at 76% bootstrap support. On the other hand, they included "*ugandae*" as a subspecies of *notata*. The results reported here conflict with their classification in identifying the clade (*ugandae* (*notata, canicapilla*)) with 99% bootstrap support. Also, *Bleda syndactyla* is found here to be sister to the rest of the genus, contra the proposal of Chappuis and Erard (1993), who postulated that *B. syndactyla* and *B. eximia* were sister taxa.

The interspecific relationships among members of the *Bleda eximia* clade were not recovered using the *fibint*5 data set (Figs. 3B): neither *eximia*, *canicapilla*, nor *notata* monophyly is recovered, although the interspecific relationships indicated by the cyt *b* tree: (*eximia* (*ugandae* (*notata*, *canicapilla*))) received 95% bootstrap support in the combined analysis (Fig. 4). The conflict between the mitochondrial and nuclear data is proposed to be the result of incomplete lineage sorting in the relatively slowly evolving nuclear locus.

Five alternative hypotheses of interrelationships among *Bleda* were subjected to Kishino-Hasegawa (K-H) tests and Shimodaira-Hasegawa (S-H) tests. A reduced dataset with a single exemplar from each of the five phylogenetic species plus *Thescelocichla* as an outgroup was constructed in order to conduct thorough likelihood searches and S-H test statistic approximations. Two hypotheses of relationships among species of *Bleda* existed before this molecular analysis was undertaken: the traditional "biological species" classification (e.g. Sclater 1930, Keith et al. 1992) and the revised classification of Chappuis and Erard (1993). The cladistic relationships derived under MP for the phylogenetic species delineated here were taken as a third hypothesis. Since no hierarchial relationship among the three subspecies in the"biological species" classification is explicit in the literature, all three were included in the topology tests. These three hypotheses were tested with MP and ML. Results of the tests are shown in Table 5. The "Phylogenetic Species" (PS) hypothesis was the shortest (402 steps) and most likely (-ln L 3329.641 under full optimization) tree. The hypothesis of Chappuis and Erard (1993) was longer and less likely, and all three biological species trees were still longest and least likely. It is interesting to note, however, that one of the three possible relationships among the three "subspecies" of the *Bleda eximia* group is shorter and more likely than the other two, *i.e.* (*notata* (*eximia*, *ugandae*)) at 421 steps and -ln L 3341.297 versus 425 steps and -ln L

3345.331. The K-H test was applied in addition to the S-H test because although Goldman et al. (2000) have emphasized that the K-H test is inappropriate when comparing topologies obtained from the same dataset, the alternative topologies tested here were not derived from nuclear sequence data. The K-H test significantly rejected all "biological species" and Chappuis and Erard (1993) topologies ($P<0.05$). The S-H test with RELL optimization using fixed model parameters rejected the two longest and least likely "biological species" topologies, and the S-H test with full optimization rejected none of the alternative topologies.

Species Limits, Distributional Patterns and Relationships within *Criniger*

Species limits and distributions. As with *Bleda*, the phylogenetic species delineated by diagnosibly distinct characters for *Criniger* are listed in Table 1; distributions of specimens examined are shown in Figure 5. Five phylogenetic species were delineated in *Criniger* (*barbatus, chloronotus, calurus, olivaceous* and *ndussumensis*). The phylogenetic species of *Criniger* are also recovered at high bootstrap values (*barbatus* 99%, *chloronotus* 100%, *calurus* 100%, *olivaceous* 100%, *ndussumensis* 100%; see Fig. 4).

Specimens of *Criniger ndussumensis* were consistently distinct from *C. olivaceous* by the white throat and chin, and from *C. calurus* by the presence of a pearly grey loral spot. Other differences (such as those noted by White, 1956 and Rand, 1958, e.g. flank and tail color) between these two taxa are not consistent across their zone of sympatry: for example, the upper surface of the tail of *Criniger calurus* varies so that it resembles the rufous tail of *C. ndussumensis* in eastern Lower Guinea. As mentioned above, ornithologists have suggested that the bill sizes of *Criniger calurus* and *C. ndussumensis* differ. Berlioz (1954) surmised that *C. ndussumensis* had a more gracile bill along with larger feet and toes, and Serle (1957) attempted to test his idea by measuring a (pooled) series of bills and tarsus lengths, but found no correlation. Here, bills of *Criniger calurus* and *C. ndussumensis* differed most in upper mandible length and width, with *C. ndussumensis* tending to have longer and narrower bills (Table 5), although this difference was not significant and indeed, is difficult to discern in the field (F. Dowsett-Lemaire, pers. comm.).

Relationships. Nuclear *fibint5* corroborates the interspecific relationships within *Criniger* shown in the cyt *b* tree ((*barbatus*, *chloronotus*) (*calurus* (*olivaceous*, *ndussumensis*))) (Fig. 3). The phylogeny suggested by the separate and combined (Fig. 4) topologies agrees with the delineation of two species groups within *Criniger* by Hall and Moreau (1970): (*C. barbatus, C. chloronotus*) and (*C. calurus, C. olivaceous* and *C. ndussumensis*).

Phylogeography within the Widespread Species *Bleda syndactyla* and *Criniger calurus*

Numerous exemplars of the widespread species *Bleda syndactyla* and *Criniger calurus* were analyzed for intraspecific phylogeographic pattern. A parsimony analysis was undertaken for these samples because the sequences were perceived to be too variable -- every haplotype was unique -- to make efficient use of population-level methods designed for relatively invariant loci. For *B. syndactyla* 162 positions (14%) were variable in 1143 bps cyt b for 26 specimens, and a heuristic search yielded 656 MP networks (length 316, CI 0.623), one of which is shown in Figure 7. The topologies differed in arrangements of terminals within the four main clades in the illustrated network. Three of these clades received fairly good bootstrap support: specimens from Upper Guinea grouped at 100% as did specimens from the central Congolian region. A group of specimens from the eastern Congolian region received 87% bootstrap support. Less well supported (70%) was a clade comprising specimens from Nigeria and western Cameroon, and the relationship of all four clades to each other was not well supported (57%). These groupings are not supported by known variation in external morphology. Three subspecies are currently recognized by Keith et al. (1992), distinguished by relative intensity of pigmentation on the tail and underparts. These characters were too difficult to determine independently and repeatedly in this study, despite study of nearly 500 specimens; in any event, the lineages discovered do not correspond with the geographic ranges ascribed to the subspecies. The phylogeographic pattern displayed by the *Bleda syndactyla* exemplars is complicated: it does not correspond clearly with known geographical features in the Guineo-Congolian biome, and the variation in branch lengths as well as the multiple lineages present in the Congo basin suggest that more than one genealogical pattern is influencing the results.

By contrast, the cyt *b* dataset for 10 *Criniger calurus* specimens with 103 (9%) informative characters resulted in only two MP networks (length 164, CI 0.878), one of which is shown in Figure 7. An Upper Guinea lineage is recovered with 100% bootstrap support, but the relationships among the Lower Guinea exemplars are also complicated, although all three lineages received 100% support. One specimen collected in the southwestern Central African Republic grouped with specimens from southwest Cameroon and Gabon, while another exemplar from the same locality in the Central African Republic grouped with specimens from the Congo basin, and specimens from the eastern Congolian region formed a unique lineage. These results suggest that lineage sorting may be incomplete (although other demographic scenarios are possible; Avise 1994). Three subspecies of *Criniger calurus* are currently recognized (Keith et al. 1992), according to pigmentation on the chin and throat. The morphotype "*verrauxi*" has a yellow chin which becomes paler in southwest Nigeria, "*calurus*" in eastern and "*emini*" in western Lower Guinea forests have white chins, and the tails change from olive-green in "*verrauxi*" to reddish-olive in "*emini*." These characters were interpreted to be clinal, and the incomplete lineage sorting in Lower Guinea exemplars supports this interpretation. However, the exclusively yellow chin of Upper Guinea populations combined with the isolation suggested by the molecular data suggest that further research on the genetics, behavior and ecology is warranted to determine the status of those populations.

DISCUSSION

Properties of molecular data

The use of multiple exemplars for examining the boundaries of phylogenetic species provided a satisfactory way to establish reciprocal monophyly with both the mitochondrial (cyt *b*) and nuclear (*fibint5*) loci. In the "no common mechanism" (*sensu* Steel & Penny 2000) model used here, these loci were less informative at recovering intergeneric relationships. The information content of *fibint5* appeared to be greater at higher phylogenetic levels: in addition to the gap regions, there were more unique, unreversed synapomorphies among *Pycnonotus* (9), among *Hypsipetes* and *Pycnonotus* (9), and among *Nicator* species (15) than there were within *Bleda* at the generic (1) and less inclusive levels (5 for *syndactyla*, 4 for the other 4 species), or *Criniger* at the generic (1) or less inclusive levels (5 for *calurus*, 1 for *barbatus* + *chloronotus*, and 2 for *olivaceous* + *ndussumensis*).

The incongruent topologies for cyt *b* and *fibint5* among *Bleda canicapilla* and the phylogenetic species of the *Bleda eximia* group (Fig. 3) are interpreted here as resulting from incomplete lineage sorting. Although past introgressive hybridization may also produce a gene tree that conflicts with another tree (e.g. Avise et al. 1990), the relatively low pairwise distances (Table 4) between *B. notata* and *B. canicapilla* are taken to indicate relatively recent differentiation. The pairwise distances are all higher between sister species of *Criniger*, and the nuclear data recovers the same topology as the mitochondrial data.

The inclusion of numerous exemplars also revealed differences in character changes among closely related species as reconstructed on the parsimony trees. Relatively little change among individuals was apparent for species of *Bleda notata*, *B. canicapilla*, *B. eximia*, and *C. olivaceous* (Fig. 3A), whereas very deep branches were reconstructed among specimens of widespread *B. syndactyla*, widespread *C. calurus*, and Lower Guinean *C. chloronotus*. Whether these patterns indicate different proportional presences of ancestral haplotypes, incomplete lineage sorting, or sampling error may be resolved by further research. However, this complex array of patterns for Guineo-Congolian endemic species could not have been discovered by the use of single specimens to represent named taxa.

Taxonomy of *Bleda* and *Criniger*

Bleda. The delimitation of basal phylogenetic species of *Bleda* and their interrelationships were highly corroborated, despite natural variation in museum specimens and multiple molecular exemplars. The status of *Bleda ugandae* —previously considered to be a subspecies of *B. eximia* or of *B. notata* — was challenged by molecular data and plumage features. For example, the condition of the lores differs between *Bleda notata* and *ugandae*, and the "song/call [of *ugandae* is] quite different" from those of *notata* recordings from Gabon (Keith et al. 1992:351); vocal samples of *ugandae* were not included in Chappuis and Erard (1993). Thus, although some workers might prefer to include *ugandae* with *notata*, "*notata*" would, according to the mt data presented here, become a paraphyletic species. If a paraphyletic species were to be avoided, than *Bleda* "*notata*" would have to include *canicapilla*, which would obscure the interrelationships of these three taxa.

The molecular data did not corroborate the subspecies of *Bleda syndactyla* as circumscribed by Keith et al. (1992) in terms of their assumed geographic distributions.

Instead, a complex situation was revealed by the molecular data (Fig. 7): specimens from Toro Forest in Uganda appear on a branch distinct from those of Mabira Forest in Uganda plus Ituri Forest in the Democratic Republic of Congo. In addition, relatively deep branches were reconstructed for specimens arrayed across the transition between southern Nigeria and the Cameroon-Gabon region. All 26 *Bleda syndactyla* exemplars are characterized by 7 unique, unreversed synapomorphies in the cyt *b* sequence. Within those, the Upper Guinea exemplars (1-4 on Table 2) share 15 synapomorphies, the specimens from Nigeria and Cameroon share three (exemplars 10-14), and the remainder of the Congolian specimens share one. More restricted sets of exemplars and populations are also characterized by small numbers of unique base positions. While further sampling across the range of *Bleda syndactyla* will be necessary to clarify distributional limits, the nature of the mitochondrial sequence differences suggests the possibility that more than one taxon is currently included in *Bleda syndactyla.*

Morphological and behavioral data would be expected to contribute to a clarification of the taxic status of populations in *Bleda syndactyla*, however, to date little is available, largely because none has been compiled in an effort to uncover evolutionary units within *B. syndactyla*. In a morphometric study, Louette (1991:479) found "marked intraspecific geographic variation" in bill sizes between specimens of *B. syndactyla* in the eastern Congolian region and all other Guineo-Congolian samples, and Keith et al. (1992) describe some variations in the calls. It may be that further behavioral and ecological studies will reveal attributes congruent with the cryptic genetic diversity suggested by the results reported here.

Criniger. All five *Criniger* species delineated in this study are also recognized in most current classifications (Keith et al. 1992, Sibley and Monroe, 1993), but Dowsett-

Lemaire and Dowsett (2001) consider *C. olivaceous* conspecific with *ndussumensis* (this has resulted in the inclusion of "*C. olivaceous*" in a northwest Congolian region avifaunal list; Dowsett-Lemaire and Dowsett 2000). Anecdotal estimates of abundances of *C. olivaceous*, however, indicate that it is a much rarer species in the (admittedly fragmented) Upper Guinea forests than is *ndussumensis* in Lower Guinea; partly for this reason, Collar and Stuart (1985) and Stattersfield et al. (1999) consider *C. olivaceous* a threatened taxon.

Another complex molecular pattern is suggested by the widespread *C. calurus*, although fewer samples were available than for the widespread *Bleda syndactyla*. Specimens from the Congolian region do not show pattern (Fig. 7) as do *Bleda syndactyla*, *B. notata* and *B. ugandae*. The gene tree is not congruent with either traditional biogeographic narrative (i.e. *Criniger calurus* populations are not treated as narrow endemics; Diamond and Hamilton 1980), geomorphological features, or variation in plumage characteristics. Three subspecies of *C. calurus* are currently recognized based on variation in tail and chin coloration following an east-to-west trend. Because Upper Guinea "*verrauxi*" has a yellow chin and Congolian "*calurus*" and "*emini*" show clinal variation from whitish-yellow to white chins. *Criniger calurus* exemplars sampled share 15 unreversed synapomorphies in the cyt *b* sequence with respect to their sister taxa *C. olivaceous* and *C. ndussumensis*; the three Upper Guinea samples share 6, and the two eastern Congolian samples (8 & 9, Table 2) share 16. No distribution of unique synapomorphies demarcates the other Congolian samples with these data. Therefore, although it is would be straightforward to interpret the entire system of plumage variation being clinal, both the Upper Guinea and easternmost Congolian lineages appear to be or have been isolated, and require further genetic, morphological, and behavioral research in order to resolve the taxonomic status of populations within *Criniger calurus*.

Phylogenetic Biogeography

In addition to showing the localities of sampled specimens, the points plotted, plus the range of habitat estimated by the ecoregions in which species occur, are taken to represent, at a broad scale, the ranges of species and congruent ranges subsequently interpreted here as historical biogeographic "areas of endemism." The vouchered points (Fig. 5) derive from a large proportion of African material held in European and North American collections and signify the distribution of sampled genetic and species-delimiting diagnostic characters. Of course, each species occurs in other localities, known from both museum collections not consulted as well as from published and unpublished observations (however, non-vouchered ornithological records are usually not informative about diagnostic characters, especially below the "biological species" level at which most surveys are conducted). For example. five of these taxa also occur in forest fragments in Senegal and/or the Gambia (*Bleda canicapilla, B. syndactyla, B. eximia, Criniger olivaceous* and *C. calurus*; Barlow and Wacher, 1997), but specimens for those areas were either not sampled or gazetted and the area not shown on these figures.

The congruent distributions of taxa in this study, as well as other Guineo-Congolian passerines, can used to postulate five areas of endemism: Upper Guinea, Lower Guinea, Guinea, Congolia, West Congolia and East Congolia (Figure 8). Upper Guinea includes the evergreen forests west of the Dahomey Gap, Lower Guinea forests east of the Dahomey Gap to the Victoria Basin forests. Guinea is proposed as a name to include the species that range east of the Dahomey Gap but not east of the Cameroon highlands, and Congolia for those taxa endemic to both East and West Congolia.

These areas differ in shape from previous treatments of this avifauna. Both the avifaunal zones of Crowe and Crowe (1982; see also Williams et al.,1998) and the zones of endemism in Dowsett-Lemaire and Dowsett (2001) delineated unique, non-overlapping areas. These and other workers (e.g. Louette 1990, 1992) have focused on the nature of the more obscure barriers and have also discussed shared elements of species ranges but do not specify groups of related taxa or consider similar ranges as hypotheses of shared phylogenetic pattern. Here, it is suggested that the recognition of a series of nested areas identifies suitable hypothetical entities for consideration as "areas" within a phylogenetic biogeographic context. The recognition of "Guinea" as an area of endemism is thus a preliminary hypothesis of shared biogeographic history among the endemics, which is predicted to differ in phylogeographic or temporal pattern from species endemic to "Upper Guinea." A comparison of phylogenetic patterns for endemic species and their sister groups, and the possible resultant detection of sequential vicariant events, may clarify the identity of discrete geomorphological or climatic historical factors that have contributed to the current biome.

The delineation of the Upper Guinea area of endemism is straightforward, limited in the east by a large break in the lowland forest, the Dahomey Gap. This boundary has long been recognized by ornithologists (Chapin 1932), and Dowsett-Lemaire and Dowsett (2001) and Louette (1992) provide recent reviews of the avifauna affected by it. Within the remaining portion of the forest block, the boundaries of two areas (Guinea and between eastern and western Congolia) are more difficult to correlate with present-day geographic factors. Marchant (1954) failed to locate specific geographic factors responsible for ranges delimited east of the Dahomey Gap in southern Nigeria, but some of the ambiguous nature of this boundary may be due to insufficient knowledge of species occurrences, and range extensions are still being recorded (Elgood 1992). Dowsett-Lemaire and Dowsett (2001) also discuss the particularly subjective nature of both the Guinean eastern barrier and the boundary between the western and eastern Congolian areas. The interpretation of congruent ranges in this paper differs from Dowsett-Lemaire and Dowsett (2001) in shifting the boundary of the northwest Congolian area further west. However, the boundary postulated here is provisional; Dowsett-Lemaire and Dowsett (2001) show that ongoing fieldwork has extended the known ranges of species thought to be restricted to a purported refuge including the coastal forests of Cameroon and Gabon, and further work may resolve the identify of one or more barriers in this region.

This study also differs from prior treatments of distributional patterns in the Guineo-Congolian avifauna by allowing areas to be redundant or nested. These areas are preliminary hypotheses of shared phylogenetic pattern among the component avifauna. When corroborated by systematic analysis of many groups, this application of vicariance biogeography (Platnick and Nelson 1978, Humphries and Parenti 1999) may facilitate the discovery of the multiple vicariant events that are sequential in time and might be identified to different nodes.

Within this biogeographic context, the area occupied by *Bleda canicapilla* and *Criniger barbatus* —"Guinea"— may be homologous, as may be the "Upper Guinea" of *Bleda eximia* and *Criniger olivaceous*. However, the area trees show that the areas relationships differ — for example, the sister area to Guinea in the *Criniger* clade is Congolia, while the sister area in the *Bleda* clade is western Congolia. The sister relationships of "Upper Guinea" also differ, in one case comprising a clade of species of *Bleda* as opposed to the more straightforward Lower Guinea relationship demonstrated by *Criniger*. Thus, although both the Dahomey Gap and a broad barrier west of the Niger River correspond to vicariant nodes between these species of *Bleda* and *Criniger*, it is not clear that these nodes are homologous in an historical sense. The molecular data might be used to arbitrate this question: the mean uncorrected p distances between *Criniger olivaceous/ndussumensis* and *Bleda eximia/(ugandae, notata, canicapilla)* are 6.1 and 9.7%, respectively, suggesting that, under the assumption of a common rate of molecular evolution within and between lineages, the times of divergences differ. Similarly, the mean uncorrected distances among *Bleda canicapilla/notata* and *Criniger barbatus/chloronotus* are 6.4 and 8.3%, respectively, again arguing against a single common vicariant event.

The pairwise differences also argue against the Pleistocene refuge hypothesis, if a molecular clock is assumed. The 2.0% per million years calibration value of Shields and Wilson (1987) puts the divergence between *Bleda notata* and *B. canicapilla* at approximately 3 million years ago, and the Kimura 2-parameter calibration value of 1.6% per million years derived by Fleisher et al. 1998 dates that divergence to roughly 6.6 million years ago (applying a gamma correction, with an empirically derived alpha value of 0.205 for the taxa in this study, adds two to seven percent to the K2P differences, making the ages of divergences even older). Again, if a molecular clock is assumed, and if demographic processes have not biased the pairwise differences (Felsenstein, 1982), then most of the divergences between the species of *Bleda* and *Criniger* would have had to occur in the late Miocene.

Although the Dahomey Gap has long been recognized as a vicariant barrier, there has been little discussion about its age. It is generally treated as a Recent (e.g. Maley, 2001) phenomenon that was subject to Pleistocene climatic vicissitudes; some have proposed that it is maintained by anthropogenic factors (Robbins, 1978) while others assign it to local wind and marine conditions (Hayward and Oguntoyinbo, 1987). The association of this barrier with nodes at different depths in the molecular trees suggest that the Gap may be associated with vicariant events of different ages. In certain Upper Guinea forests, 6 of the 10 species studied are sympatric or nearly so (e.g. Allport et al., 1989), and combined with the presence of deep, possibly long isolated lineages evidenced by the widespread species, the number of nodes (or phylogenetic diversity, Faith 1992) of some Upper Guinea forests is quite high. The Upper Guinea avifauna does have a number of endemics (22 under the polytypic species concept of Dowsett-Lemaire and Dowsett, 2001), and if the basal position of several Upper Guinea taxa described in this paper and in Beresford and Cracraft (1999) are interpreted to be older in time, then these data indicate that some historical relationships of the highly fragmented and vulnerable Upper Guinea forests may be found in the Miocene. The end-Miocene forest is reconstructed (Axelrod and Raven, 1978) as having a more northerly distribution than at present, and it is possible that connections to the Asian fauna, such as may be clarified by a more comprehensive systematic analysis of the Pycnonotidae, may contain the key for understanding the area relationships of many Upper Guinea birds.

As discussed above, the eastern limit of the west Congolian avifauna is not sharply demarcated by many congruent ranges at present. This broad boundary appears to correspond to a relatively marked zone of turnover in Williams et al. (1999) and could encompass two separate barriers, possibly associated with the phytogeography and topography of the Ogooué headwaters as well as the Congo-Ubangi watershed. Alternatively, formation of a refuge by past climatic changes may have caused the perceived vicariance east of the coastal rainforests. Recent stratigraphic and seismic reconstruction studies have proposed relatively rapid uplift of the Congo margin in the Miocene (Lavier et al. 2001), which affected the development of the Congo river drainage system; this in turn was followed by the establishment of the cold Bengeula current Uenzelmann-Neben et al. (1997) which continues to affect the climate of the western forests (Hayward and

Oguntoyinbo, 1987). The single or combined influences of these events may have shaped the diversification of forest taxa.

Should the basal position of Upper Guinea endemics prove to be a more general pattern shared by other species, few explanatory hypothesis are presently available besides cyclical Plio-Pleistocene changes in climate and vegetation cover. The current Upper Guinea landscape is characterized by several features that are thought to promote speciation, specifically, topographical heterogeneity, an extensive coast with complex offshore weather patterns, and a highly fragmented forest habitat that is home to the species in this study. However, a vicariant history of the African lowland forest has not been explored in terms of regional, as opposed to global, climate affects; yet the late Neogene tectonic and volcanic activity (Partridge et al., 1995), the Tibetan plateau uplift, the closing of the Indonesian seaway (Cane and Molnar, 2001) all have potential to have influenced the distribution of forest. Discriminating among these factors will be challenging, however, since they all fall within the realm of 4 to 2 million years ago, as does the major shift in the global climate regime (Denton, 1999).

The general impression obtained from the literature on patterns of species richness in African lowland forests is that the central Congolian region, or Congo basin, is depauperate (Diamond and Hamilton, 1980; Crowe and Crowe, 1982; Prigogine, 1987). Although sampling effects have been recognized (Louette, 1984; Beresford and Cracraft, 1999; Dowsett-Lemaire and Dowsett, 2001), this pattern continues to be recovered (Williams et al., 1999; Brooks et al., 2001). Neither the refuge model (Diamond and Hamilton, 1980) nor the he accumulation model (Fjeldsaa and Lovett, 1997) make explicit predictions about patterns of genetic diversity among populations or species within Congolia. This study has provided the first description of some such patterns, and this molecular survey indicates that a variety of demographic histories are present in the central Congolian region. The presence of two sympatric lineages of *Criniger calurus* with low pairwise distances in the northwestern Congolian region, the differentiation between *Bleda notata* and *Bleda ugandae*, and the three lineages of *Bleda syndactyla* in Lower Guinea suggest higher genetic diversity than could have been anticipated by scenarios based on refugial dynamics.

In the light of these observations, it seems reasonable to conclude that both the distributions and the taxonomy of Guineo-Congolian birds is poorly resolved at present. As many studies of other African bird species have recently shown (e.g., raptors: Clark 1999; larks: Ryan and Bloomer 1999, Ryan et al. 1998; bustards: Crowe et al., 1994), species require modern revision in order to delineate basal evolutionary units. These findings also carry implications for the accuracy of applications of conservation science. First of all, although current taxonomic practice does not recognize many vicars within the Congolian region, cases of cryptic genetic variation such as that seen in *Bleda syndactyla* may be numerous. Secondly, Fjeldsaa (2001) compared the effects of using genera, biological species and subspecies on complementarity approaches and found the more finely delineated subspecies performed best at delineated priority areas, especially in terms of range-size rarity. Finally, this study suggests that much of the lowland forest avifauna may have resulted from evolutionary processes at a larger amplitude than those promoting Plio- Pleistocene speciation in non-lowland landscapes and, ideally, should also be of conservation concern (Vane-Wright et al., 1991).

A geologically driven model of vicariant, allopatric speciation (e.g. Cracraft 1985) can be treated as the null model against which adaptive process-based models might be compared, and at the same time inferences about evolutionary processes within the

Guineo-Congolian biome that are presently based on relatively few detailed systematic studies (see Moritz et al. 2000) will be significantly improved once additional revisionary species-level studies are undertaken. Although the role of refuges may be ineluctable to interspecific biogeographic analyses (Lynch 1988; Patton and da Silva 1998), intraspecific molecular analyses may be brought to bear on demographic historical patterns (e.g. Crandall and Templeton 1996) and reveal the shared histories that refuge scenarios dictate. However, the "test of time" that the refuge hypothesis is claimed to have withstood (Meadows 1996) has come from neither modern systematic revision nor the application of phylogenetic biogeographic analysis. Indeed, neither the refuge hypothesis nor the accumulation model formulate explanations for congruent elements among species endemic to the Guineo-Congolian biome. A new model for the evolution of the lowland rainforest avifauna based on a rigorous analysis of the distributions, phylogenetic and area relationships of groups of related species may one day be articulated.

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Table 1. Summary of morphological and molecular sampling in relation to classification status of focal species.

				Taxonomic status	
Phylogenetic species	**Characters used**	**Morphological specimens**	**Molecular specimens**	Traditional classification (Keith et al. 1992, Rand 1958)	Alternative classifications: Chappuis and Erard 1993
Bleda syndactyla (Swainson 1837)	Red tail	499	26	*Bleda syndactyla syndactyla* *Bleda syndactyla woosnami*	*Bleda syndactyla syndactyla* *Bleda syndactyla woosnami* *Bleda syndactyla multicolor* *Bleda syndactyla nandensis*
Bleda canicapilla (Hartlaub 1854)	Grey head	84	5	*Bleda canicapillla*	*Bleda canicapilla*
Bleda eximia (Hartlaub 1855)	Green head, large yellow postocular spot	26	3	*Bleda eximia eximia*	*Bleda eximia*
Bleda notata (Cassin 1856)	Loral feathers yellow at base, small pale yellow postocular spot	109	6	*Bleda eximia notata*	*Bleda notata notata*
Bleda ugandae (van Someren 1915)	Loral feathers olive distally washed yellow-green	236	10	*Bleda eximia ugandae*	*Bleda notata ugandae*
					Dowsett and Forbes Watson 1993
Criniger barbatus Temminck 1821	Yellow chin	86	4		
Criniger chloronotus Cassin 1860	White chin	93	4		
Criniger calurus (Cassin 1857)	Dull brick forehead and crown, bill size	255	5		
Criniger olivaceous (Swainson 1837)	Yellow chin & throat	23	3		*Criniger olivaceous olivaceous*
Criniger ndussumensis Reichenow 1904	Grey lores, ash brown forehead tinged olive, white chin and throat, bill size	51	10		*Criniger olivaceous ndussumensis*

Table 2. Specimens used for molecular analysis. Source of DNA indicated as tissue (ts), blood (bl) or museum study skins (sk). Localities given in degrees minutes

Taxon	Specimen	Source	Institution	Accession	Country	N/-S	E/-W
Bleda eximia	1	ts	AMNH	827541	Liberia	7 35	-8 28
	2	ts	AMNH	827543	Liberia	7 35	-8 28
	3	ts	AMNH	18908	Liberia	7 35	-8 28
Bleda notata	1	ts	AMNH	831837	C A R	2 59	16 14
	2	ts	AMNH	831836	C A R	2 59	16 14
	3	ts	AMNH	24729	C A R	2 59	16 14
	4	ts	AMNH	24853	C A R	2 55	16 15
	5	ts	MNHN	not vouchered	Cameroon	5 21	11 14
	6	ts	MNHN	not vouchered	Cameroon	5 21	11 14
Bleda ugandae	1	ts	FMNH	357226	D R C	1 26	28 36
	2	ts	FMNH	357229	D R C	1 26	28 36
	3	ts	FMNH	357228	D R C	1 26	28 36
	4	ts	FMNH	357227	D R C	1 26	28 36
	5	sk	MRAC	84237	D R C	2 57	19 48
	6	sk	MRAC	84892	D R C	2 57	19 48
	7	sk	AMNH	296943	D R C	-1 07	17 11
	8	sk	AMNH	296945	D R C	-1 07	17 11
	9	sk	MRAC	74610	D R C	1 13	19 49
	10	sk	MRAC	74871	D R C	1 13	19 49
Bleda canicapilla	1	ts	AMNH	827547	Liberia	7 35	-8 28
	2	ts	AMNH	18917	Liberia	7 35	8 28
	3	ts	AMNH	827550	Liberia	7 35	8 28
	4	ts	AMNH	827555	Liberia	7 35	-8 28
	5	bl	ZMUC	DMC20	Ghana	5 2	-1 22
Bleda syndactyla	1	ts	AMNH	827534	Liberia	7 35	-8 28
	2	ts	AMNH	827535	Liberia	7 35	-8 28
	3	ts	AMNH	827534	Liberia	7 35	-8 28
	4	ts	AMNH	18892	Liberia	7 35	8 28
	5	ts	AMNH	831831	C A R	2 59	16 14
	6	ts	AMNH	831833	C A R	2 59	16 14
	7	ts	AMNH	831832	C A R	2 59	16 14
	8	ts	AMNH	24851	C A R	2 55	16 15
	9	ts	AMNH	832099	C A R	2 55	16 15
	10	ts	MNHN	not vouchered	Cameroon	5 21	11 14
	11	ts	MNHN	not vouchered	Cameroon	5 21	11 14
	12	ts	MNHN	not vouchered	Cameroon	3 2	12 45
	13	bl	UMMZ	A876	Nigeria	6 21	9 07
	14	bl	ZMUC	3196	Uganda	0 12	29 43
	15	bl	ZMUC	3216	Uganda	0 12	29 43
	16	ts	FMNH	384952	Uganda	-1 17	29 41
	17	ts	FMNH	384951	Uganda	1 17	29 41
	18	ts	FMNH	357222	D R C	1 26	28 36
	19	ts	FMNH	357217	D R C	1 26	28 36
	20	ts	FMNH	357219	D R C	1 26	28 36
	21	sk	AMNH	296953	D R C	-1 07	17 11
	22	sk	AMNH	296949	D R C	-1 07	17 11
	23	sk	MRAC	74872	D R C	1 13	19 49
	24	sk	MRAC	74488	D R C	1 13	19 49
	25	sk	MRAC	67611	D R C	0 46	22 49
	26	sk	MRAC	66541	D R C	0 46	22 49
Criniger barbatus	1	bl	ZMUC	DCM21	Ghana	5 2	-1 22
	2	ts	AMNH	827566	Liberia	7 35	-8 28
	3	ts	AMNH	827561	Liberia	7 35	-8 28
	4	ts	AMNH	827567	Liberia	7 35	8 28
Criniger calurus	1	sk	AMNH	565881	Gabon	-1 08	10
	2	ts	AMNH	24860	C A R	2 55	16 15
	3	ts	AMNH	831828	C A R	2 59	16 14
	4	ts	AMNH	831829	C A R	2 59	16 14
	5	ts	AMNH	832104	C A R	2 55	16 15
	6	sk	MRAC	74862	D R C	1 13	19 49
	7	sk	MRAC	74880	D R C	1 13	19 49
	8	ts	FMNH	357240	D R C	1 26	28 36
	9	ts	FMNH	357238	D R C	1 26	28 36
	10	ts	AMNH	18928	Liberia	7 35	-8 28
	11	sk	AMNH	827571	Liberia	7 35	-8 28
	12	sk	AMNH	825457	Liberia	5 32	-8 14
Criniger chloronotus	1	bl	UMMZ	A875	Nigeria	6 21	9 07
	2	ts	FMNH	357232	D R C	1 26	28 36
	3	ts	FMNH	357233	D R C	1 26	28 36
	4	sk	MRAC	81025	D R C	1 14	19 48
	5	sk	MRAC	81198	D R C	2 14	20 48
Criniger ndussumensis	1	ts	AMNH	831827	C A R	2 59	16 14
	2	ts	AMNH	832103	C A R	2 55	16 15
	3	ts	MNHN	not vouchered	Cameroon	2 4	13 06
	4	ts	FMNH	357235	D R C	1 26	28 36
Criniger olivaceus	1	ts	AMNH	827574	Liberia	7 35	-8 28
	2	ts	AMNH	827573	Liberia	7 35	8 28
	3	ts	AMNH	827575	Liberia	7 35	-8 28
Outgroups							
Andropadus curvirostris		ts	AMNH	832077	C A R		
Andropadus gracilis	1	ts	AMNH	831826	C A R		
Andropadus gracilis	2	ts	AMNH	832075	C A R		
Andropadus latirostris	1	ts	AMNH	24835	C A R		
Andropadus latirostris	2	ts	AMNH	832080	C A R		
Andropadus virens		ts	AMNH	831822	C A R		
Andropadus gracilirostris	1	ts	AMNH	832081	C A R		
Andropadus gracilirostris	2	ts	AMNH	24841	C A R		
Hypsipetes mcclellandii		ts	AMNH	833142	Viet Nam		
Nicator chloris		ts	AMNH	832108	C A R		
Nicator vireo		ts	AMNH	832107	C A R		
Phyllastrephus xavieri		ts	AMNH	832093	C A R		
Phyllastrephus icterinus		ts	AMNH	832088	C A R		
Pycnonotus barbatus		ts	AMNH	24822	C A R		
Pycnonotus jocosus		ts	AMNH	833139	Viet Nam		
Thescelocichla leucopleura	1	ts	AMNH	24844	C A R		
Thescelocichla leucopleura	2	ts	AMNH	24845	C A R		
Alophoixus pallidus		ts	AMNH	prs2198	Viet Nam		

Table 3. Primer Information. Primer numbers for mt cyt *b* 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. Nucelar beta-*fibrinogen* intron 5 primers provided by S. Hackett.

Cyt b

L14578 (ND5)	5-ctaggaatcatcctagccctaga-3	H15104	5-tgtgtcagccatattggacgtctcggc-3
L15068	5-actagcaatacactacacagcaga-3	H15134	5-ccgcaacctccacgccaatggagcctcct-3
L15236	5-ttcctatacaaagaaacctgaaa-3	H15478	5-gtccacctcaccctcctacacga-3
L15320	5-tgaggacaaatatcattctgagg-3	H15505	5-tgcatgaattcctattgggttgtttgatcc-3
L15413	5-ggattctcagtagacaaccc-3	H15710	5-atagcgtaggcgaataggaagtatc-3
L15510	5-ttcgcctccgtctcacatatctgccgaga-3	H15742	5-tccatcccaaacaaacttggagg-3
L15656	5-ccagacctcctaggagacccaga-3	H16065	5-aacgcagtcatctccggtttacaagac-3
L15725	5-gaatgatacttcctattcgc-3		
L15872	5-ccactgtcacaaatcctattctg		
L15895	5-gtcctaacctgagtaggaacca		

Fibint-5

F5 (sense)	5-cgccatacagagtatactgtgacat-3
F6 (antisense)	5-gccatcctggcgattctgaa-3

Table 4. Pairwise sequence divergeces: First data column, uncorrected p distances within taxa, followed by (above diagonal) total uncorrected p distaces and (below diagonal) Kimura 2 parameter p distances.

Taxon	**N**	**mean (range) within**	*eximia*	*canicapilla*	*notata*	*ugandae*	*syndactyla*
Bleda eximia	3	0.009 (0.002-0.014)		0.094	0.099	0.099	0.112
Bleda canicapilla	5	0.004 (0-0.009)	0.102		0.061	0.070	0.116
Bleda notata	6	0.001 (0-0.003)	0.107	0.065	.	0.070	0.112
Bleda ugandae	10	0.017 (0-0.029)	0.109	0.074	0.075	.	0.112
Bleda syndactyla	26	0.053 (0.002-0.099)	0.121	0.129	0.124	0.125	
			barbatus	*chloronotus*	*olivaceous*	*ndussumensis*	*calurus*
Criniger barbatus	4	0.046 (0.003-0.068)		0.083	0.128	0.115	0.119
Criniger chloronotus	4	0.023 (0.005-0.028)	0.092		0.121	0.108	0.118
Criniger olivaceous	3	0.003 (0.002-0.004)	0.142	0.135		0.061	0.097
Criniger ndussumensis	5	0.006 (0.003-0.011)	0.127	0.120	0.067		0.087
Criniger calurus	10	0.037 (0.002-0.060)	0.133	0.131	0.106	0.096	

Table 5. Results of topology tests. Kishingo-Hasegawa (K-H) test results conducted with parsimony optimality criterion. Shimodaira-Hasegawa (S-H) tests with model parameters estimated on each tree for RELL test statistic approximation and fixed for full approximation. Asterisked values indicate tree scores are significantly different from the first topology (at $P<0.05$).

Topology		**K-H**	**S-H (RELL)**	**S-H (Full)**
Phylogenetic species	*(syndactyla (eximia (ugandae (notata, canicapilla))))*	402	3329.641	3331.544
Chappuis and Erard (1993)	*(syndactyla, eximia) ((notata, ugandae) canicapilla)*	420*	3339.462	3340.381
Biological species	*(syndactyla (canicapilla (eximia (notata, ugandae)))*	425*	3344.208*	3345.331
	(syndactyla (canicapilla (ugandae (notata, eximia)))	425*	3344.368*	3345.506
	(syndactyla (canicapilla (notata (eximia, ugandae)))	421*	3339.746	3341.297

Table 6. Measurements (in milimeters) of upper mandibles of two *Criniger* species.

Taxon	N	Upper mandible length		Upper mandible width	
		Mean	Range	Mean	Range
ndussumensis	23	18.09	17.73-20.48	5.93	5.21-6.95
calurus	43	20.46	17.35-22.11	6.65	5.75-7.53

Note: Results were not significant under an F test or a t test assuming equal or unequal variances.

Figure captions

Figure 1. Left: Overview of morphological diversity in bulbuls (Pycnonotidae) according to Delacour (1943:19). Right: Strict consensus of 1368 MP trees (length 2392, CI 0.323) for 96 individuals sampled for complete mt cyt *b*; nodes subtending species where N>1 exemplars (indicated in parentheses) removed from topology (rooted with *Nicator* species). Fast-heuristic bootstrap (10,000 replicates) values shown for nodes supported above 70%. Based on these results, some outgroup taxa were removed from further analyses. Taxa subsequently sampled for nu*fibin5* marked with asterisk.

Figure 2. Characteristics of loci sampled. Above, percent base composition (left, cyt-b; right, beta*fibint5*). Below, frequency (%) unambiguous changes mapped over phylograms in Figure 3.

Figure 3. Representative phylograms with terminals labelled according to Table 1. A: one of two MPTs (length 1546) for mt cyt *b* data, rooted with *Pycnonotus*. B:one of six MPTs (length 182) for nu*fibint5* data, rooted with *Nicator*. Bootstrap values (1000 reps) shown above, decay indices shown below nodes recovered on bootstrap majority-rule consensus tree (* not recovered); values not shown for nodes within phylogenetic species.

Figure 4. Strict consensus of 3 MP networks (length 1697, CI 0.499) for 1686 mt cyt *b* and nu *fibint5* characters, midpoint rooted. Bootstrap values (1000 reps) shown above, decay indices shown below nodes recovered on bootstrap majority-rule consensus tree (* not recovered); values not shown for nodes within phylogenetic species.

Figure 5. Distributions of morphological specimens (solid) examined to determine diagnosibly distinct units and molecular samples (hollow). Shaded areas include Guineo-Congolian forest ecoregions on the WWF Ecoregions map (Underwood et al. 1998) distributed with ArcView 3.2 (ESRI 1999).

Figure 6. Revised classification of the genus *Bleda*: topology, sonograms and morphological characters reproduced from Chappuis and Erard, 1993.

Figure 7. Unrooted networks and distributions of morphological specimens of widespread taxa. Branch lengths >10 and bootstrap (1000 reps) support shown. Hollow symbols represent molecular sample localities; asterisked exemplars obtained from museum study skins. Left, *Bleda syndactyla*: one of 676 MP networks (length 316, CI 0.623). Right, *Criniger calurus*: one of two MP networks (length 164, CI 0.878). Arrows show outgroup placement of congeneric taxa.

Figure 8. Areas of endemism and area trees inferred from molecular systematics and distributions of phylogenetic species.

Figure 1

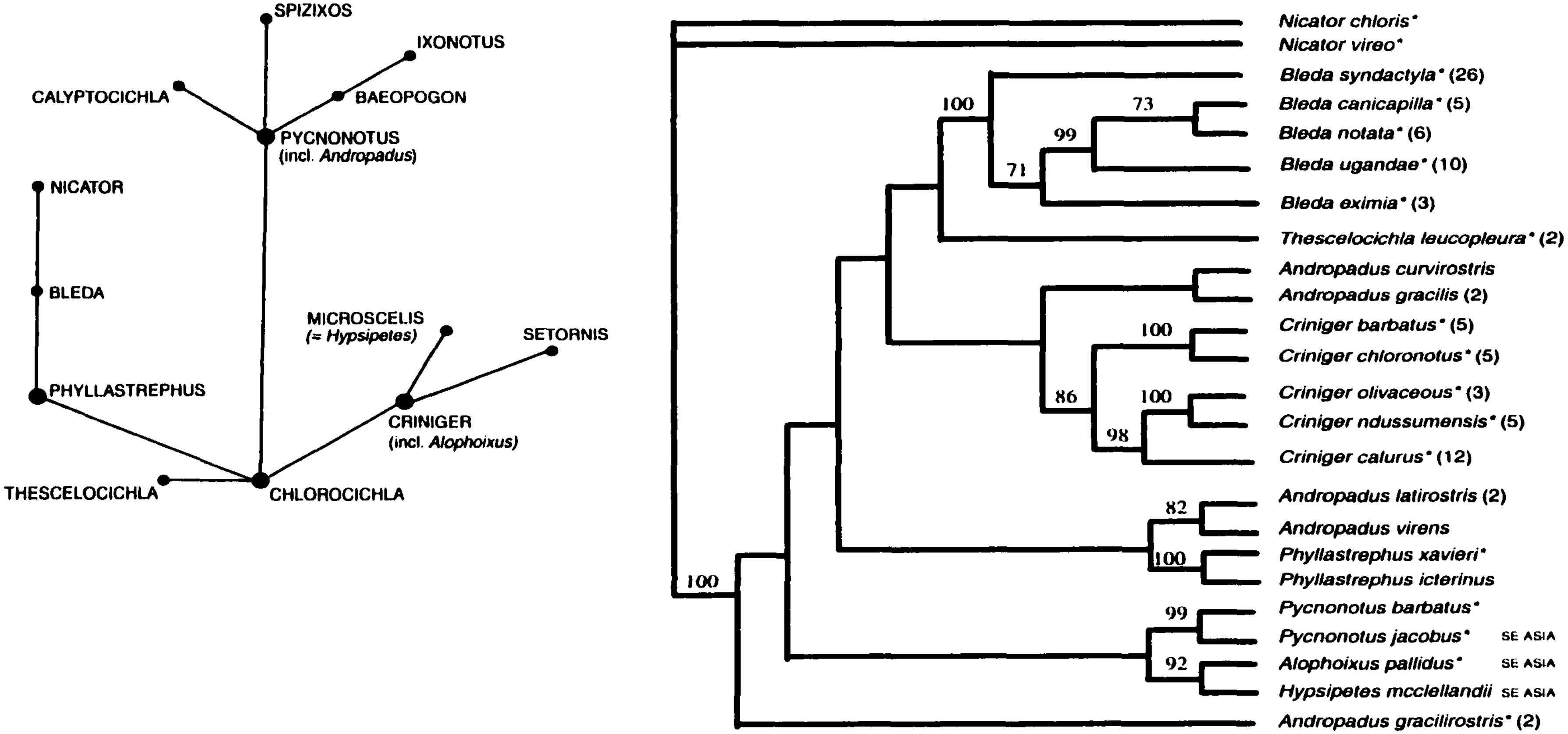

SPIZIXOS
IXONOTUS
CALYPTOCICHLA
BAEOPOGON
PYCNONOTUS (incl. *Andropadus*)
NICATOR
BLEDA
MICROSCELIS (= *Hypsipetes*)
SETORNIS
PHYLLASTREPHUS
CRINIGER (incl. *Alophoixus*)
THESCELOCICHLA
CHLOROCICHLA
*Nicator chloris**
*Nicator vireo**
*Bleda syndactyla** (26)
*Bleda canicapilla** (5)
*Bleda notata** (6)
*Bleda ugandae** (10)
*Bleda eximia** (3)
*Thescelocichla leucopleura** (2)
Andropadus curvirostris
Andropadus gracilis (2)
*Criniger barbatus** (5)
*Criniger chloronotus** (5)
*Criniger olivaceous** (3)
*Criniger ndussumensis** (5)
*Criniger calurus** (12)
Andropadus latirostris (2)
Andropadus virens
*Phyllastrephus xavieri**
Phyllastrephus icterinus
*Pycnonotus barbatus**
*Pycnonotus jacobus** SE ASIA
*Alophoixus pallidus** SE ASIA
Hypsipetes mcclellandii SE ASIA
*Andropadus gracilirostris** (2)
100
73
99
71
100
86
100
98
82
100
100
99
92

Figure 2

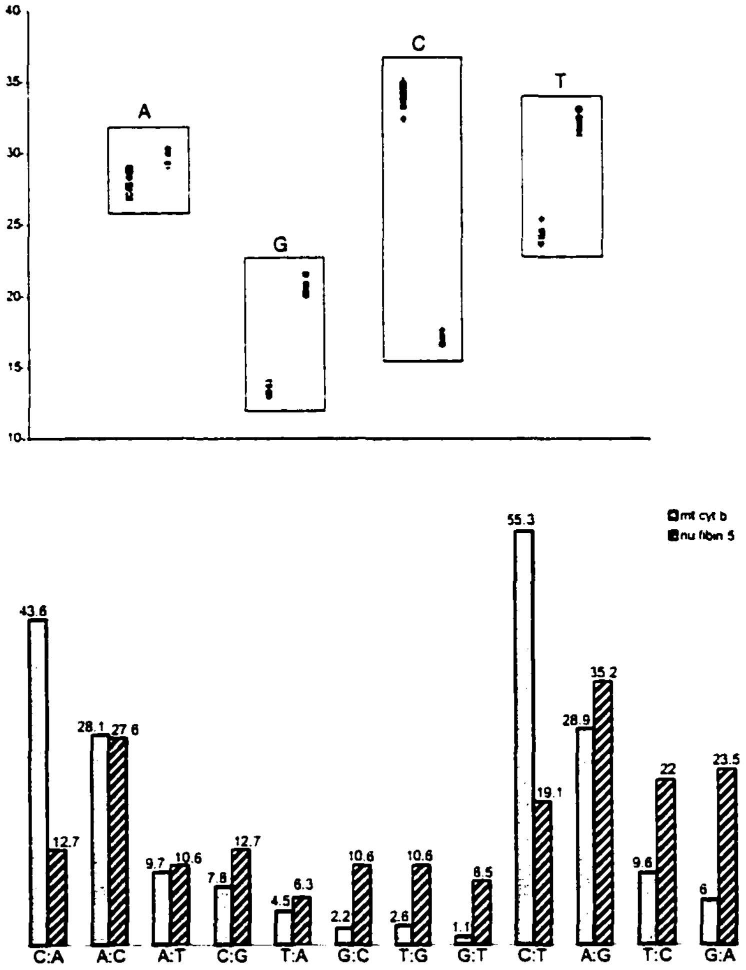

40
35
30
25
20
15
10
A
G
C
T
□ mt cyt b
▨ nu fibin 5
43.6
12.7
28.1
27.6
9.7
10.6
7.8
12.7
4.5
6.3
2.2
10.6
2.6
10.6
1.1
8.5
55.3
19.1
28.9
35.2
9.6
22
6
23.5
C:A
A:C
A:T
C:G
T:A
G:C
T:G
G:T
C:T
A:G
T:C
G:A

Fig 3

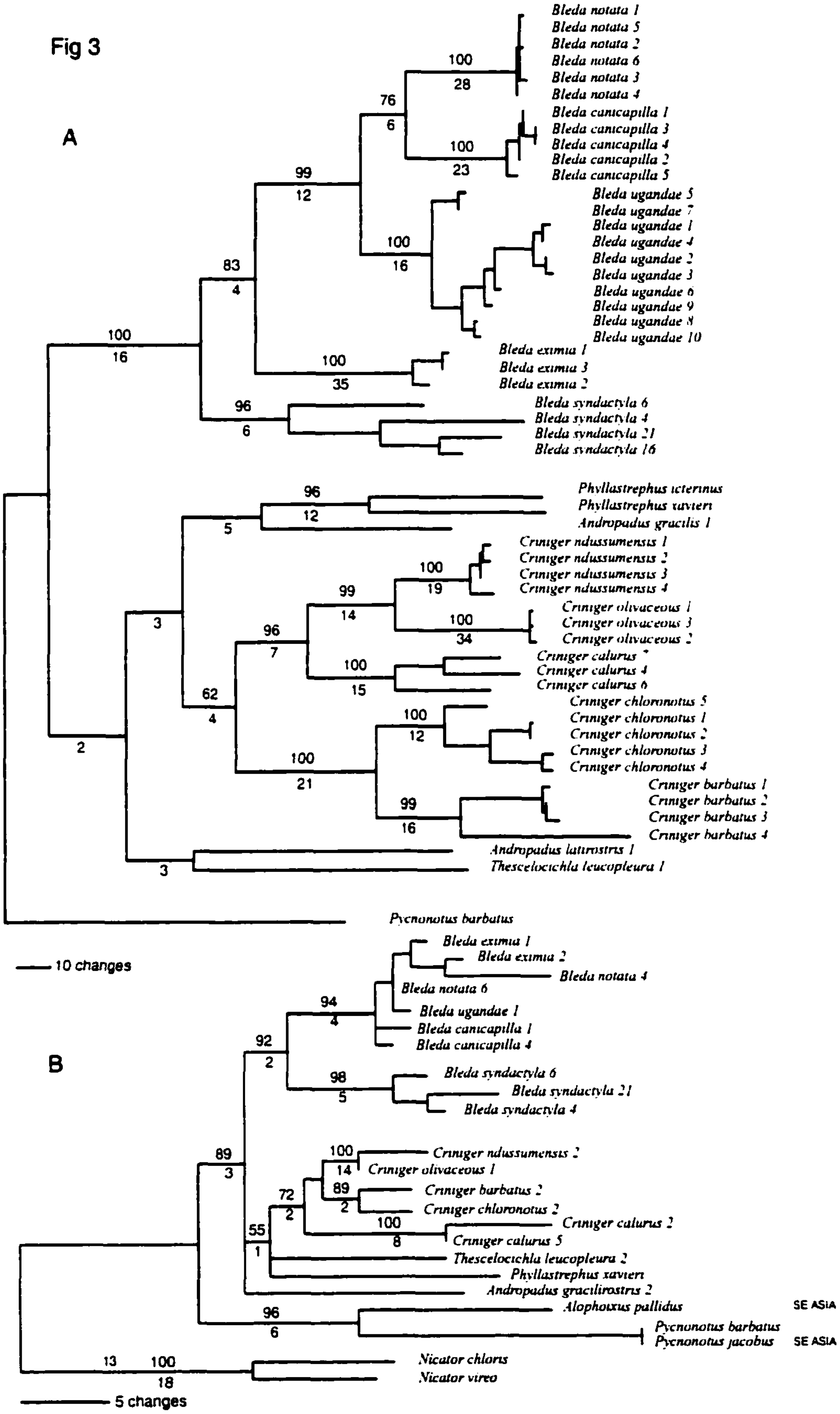

A
Bleda notata 1
Bleda notata 5
Bleda notata 2
Bleda notata 6
Bleda notata 3
Bleda notata 4
Bleda canicapilla 1
Bleda canicapilla 3
Bleda canicapilla 4
Bleda canicapilla 2
Bleda canicapilla 5
Bleda ugandae 5
Bleda ugandae 7
Bleda ugandae 1
Bleda ugandae 4
Bleda ugandae 2
Bleda ugandae 3
Bleda ugandae 6
Bleda ugandae 9
Bleda ugandae 8
Bleda ugandae 10
Bleda eximia 1
Bleda eximia 3
Bleda eximia 2
Bleda syndactyla 6
Bleda syndactyla 4
Bleda syndactyla 21
Bleda syndactyla 16
Phyllastrephus icterinus
Phyllastrephus xavieri
Andropadus gracilis 1
Criniger ndussumensis 1
Criniger ndussumensis 2
Criniger ndussumensis 3
Criniger ndussumensis 4
Criniger olivaceous 1
Criniger olivaceous 3
Criniger olivaceous 2
Criniger calurus 7
Criniger calurus 4
Criniger calurus 6
Criniger chloronotus 5
Criniger chloronotus 1
Criniger chloronotus 2
Criniger chloronotus 3
Criniger chloronotus 4
Criniger barbatus 1
Criniger barbatus 2
Criniger barbatus 3
Criniger barbatus 4
Andropadus latirostris 1
Thescelocichla leucopleura 1
Pycnonotus barbatus
100
28
76
6
100
23
99
12
100
16
83
4
100
16
100
35
96
6
96
12
5
100
19
99
14
100
34
3
96
7
100
15
62
4
100
12
100
21
2
99
16
3
10 changes
B
Bleda eximia 1
Bleda eximia 2
Bleda notata 4
Bleda notata 6
Bleda ugandae 1
Bleda canicapilla 1
Bleda canicapilla 4
Bleda syndactyla 6
Bleda syndactyla 21
Bleda syndactyla 4
Criniger ndussumensis 2
Criniger olivaceous 1
Criniger barbatus 2
Criniger chloronotus 2
Criniger calurus 2
Criniger calurus 5
Thescelocichla leucopleura 2
Phyllastrephus xavieri
Andropadus gracilirostris 2
Alophoixus pallidus
SE ASIA
Pycnonotus barbatus
Pycnonotus jacobus
SE ASIA
Nicator chloris
Nicator vireo
94
4
92
2
98
5
89
3
100
14
89
2
72
2
100
8
55
1
96
6
13
100
18
5 changes

Figure 4

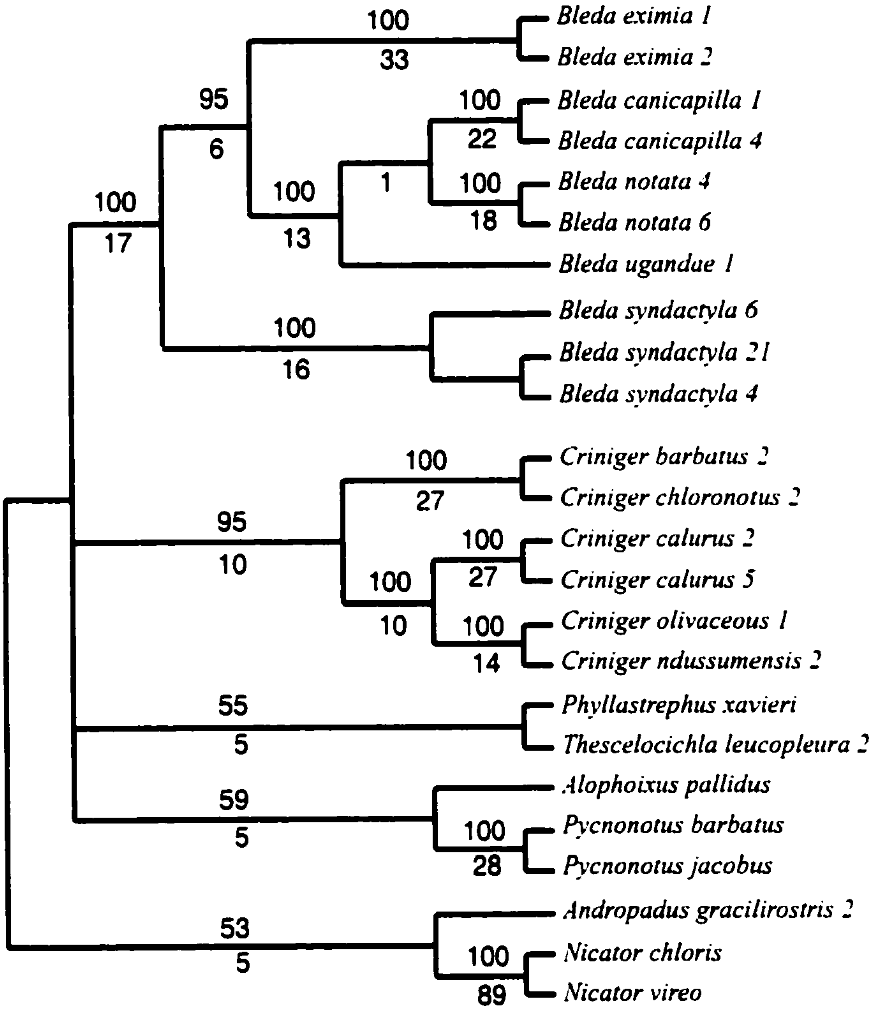

100
33
Bleda eximia 1
Bleda eximia 2
95
6
100
22
Bleda canicapilla 1
Bleda canicapilla 4
100
17
100
13
1
100
18
Bleda notata 4
Bleda notata 6
Bleda ugandae 1
100
16
Bleda syndactyla 6
Bleda syndactyla 21
Bleda syndactyla 4
100
27
Criniger barbatus 2
Criniger chloronotus 2
95
10
100
27
Criniger calurus 2
Criniger calurus 5
100
10
100
14
Criniger olivaceous 1
Criniger ndussumensis 2
55
5
Phyllastrephus xavieri
Thescelocichla leucopleura 2
59
5
Alophoixus pallidus
100
28
Pycnonotus barbatus
Pycnonotus jacobus
53
5
Andropadus gracilirostris 2
100
89
Nicator chloris
Nicator vireo

Figure 5

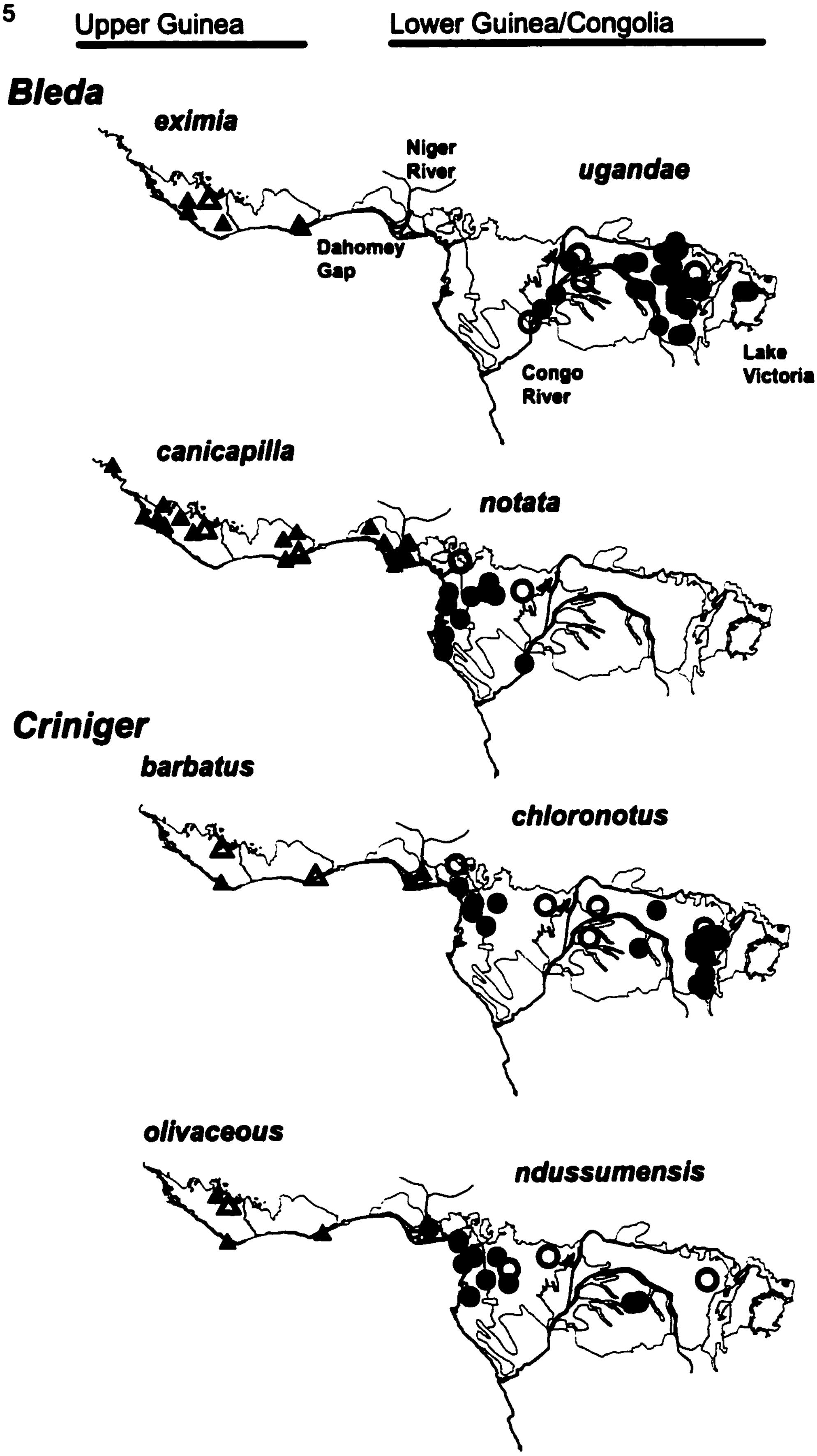

Upper Guinea
Lower Guinea/Congolia
Bleda
eximia
Niger River
ugandae
Dahomey Gap
Congo River
Lake Victoria
canicapilla
notata
Criniger
barbatus
chloronotus
olivaceous
ndussumensis

Figure 6

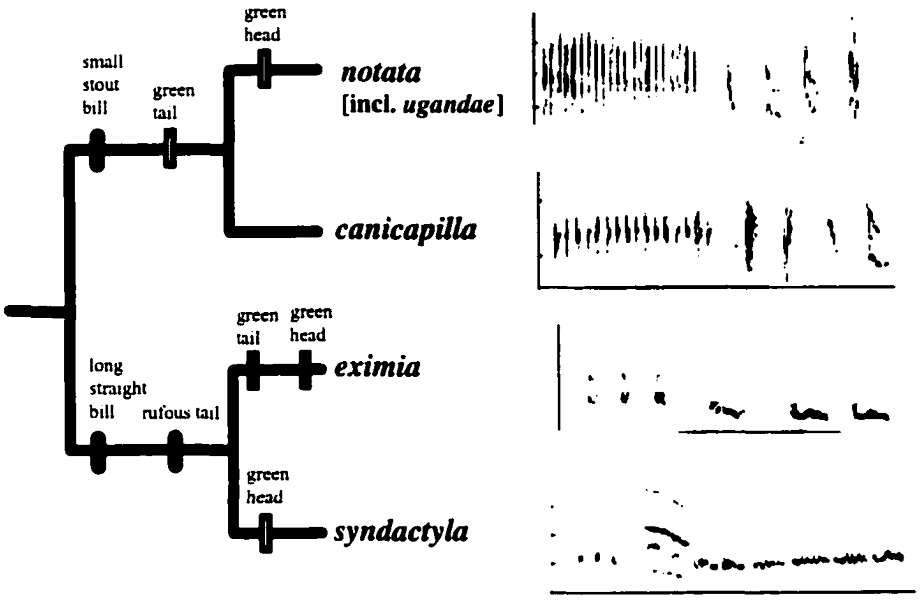

green
head
small
stout
bill
green
tail
notata
[incl. ugandae]
canicapilla
green
tail
green
head
long
straight
bill
rufous tail
eximia
green
head
syndactyla

Figure 7

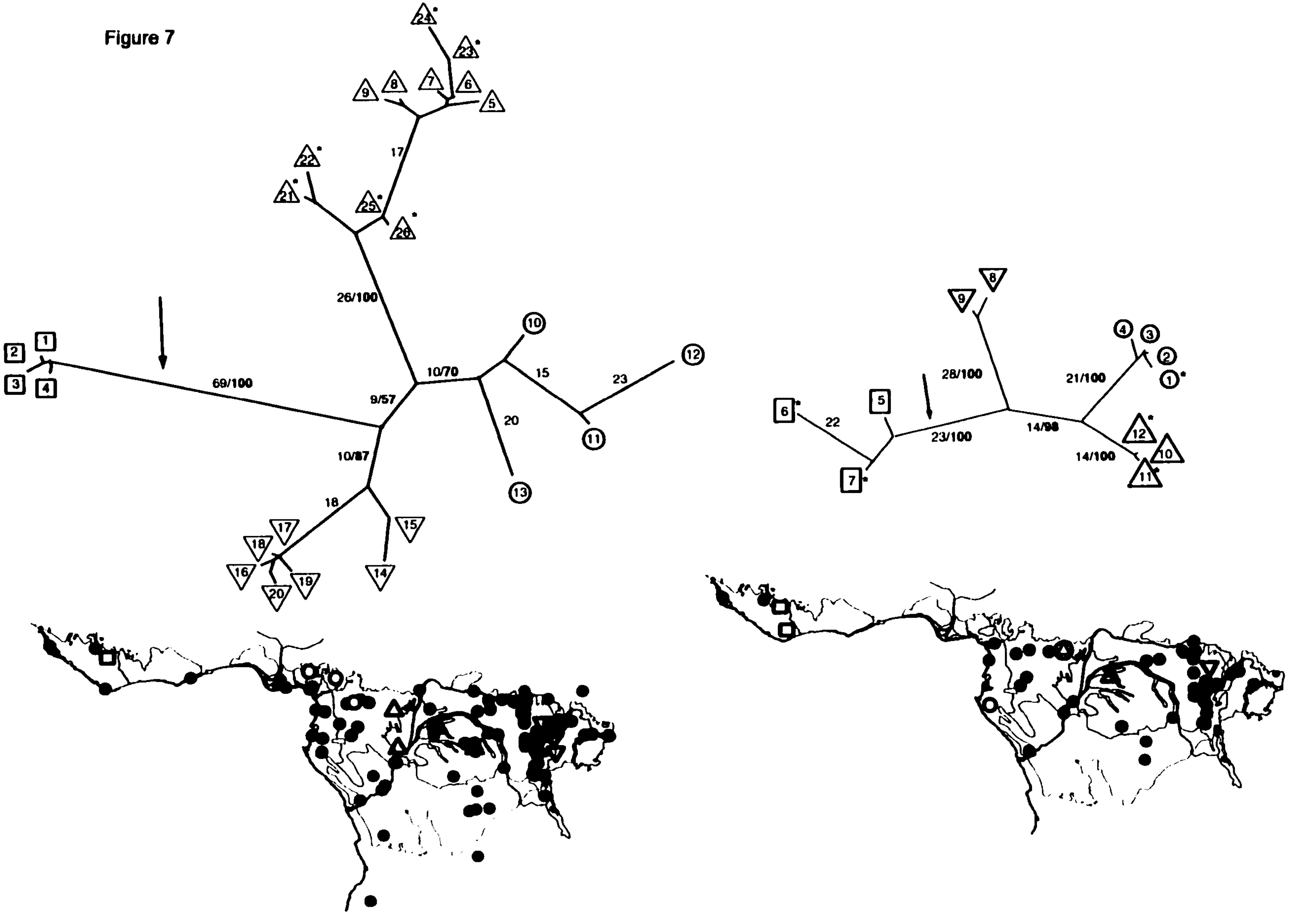
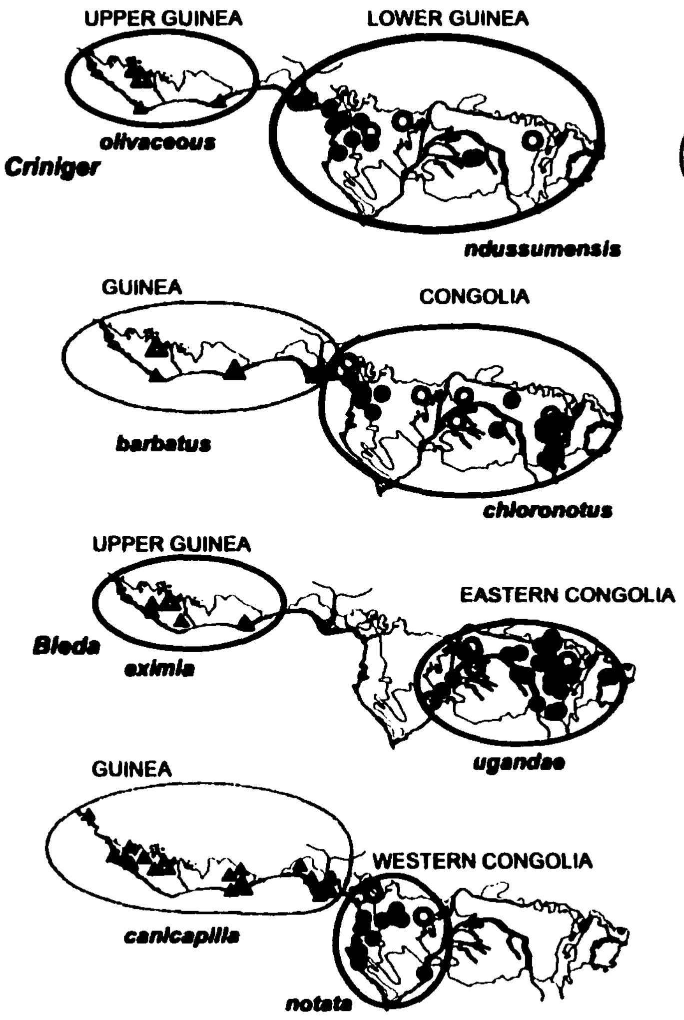
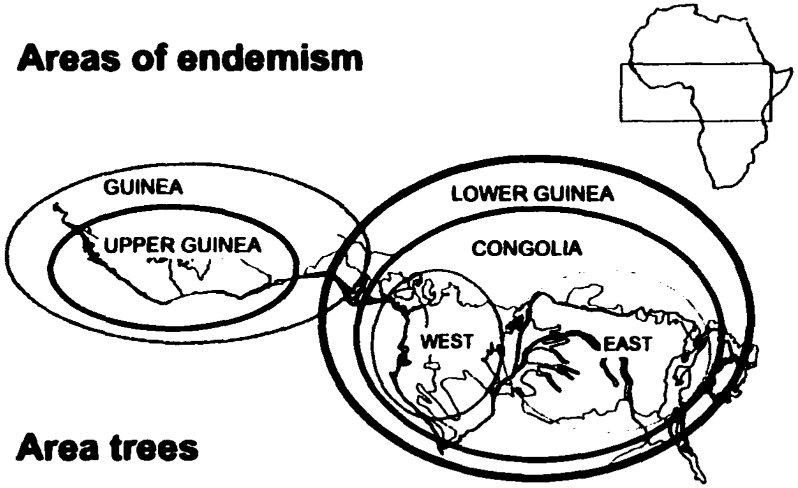

1
2
3
4
69/100
9/57
10/70
26/100
10/87
5
6
7
8
9
17
21
22
23
24
25
26
10
11
12
13
15
23
20
18
14
15
16
17
18
19
20
6
7
5
22
23/100
28/100
8
9
14/98
21/100
14/100
1
2
3
4
10
11
12

Figure 8

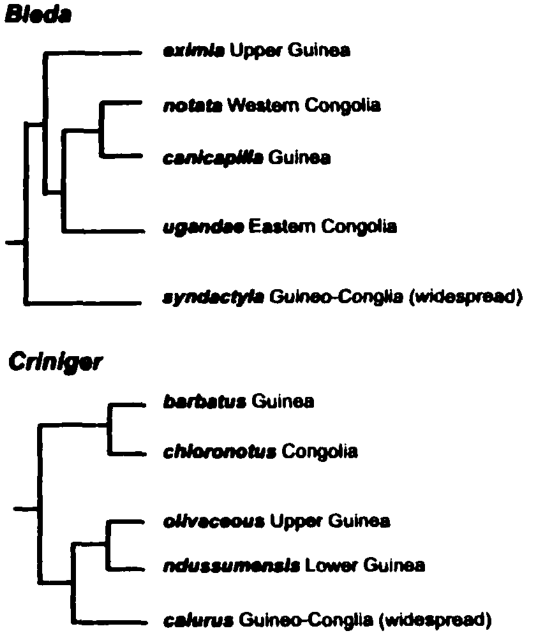
Distributions



Areas of endemism



Area trees



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CHAPTER 3

THE IMPACT OF MOLECULAR SYSTEMATICS ON THE CONTROVERSIAL COMPOSITION OF Alethe AND Sheppardia (Aves: Turdidae).

ABSTRACT

Phylogenetic relationships between species of akalats (*Sheppardia*) and alethes (*Alethe*) were derived from mitochondrial and nuclear sequence data in order to explore the historical biogeography of the two groups. Phylogeographic pattern was also investigated in three widespread species (two *Alethe* and one *Sheppardia*) endemic to the African lowland rainforest biome. Co-distributed species of *Alethe* and *Sheppardia* showed similar spatial relationships between the Guineo-Congolian biome and the Western Rift mountains. Biogeographic pattern was also revealed for other species of *Sheppardia* and *Alethe* distributed in the Cameroon highlands, the woodland areas north and south of the lowland forest block, and east African montane and lowland forest. Within widespread species, phylogeographic pattern was broadly similar in displaying a long branch between Upper and Lower Guinea populations, and between eastern and western Congolian populations. At the interspecific level, the nuclear intron used gave more resolution than the mitochondrial data, which gave poor resolution at basal nodes. While the affinities of some species groups was weakly supported, no support was suggested for the monophyly of either *Alethe* or *Sheppardia* as those genera are currently circumscribed. The membership of these genera has changed with each revision since the mid-20th

century, and this study followed in that tradition, specifically by erecting a new genus for certain alethes and returning some akalats to *Dryocichloides* Irwin and Clancey 1974.

INTRODUCTION

The group of small to medium-sized, forest-dwelling robin-like birds known as alethes (*Alethe*), akalats (*Sheppardia*), and robin-chats (*Cossypha*; Aves: Turdidae) appear to include several radiations that promise to reveal information about evolutionary pattern in the African avifauna. Since many of the alethes and akalats have restricted, allopatric ranges that share geographic and ecological similarities in distribution, a systematic analysis should provide historical signal about biogeographic pattern. This study focuses on alethes and akalats, mainly restricted to lowland and montane forest habitat in Africa; a few species also occur in savanna-woodland mosaic habitat. Here, spatial pattern is explored particularly for taxa distributed in the Eastern Arc montane forests, the Western Rift montane forests and the Guineo-Congolian lowland forest. For three species, phylogeographic pattern is also investigated for taxa occurring in all or part of the Guineo-Congolian lowland forest biome (sensu White, 1983).

A preliminary survey of the genera *Alethe* and *Sheppardia* as currently classified would delineate species with allopatric distributions, but an analysis of the spatial or temporal mode of speciation is not possible without a branching phylogenetic hypothesis. Previous taxonomic work on the akalats, alethes and robin chats, however, has resulted in many conflicting rearrangements of species to genera, and this study was designed to investigate the monophyly of *Alethe* and *Sheppardia* using molecular data; certain *Cossypha* were included as outgroup taxa as well as to test purported affinity of some of them to *Sheppardia*.

Although *Alethe*, *Sheppardia*, and *Cossypha* have been thought to be related to each other (e.g. Hall and Moreau 1970), most systematic treatments have assigned them to a large group of thrushes without hypothesizing any scheme of relationship among the genera. Wolters' (1983) revision put *Alethe* with most *Cossypha* in one group, and *Sheppardia* and some African flycatchers (e.g. *Alseonax*, now *Muscicpa*: Muscicapidae) and another, the two groups separated by several genera (*Pogonocichla*, *Swynnertonia*, *Stiphrornis*). The classification of Sibley and Monroe (1990) rendered these taxa into still more distant groups by keeping *Alethe* in the subfamily Turdinae (Muscicapidae) and assigning *Sheppardia* and *Cossypha* to the Saxicolini tribe in the subfamily Muscicapinae (Muscicapidae). Dowsett and Forbes-Watson (1993) kept *Alethe* in Turdinae: Turdidae; *Sheppardia* and *Cossypha* were assigned to Saxicolinae: Turdinae. The issue of the higher level affinities between *Alethe*, *Sheppardia*, Old World flycatchers and other thrushes is not addressed further here. Instead, the problems evidenced by much reassignment of certain species to genera are explored. Several species have been particularly unstable in recent years, such as (sensu Jensen 1989) *Sheppardia polioptera*, *S. bocagei*, *S. montana* and *S. lowei*. Much of this uncertainty can only be partly ascribed to past approaches to taxonomy that have attempted to reconcile the frustratingly conflicting array of characters in plumage, size, behavior, and vocalization type among these African thrushes.

At first glance, the alethes and akalats seem well defined by a suite of morphological characters. Alethes are relatively large-bodied with plumages dominated by grays and browns and most have a patch of orange feathers on their upperparts. Akalats are smaller, with broader bills surrounded by prominent rictal bristles, and most have orange-hued plumage ventrally. Most of the currently recognized 14 species of *Cossypha* are easily diagnosable: they are larger birds with relatively long tails and conspicuously contrasting red or orange and black plumage patterns.

The uncertainties about generic affinities in past classification are largely due to the distribution of characters that seem to diagnose genera in taxa that have unusual combinations of those characters. Thus, a species may have one character that assigns it to a genus as well as another character that would assign it to a different genus. For example, *Cossypha isabellae* and *C. archeri* are like *Sheppardia* in size and leg and wing proportions, but have red and black plumages typical of *Cossypha*. Hall and Moreau (1970) put *archeri* in *Dessonornis* and *isabellae* in *Sheppardia*, but Irwin and Clancey (1974) assigned them both to their new genus *Dryocichloides*. Wolters (1983) followed this arrangement for *archeri*, but erected a new, monotypic genus for *isabellae*: *Oreocossypha* (which has not been adopted by subsequent taxonomists). Since Jensen (1989), *isabellae* and *archeri* have been placed in *Cossypha*, along with 12 other species (type *C. dichroa*). Hall and Moreau (1970:128) included a supraloral spot among the attributes of the genus *Sheppardia*, but excluded *Cossypha bocagei*, *C. polioptera*, and *C. isabellae*, which they placed in a species group within *Cossypha*. However, Hall and Moreau (1970) noted the presence of a supraloral spot in *C. bocagei* and admitted it "possible that *bocagei* should be transferred to *Sheppardia*," they noted the absence of this feature for *C. polioptera* and *C. isabellae*. Jensen (1989) realized that "*Cossypha*" *polioptera* did indeed have a supraloral spot, albeit concealed, and noted that all *Sheppardia* had such concealed supraocular feathers. Jensen (1989:164) therefore applied a "new concept" of *Sheppardia*, "diagnosed by concealed supraocular feathers," including the type *gunningi*, *sharpei*, *montana*, *lowei*, *cyornithopsis*, *aequatorialis*, *polioptera*, *gabela* and *bocagei*.

Unfortunately, Jensen (1989) found no single or suite of characters to diagnose the genus *Alethe*, and followed past workers in grouping them based on size, overall dull brown or grayish hued plumage, and the absence of characters diagnostic for *Sheppardia*, *Cossypha* or other thrushes. The alethes have nonetheless enjoyed more taxonomic stability than have the akalats and robin-chats, although it has been noted that *Alethe diademata* and *castanea* differ from their congeners in having longer legs and shorter tails. Many workers (Hall and Moreau, 1970; Jensen, 1989; Keith et al., 1992) have included *Alethe poliocephala*, *A. poliophrys*, *A. fuelleborni* and *A. choloensis* in a superspecies group.

Sheppardia montana and *S. lowei* have also been placed in a variety of genera because of an anomalous distribution of features. They are larger than other akalats with plumages dominated by grays and browns, like alethes, but have the concealed supraocular feathers of *Sheppardia*. This study includes exemplars of a new species of akalat, first discovered in 2000 in the Ukuguru mountains of eastern Tanzania. The new akalat shares the bicolored lores otherwise unique to *Sheppardia montana* and *lowei*, and a formal description, including molecular systematic analysis, is in preparation (Beresford et al., in prep.). Although *montana* and *lowei* have been assigned to *Sheppardia* by Jensen (1989) based on the presence of a concealed supraloral spot, previous workers have either assigned them to *Alethe* (Reichenow, 1906; Mackworth-Praed and Grant, 1941), *Dryocichloides* (Irwin and Clancey, 1974; Wolters, 1983), or *Dessonornis* (Hall and Moreau, 1970) on the basis of one or more features that they share characteristic of both *Alethe* and *Sheppardia.*

In addition to the ambiguous generic affinities of these assorted akalats, the species status of *Alethe diademata* and *A. castanea* has differed in recent classifications. The application of the biological species concept in some cases (Keith et al., 1992; Dowsett and Forbes-Watson, 1993) has led to the recognition of *Alethe diademata diademata*, *A. d. castanea* and *A. d. woosnami*, while the classification of Sibley and Monroe (1990) recognize *Alethe castanea* and *Alethe diademata*. *Alethe diademata* is endemic to Upper Guinea, the westernmost part of the Guineo-Congolian lowland forest biome, and has large terminal white spots on the outer 6 tail feathers. *Alethe castanea*, endemic to the Congolian or Lower Guinea lowland forest, from the east of the Dahomey Gap to Uganda, lacks the white spots on the tail. The two are clearly related by virtue of sharing the unique, erectile orange crest that gives the nominate *diademata* the common name "fire-crested alethe." But the inclusion of both diagnosibly distinct forms in a single biological species obscures the probable vicariant history that has isolated each taxon. Many species with similar allopatric distributions on either side of the Dahomey Gap were subsumed into more inclusive biological species by taxonomists in the mid-20th century, and recent work is beginning to reveal deep historical isolation in such taxa (e.g. Chappuis and Erard 1993, Beresford and Cracraft 1999). Here, molecular and other plumage characters are investigated to establish the status of the phylogenetic species of *Alethe diademata* and *A. castanea.*

In addition to exploring monophyly of the genera *Alethe* and *Sheppardia* and resolving the species status of *A. diademata* and *castanea*, this study also seeks preliminary phylogeographic pattern for three species widespread in the Guineo-Congolian biome: *Alethe castanea* (Lower Guinea only), *A. poliocephala* and *Sheppardia cyornithopsis*. Since a phylogeographic analysis of widespread *Bleda syndactyla* and *Criniger calurus* (Pycnonotidae: Beresford, in prep.) indicated geographic structure (congruent with area relationships seen among species in those genera) as well as remarkably deep lineages (as measured by genetic differences), there was an expectation that phylogeographic structure might also be revealed in these three widespread thrushes.

To date, few molecular systematic studies have investigated interspecific relationships in African passerine birds. Beginning with Moreau (1966), the evolution of the African avifauna has overwhelmingly been cast in terms of Pleistocene glaciation cycles and their effect on the distribution of habitat. Recently, Fjeldsaa and Lovett (1997) applied a molecular clock approach to the phenograms in Sibley and Ahlquist (1990) to propose that much of the endemic lowland rainforest fauna was 'relict', the biogeographic signal of which was expected to have been erased, and that more recent radiations were driven by Plio-Pleistocene changes in climate. Unfortunately, Sibley and Ahlquist (1990) did not include any exemplars of *Sheppardia* or *Alethe* in their phenograms, so their "ages" are not known and were excluded from Fjeldsaa and Lovett's (1997) model. In order to clarify the evolutionary history of some akalats, Roy et al. (2000) undertook a molecular phylogeny of seven *Sheppardia* species and described three independent radiations, the origin of each ascribed to late Miocene orogenesis. This study expands the taxonomic sampling of *Sheppardia*, and by including alethes, explores biogeographic pattern across a broader geographic area in an effort to achieve a more detailed analysis of their biogeographic history.

At present there is a vacuum of hypotheses to explain vicariant patterns among African birds due to the aforementioned dominance of models based on glacial-driven climatic change. It seems surprising that given the topographic complexity of eastern Africa, and the ongoing activity of tectonic activity in the rift system, that other abiotic factors have not been sought to explain vicariant patterns among African birds. This paper suggests that the paucity of explanatory hypotheses is due to the corresponding absence of rigorous phylogenetic hypotheses among closely related groups, an absence this study hopes to correct.

MATERIALS AND METHODS

Museum study skins were examined for evidence of variation and diagnosability in features of external morphology and to obtain distributional data. Mitochondrial and nuclear DNA sequence data were collected to infer phylogenetic relationships.

Materials Examined

1,050 specimens of *Alethe*, *Sheppardia*, and selected *Cossypha* were examined from collections at the American Museum of Natural History (AMNH), the Smithsonian

National Museum of Natural History (NMNH), the Royal Museum for Central Africa (MRAC), the Zoological Museum of the University of Copenhagen (DMZ) and the Natural History Museum at Tring (BMNH). Geographic coordinates for the collecting locality of each specimen were obtained from digital (the Digital Gazetteer of the Vertebrate Section, Royal Museum for Central Africa (D. Meirte and H. Schmitz), printed and online gazetteers. For certain species coordinates were converted to decimal degrees, and specimens for which localities could be determined were mapped in ArcView 3.2 (ESRI, 1999) with the WWF ecoregion shapefile (wwf_eco), and layouts were modified in Adobe Illustrator 8. While the published distributions of species are depicted as continuous ranges (e.g. Keith et al. 1992), at the broad spatial scale applied here, the ranges of the focal taxa as depicted by vouchered specimens are not significantly different from those ranges; these species do not occur in regions not represented by point localities shown here.

Molecular Methods

Sequence data were obtained for all 1143 base pairs (bps) of the mitochondrial cytochrome *b* gene (mt cyt *b*) and 550 bps of intron 5 of the nuclear beta-fibrinogen gene (nu *fibint*5). Collecting locales and other information pertaining to the 58 individuals sampled for the molecular analysis are presented in Table 1. Several species of *Cossypha* and a species of *Zoothera* were included as outgroups, as well as representatives of the forest robins *Pogonocichla*, *Swynnertonia* and *Stiphrornis*; these genera are thought to be closely related to the akalats. Tissue or blood genomic DNA was extracted by boiling in 5% (w/v) Chelex (Bio-Rad, Hercules, CA) solution or with the Qiagen amplification kit;

museum study skin DNA was amplified with the Qiagen kit according to the protocol in Mundy et al. (1997). PCR amplification for both loci followed standard protocols (e.g. Beresford and Cracraft 1999). For specimens of museum study skins, usual precautions were taken to prevent contamination, including use of a separate lab, irradiated reagents and disposable components, and "hot-start" PCR reactions were performed exclusively with high annealing temperatures to amplify overlapping fragments of approximately 260bp with primers designed using sequences from conspecific tissue samples (Table 2). Final products were suspended in a Blue Dextran-150 mM EDTA:formamide loading buffer, and samples were run out on 5% Long Ranger (FMC, Philadelphia, PA) gels in TBE buffer in an Applied Biosystems, Inc. (Foster City, CA) 377 automated sequencer.

Systematic Methods

Sequences were assembled and aligned with Sequencher 3.0 (Gene Codes Corporation, Ann Arbor, MI) and verified by eye. No gaps were apparent in either locus, so alignment was straight-forward for both the coding mtDNA cyt *b* and the nuDNA *fibint5* gene. For phylogenetic analysis, most-parsimonious trees were obtained through branch-and-bound searches using PAUP* (Swofford, 2001). No outgroup taxon was defined and trees were rooted after searches with the distantly related turdid *Zoothera princei*. Bootstrap values were obtained with 1000 replicates of parsimony heuristic searches (20 replicates each). Decay indices were calculated in PAUP* with command files generated by MacClade 4.0 (Maddison and Maddison, 2000). Sequence divergence measures were estimated for all pairwise comparisons both as uncorrected (p) distances and under the Kimura 2-parameter model as implemented in PAUP*. Base frequencies were based on observed values reported by PAUP*, and patterns of nucleotide substitution and transition/transversion substitution rates were obtained with MacClade 4.0.

RESULTS

Properties of nucleotide data and genetic diversity. Base compositions were different in mt cyt *b* (A=0.279, C=0.336, G=0.135, T=0.248) compared to nu *fibint5* (A=0.313, C=0.170, G=0.202, T=0.313), and their relative GC content is similar to those found for woodpeckers by Prychitko and Moore (2000) for cyt *b* and fibrinogen intron 7. Patterns of nucleotide substitution in mt cyt *b* were dominated by C:T transitions, and transversions were dominated by A:C changes. The transition:transversion ratio was higher in mt cyt *b* (1:3.8) than for nu *fibint*5 (1:1.4). Similar to the findings of Prytchiko and Moore (2000) and in this study for bulbuls (Chapter 2), patterns of nucleotide substitution were evenly distributed among the 6 types in the nuclear intron and biased toward .

Mean uncorrected pairwise distances for cyt *b* (Table 3) within alethes ranged from 6.5% between *Alethe castanea* and *A. diademata* to 13.8% between *A. poliocephala* and *A. diademata*; Kimura 2-parameter corrected distance ranged from 6.8% between *A. castanea* and *A. diademata* to 16% between *A. choloensis* and *A. diademata*. Within akalats, the uncorrected distances ranged from 7.6% between *Sheppardia cyornithopsis* and *S. aequatorialis* to 12.4% between *S. sharpei* and *S. lowei*; corrected distances ranged from 8.2% between *S. cyornithopsis* and *S. aequatorialis* and 14% between *S. sharpei* and *S. lowei*.

Phylogenetic relationships. In 1143bps mt cyt *b* for 58 exemplars, 416 characters were parsimony informative, and a heuristic search resulted in six most-parsimonious (MP) trees of length 1957, one of which is shown (Figure 1A) with bootstrap support and decay index values. The six trees differed only in the arrangements among terminals within species. These data do not recover any clade including all *Sheppardia* (sensu Jenson 1989); most *Sheppardia* fell into a clade polyphyletic with two typical *Cossypha*, while *S. montana, S. lowei* and *S. spp. nov.* formed a separate, well-supported (85%) clade. While the *Alethe poliocephala* species group of many workers (*poliocephala, poliophrys, fuelleborni* and *choloensis*) is recovered, although without strong support (75%), the species-pair *Alethe diademata/castanea* did not group with the other alethes.

Fewer taxa were sampled for the nuclear intron because of the difficulty in amplifying nuclear DNA from old museum study skins. In 550bps of nu*fibint*5 for 29 exemplars, 70 characters were parsimony-informative, and a heuristic search gave a two MP trees of length 166, one of which is shown in Figure 1B with bootstrap support and decay index values. The two trees differed only in the resolution among exemplars of *Sheppardia cyornithopsis* and *S. aequatorialis*. The nuclear data provide stronger bootstrap support for the *Alethe poliocephala* group (97%) than does mtDNA, and, like the cyt *b* data, provide no support for a clade including that group plus *Alethe castanea* and *Alethe diademata*. Although less well represented in the dataset, a monophyletic clade of *Sheppardia* is recovered with good bootstrap support (88%), but *Sheppardia montana/lowei/spp. nov.* are still excluded from this group although their affinity to each other is well supported (84%).

A reduced dataset was compiled including taxa for which both mitochondrial and nuclear sequence were available. For 29 exemplars and a total of 1693bps, 427 characters were parsimony informative and a heuristic search resulted in a single MP tree of length 1420, shown in Figure 2A. The *Alethe poliocephala* group receives good bootstrap support (95%), as does a clade including members of Hall and Moreau's (1970) *Sheppardia cyornithopsis* group (90%). The monophyly of the *Sheppardia montana* group is well supported at 95%, as is the sister relationship between *Alethe castanea* and *A. diademata* (100%), but the combined data do not support an affinity of either group with their purported congeners.

Since the separate mitochondrial, nuclear and combined topologies were similar (a partition homogeneity test using PAUP* found no significant conflict between the loci), all data for *Sheppardia* and *Alethe* exemplars was combined, regardless of missing data (i.e., nu *fibint5* missing for *S. polioptera, S. bocagei* and *Cossypha isabellae*). This dataset included 36 exemplars and 1683 bps; 445 characters were parsimony-informative. The single MP tree found (length 1836) is shown with bootstrap support and decay indices (Fig. 3B). A *Sheppardia cyornithopsis clade* is recovered (97%) including *S. cyornithopsis, S. aequatorialis* and *S. gabela*, as is a clade including the three species in the *S. montana* group (95%). As with the smaller datasets, the *Alethe poliocephala* group is well supported (94%). The topology suggests that *Sheppardia sharpei* and *gunningi* are more closely related to the *bocagei* group than they are to the *cyornithopsis* group.

Phylogeographic pattern. Three mt cyt *b* datasets were assembled to obtain a preliminary understanding of the depth of genetic differentiation and geographical signal among three relatively widespread taxa, including *Alethe poliocephala* (11 exemplars) and *Sheppardia cyornithopsis* (6 exemplars), both distributed throughout the Guineo-Congolian biome (*A. poliocephala* has populations in forests outside that biome), and also the Lower Guinea (Congolian) endemic *Alethe castanea* (11 exemplars). For *Alethe poliocephala*, 96 characters were parsimony informative and a heuristic search resulted in a single MP network of length 234, shown in Figure 3A. Fewer samples were available for *Sheppardia cyornithopsis*, which appears to be relatively rare and patchily distributed (Keith et al. 1992, pers. obs.); 73 parsimony-informative characters resulted in a single MP network (length 151, Fig. 3B). For *Alethe castanea*, 32 informative characters resulted in a single MP network of length 102 (Fig 3C). All three networks display a similar phylogeographic pattern, with the outgroup falling on a branch separating the Upper Guinea exemplars and the rest, and a bifurcation between eastern and western Congolian exemplars.

DISCUSSION

Whereas the cladistic relationships recovered for species of *Sheppardia* and *Alethe* are in conflict with the classification of Jensen (1989), they are not without precedent in previous classifications (Table 1). Some taxonomic changes are recommended below.

Interspecific relationships of *Sheppardia*. Although few alternative trees were recovered for the data explored here, the bootstrap and decay index support for each topology was much worse for the mt cyt *b* data (with 416 parsimony informative characters) than it was for the nu *fibint5* data (with 70). This poor performance of the mitochondrial data may be due to the evolutionary history of the species in question, since similar results were obtained by Roy et al. (2000). For 648bps of mitochondrial ND2 and ND5 genes, Roy et al. (2000) sampled 7 *Sheppardia* species and, using *Cossypha cyanocampter* and *Cossypha anomala* as outgroups, reported a monophyletic *Sheppardia* that included *bocagei, montana, lowei, gunningi, sharpei, cyornithopsis* and *aequatorialis*. Although Roy et al. (2000) did not set out to test the monophyly of *Sheppardia*, they nonetheless failed to obtain bootstrap support for that clade. That is, similar to the results reported here, the mitochondrial markers sampled by Roy et al. (2000) also failed to include *Sheppardia montana* and *lowei* in the remainder of *Sheppardia*. Furthermore, Roy et al. (2000) did not find much support for relationships among species, beyond recovering a sister relationship for *S. cyornithopsis* and *S. aequatorialis* (at 79% bootstrap support). Therefore, the poor signal provided by cyt *b* for nodes basal to those of sister species (Fig. 1A) was replicated by the other mitochondrial markers used by Roy et al. (2000). Roy et al. (2000) concluded that short basal internodes caused the lack of support, but the phylogram in Figure 1A weakly supports that interpretation for cyt *b*; instead, given the relatively high pairwise distances between species of *Sheppardia* (Table 3), it is likely that homoplasious replacements have precluded the resolution of well-supported nodes.

The results reported here corroborate Jensen's (1989) inclusion of *polioptera* in *Sheppardia*; however, the consistency of the "concealed supraocular feathers" character was cast in doubt. No support was found for including the *montana* group in *Sheppardia*, yet the three species have the supraocular spot, and "*Cossypha*" *isabellae* appears to belong to the *S. bocagei* group but does not have the character. The affinity recovered here between *Sheppardia bocagei, isabellae* and *polioptera* has been suggested many times in the past, i.e. these species have been put in a species group (e.g. Hall and Moreau 1970, Irwin and Clancey 1974, Wolters 1983). Based on the results presented here the genus *Sheppardia* should now include these three species as well as *S. gunningi, S. sharpei,* and the *S. cyornithopsis* group (*cyornithopsis, aequatorialis and gabela*; Table 4). This arrangement differs from Jensen's (1989) in including *isabellae*, but is similar to Hall and Moreau's (1970) species group. This conception of *Sheppardia* means that the character, supraocular erectile feathers, is homoplastic.

Previous workers have also kept *montana* and *lowei* out of *Sheppardia*, and no support was found in this study for the inclusion of that group in *Sheppardia*. Therefore a new generic name should be assigned to them, but this must ultimately rely on further systematic work. If the close relationship between these species and *Alethe castanea* and *diademata*, suggested by the mitochondrial data (Figure 1) is further supported, they may revert to *Alethe*, the genus in which they were originally described (in which case the five species would share the ecological attribute of following driver ant columns; J. Fjeldsaa, pers. comm.). Another possibility may be to follow Hall and Moreau (1970) and maintain them in *Dessonornis* (the type of which is *D. humeralis*) but the composition of *Dessonornis* was not supported by either Irwin and Clancey (1974) or Wolters (1983). Wolters (1983) kept *montana* and *lowei incertae sedis* in *Dryocichloides*. The results of this study show that the supraocular feathers that prompted Jensen (1989) to include them in *Sheppardia* have proved to be a poor indicator of the affinity of this group of species. It is suggested here that the *montana* group revert to the genus *Dryocichloides* Irwin and Clancey 1974 (Table 4); by re-establishing *Dryocichloides*, this study precludes that single character from allocating the *montana* group to *Sheppardia*. Although the monophyly of that genus (the type of which is the polytypic *D. anomala* and includes *D. archeri*) was not tested here, it seems more accurate to keep them in *Dyrocichloides* (*incertae sedis)* to signal their lack of affinity with *Sheppardia*.

Interspecific relationships of *Alethe*. The molecular data supported the separation of *Alethe castanea* from *diademata*. Although very similar, these species differ by white spots on tail, coloration of dorsal plumage, and also by juvenile plumages. Immature *castanea* have dark rufous, spotted vents, while immature *diademata* have white spotted vents. These fixed differences, taken in consideration with the reciprocal monophyly displayed by the mitochondrial data, indicate that it is more accurate to recognize each as separate species. Recognizing these phylogenetic species follows the classification of Sibley and Monroe (1990) but conflicts with that of Dowsett-Lemaire and Dowsett (1993) who felt the similarity in song types warrants conspecificity.

In general, the cladistic relationships among the remaining alethes were better supported by both the mitochondrial and nuclear data than they were for the akalats, with the monophyly of the *Alethe poliocephala* species group (including *poliophrys*, *fuelleborni* and *choloensis*) recovered with all datasets. At the same time, there was never any support for the inclusion of *Alethe castanea* and *A. diademata* with the other alethes, and they have often (Hall and Moreau, 1970; Keith et al. 1992) been kept out of the *poliocephala* species group by virtue of longer legs and erectile crest. Furthermore, there are no character-based reasons to ally *castanea/diademata* with the *poliophrys* group, since the shared presence of dull, uniform plumage is pleisiomorphic within Turdidae. Unfortunately, *Alethe castanea* is the type of the genus, so the *poliocephala* group (all of which were originally described as *Alethe*) must be given a different generic name: the name *Pseudalethe* is proposed (Table 4). This designation may change depending on future systematic analysis of other *Cossypha* species. If the type of the genus *Cossypha (dichroa)* groups with *C. niveicapilla* and *C. cyanocampter* in a clade paraphyletic to, or sister to, these "false alethes," it will be more efficient to assign these species to *Cossypha*.

New genus

Pseudalethe nomen novum

(Aves: Passeriformes (Turdidae))

Type *Trichophorus poliocephalus* Bonaparte 1850

Including

Pseudalethe poliocephala (Bonaparte 1850)

Pseudalethe fuelleborni (Reichenow 1900)

Pseudalethe poliophrys (Sharpe 1902)

Pseudalethe choloensis (Sclater 1927)

DIAGNOSIS:

Medium sized ground-dwelling thrushes distributed in forested habitats in subsaharan Africa. All species have dorsally unpatterned, sexually monomorphic plumage with white or off-white underparts. Dorsal plumages are chestnut brown or gray brown.

INTERSPECIFIC VARIATION:

Pseudalethe poliocephala has a dark gray crown and a white superciliary stripe. *P. poliophrys* has a faint gray superciliary stripe and a rufous chin and throat patch. *P. choloensis* has a white chin and throat patch, and *P. fuelleborni* has a white chin, throat and upper breast.

DISCUSSION:

These species are being removed from the genus *Alethe* based on evidence from mitochondrial and nuclear data that they do not form a monophyletic clade with the type of that genus, *Alethe castanea* (Cassin 1857). This recommendation does not contradict any character-based evidence for including them in *Alethe*, as no phenotypical synapomorphies for that genus have been described. Past workers (White, 1962; Irwin and Clancey, 1974; Jensen, 1989) have assigned these four species to Alethe based on absences of characters diagnostic for other genera of thrushes.

Implications for taxonomy of *Cossypha*. The recovered paraphyly for the few *Cossypha* sampled here is reflected in the historical treatments for the genus (Table 1), as is true for *Sheppardia* and *Alethe*. Although Jensen (1989) diagnosed the genus on the presence of red and black patterned tails, he admitted that *Cossypha anomala* was an exception. *Cossypha anomala* is currently treated as a polytypic species, with one subspecies (sensu Keith et al., 1992) bearing the bicolored tail (*C. a. mbuluensis*) and the nominate subspecies having a plain rufous tail. There are other plumages differences between these taxa and they should be recognized as separate phylogenetic species; furthermore, if the red and black tail is strictly synapomorphic for the genus *Cossypha*, the two forms of *C. anomala* may not even be sister taxa. However, the red and black tail is also variable among populations of *Cossypha heuglini*, so the extent to which this character, like the supraocular feathers, define a monophyletic group is rendered doubtful by the results here. The composition of the genus *Cossypha* must be investigated rigorously.

Biogeographic pattern among species. Absence of generic monophyly notwithstanding, several clades recovered here may be explored for biogeographic signal in the spatial patterns displayed. The following description of the spatial pattern revealed by this analysis refers to 'area relationships' while relaxing the cladistic biogeographic definition of "areas" (characterized by many codistributed taxa with homologous sister relationships; e.g., Humphries and Parenti, 1999); nomenclature follows the revised taxonomy presented here (Table 4). Area relationships for the *Pseudalethe* group show (Fig. 4A) that the range of *P. poliophrys*, in mid to high elevation forest on the Western Rift, is the sister area to the Guineo-Congolian and outlying lowland forest habitat occupied by *P. poliocephala*. Their sister clade includes a sister relationship between *Pseudalethe fuelleborni* in montane forests of the Eastern Arc and *P. choloensis* in the Mozambique mountain forests.

A similar area relationship between the Guineo-Congolian biome and the Western Arc is shown by the *Sheppardia cyornithopsis* group (even though *S. cyornithopsis* and *S. aequatorialis* co-occur in lower elevation forests in the Western Arc), but the cladistic relationship between these areas differs from *Pseudalethe poliophrys/ poliocephala* in that this Western Arc endemic is most closely related to the lowland *S. gabela* in Angola (Figure 4B). The molecular data suggest that the *S. cyornithopsis* clade is sister to the "*bocagei*" group, the distributions of which are shown in Figure 4 along with the topology from the combined consensus tree. Here the Cameroon highlands endemic *isabellae* is sister to *Sheppardia bocagei*, presently including northern (Cameroon highlands) and southern lowland populations, although as discussed further below, the monophyly of the polytypic species *bocagei* remains to be demonstrated, and the area relationships to *isabellae* may change accordingly. *Sheppardia polioptera*, in woodland and gallery forest surrounding the Guineo-Congolian forest zone, is the sister taxon to *S. bocagei* and *S. isabellae*. Related to this group is the sister species pair *Sheppardia gunningi* and *Sheppardia sharpei*, the former distributed in lowland forest in the east, and the latter in Eastern Arc montane forest.

The distributions and sister relationships of *Alethe castanea* and *diademata*, and the *Dyrocichloides montana* group are straightforward (Figure 5), but at this time the area relationships beyond these clades are not known. If the patterns shown by the "false alethes" and akalats should prove to be general, then it might be expected that the sister taxon to *Alethe castanea/diademata* may be or have been distributed in the Western Arc, and that the sister to the *Dryocichloides montana* group may be found in eastern lowland forests.

In order for "areas" as entities in biogeographic analysis to be defined, they should first be characterized by congruent distributions of many taxa and, in order to be strictly homologous in a historical sense, subsequently show the same area relationships via systematic analysis. Too few distributions were shared among the clades studied here for a strict delineated of "areas;" nonetheless, the spatial patterns shown represent a preliminary set of relationships to which subsequent area relationships from future studies can be compared. The question as to the homology of the vicariant nodes shared among clades in this study remains to be addressed: that is, can they be interpreted to represent the same historical, abiotic event? Besides evidence of congruence in sister area relationships, one way to approximate such historical similarity is by comparing genetic distance between homologous nodes, under the assumption that the rate of molecular evolution is both constant within lineages and shared between clades. Workers customarily use either the 0.2/million years uncorrected sequence divergence values (based on Shields and Wilson, 1987; e.g., Avise and Walker, 1998) or 0.15/my Kimura 2-parameter corrected values (based on Fleischer et al, 1998; e.g., Zink et al. 2000), although neither value has been shown to be general for African passerines. Application of these values to the similar Guineo-Congolian/Western Rift nodes show these mean values to be 8.8% (uncorrected) between *Pseudalethe poliocephala* and *P. poliophrys* and 7.7% between *Sheppardia cyornithopsis* and (*S. aequatorialis*, *S. gabela*). It is not clear whether the 1.1% difference, which some workers would translate to half a million years, should be taken to represent different evolutionary histories within the groups of taxa, different rates of cyt *b* evolution, or merely represents standard deviation of pairwise differences. More precise interpretations may be possible once additional species groups are studied.

Phylogeographic pattern. While the sampling of widespread taxa was limited, the networks recovered (Fig. 3) were broadly similar. As has been found with two widespread bulbuls (Chapter One.), Upper Guinea populations are on long branches and, if when the networks are rooted, they are also basal. Phylogeographic structure is also apparent in Lower Guinea, although what factors may be responsible for the east-west division shown here remain to be explored with more sampling. The phylogeographic structure and genetic distances within *Pseudalethe poliocephala* (7.3% between exemplars from Liberia and Uganda) indicate the presence of relatively old intraspecific lineages. Exemplars of *Sheppardia cyornithopsis* from Liberia and the Ituri forest in the Democratic Republic of Congo (D.R.C.) were 5.8% divergent, a value that is higher than those displayed between many other species of birds (Avise and Walker, 1998). These two species are therefore good candidates for future investigations of intraspecific population history. By contrast, the Congolian *Alethe castanea* displayed much lower interindividual divergence value (maximum 2.2% between exemplars from Gabon and the Ituri).

Further comments on intraspecific variation. Many alethes, chats and robin-chats are characterized by marked intraspecific variation. As mentioned above, populations of *Cossypha anomala* differ by the presence or absence of a superciliary stripe, a red and black tail, and sooty grey crown plumage. These isolated populations should be split under a phylogenetic species concept. Keith et al. (1992) recognize ten subspecies for *Alethe poliocephala*, according to degrees of color saturation in parts of the plumage. While those difference appear to change in a gradual way in the bulk of the species' distribution, the status of some of the outlying populations (e.g., in Sudan and in Uganda) needs to be investigated further. The three subspecies of *Sheppardia cyornithopsis* of Keith et al. (1992) also appear to represent clinal variation, and the resemblance of western *cyornithopsis* with eastern *aequatorialis* has led some workers to suggest that they are conspecific. In the latter case, however, specimens of each species collected in the same mid-altitude forest at Kakonda, D.R.C. (0°25'N, 29°46E) differ strongly (e.g. *aequatorialis* MRAC 111540, 111539 and *cyornithopsis* MRAC 64716, 107397). Furthermore, each species was reciprocally monophyletic in the molecular analysis.

A more complicated taxonomic issue is suggested by the intraspecific variation in *Sheppardia bocagei* (sensu Keith et al. 1992; "*bocagei*" in this study is polytypic). Sibley and Monroe (1990) split *Sheppardia bocagei* into *bocagei* and *poensis*, the latter including northern subspecies of *Sheppardia bocagei*. Hall and Moreau (1970) also recognized two different forms for this taxon, and Prigogine (1987) argued convincingly for recognizing the northern, montane populations as a separate species from the southern, lowland populations, based on tail and wing proportions as well as the coloration of the eyelids. However, the preliminary survey of specimens undertaken here arrived at a different arrangement of diagnosibly distinct populations (primarily based on dark gray crown plumage differentiated from dorsal plumage) than did either Prigogine (1987) or Keith et al. (1992), and time limitations prevented a more thorough review of the polytypy in this study. Interestingly, Prigogine (1987) also described a new subspecies ("*ilyae*") of the northern morphotype from western Tanzania, which represent a remarkable range extension of the distribution of northern birds. Further research on the status of the several isolated populations of both *Sheppardia bocagei* and *Sheppardia poensis* must be conducted, as morphological variation among populations (as described in Prigogine (1987) and Keith et al. (1992)) suggest that more than two phylogenetic species may be involved.

Evolutionary history of akalats and alethes. The largely allopatric distributions and phylogenetic relationships among the akalats and alethes examined in this study seem to be good candidates for a vicariant-based historical analysis. Ideally, a geological or abiotic cladogram (i.e. a series of events) should be compared to cladograms from many codistributed species (Rosen, 1978), but late Tertiary to Recent eastern African history is marked by a complex series of tectonic events that have affected both the physical landscape and climatic regimes. Rifting in the Western Arc and the Gregory Rift is thought to be characterized by three bursts of activity from the late Miocene to the late Pleistocene (Partridge et al., 1995), and although the Eastern Arc mountains are Karoo-era, block-faulted non-volcanic mountains of Karoo age origin (i.e. about 250MYA), their faults are thought to have been affected by Pleistocene activity in the Gregory Rift (Griffiths, 1993). Major periods of rifting may be associated with vicariant nodes within the *Pseudalethe* and *Sheppardia cyornithopsis* groups, but given the repeated nature of the abiotic events, it may be difficult to assign specific periods of geomorphological activity to them without both evidence from additional co-distributed species groups as well as from more precise models of geological history.

Possible explanations for patterns of differentiation among the *Sheppardia bocagei* group, including several endemics on the Cameroon highlands, and among the species of *Dryocichloides* in the Eastern Arc might best be sought from models of past changes in climate regimes. Fjeldsaa and Lovett (1993) suggested that the forests of the Eastern Arc have enjoyed stability during adverse Plio-Pleistocene climatic regimes by virtue of their receiving moisture from the Indian Ocean, yet on a finer scale, ecological instability is implied by the pattern of speciation in the *Dryocichloides montana* group.

Roy et al. (2000) suggested that the difficulty in recovering well-supported interspecific nodes among species of *Sheppardia* was due to compression of basal nodes caused by a rapid radiation. It is also possible that the shallow nodes recovered by those workers were artifacts of taxon sampling. The nodes recovered here in the mtDNA phylogram (Figure 1A) among species of "*Sheppardia*" and "*Alethe*" are not particularly short. These results suggest that, as an alternative to the interpretation of Roy et al. (2000), the poor support for intrageneric relationships may be due to taxon sampling, the homoplasious nature of the mitochondrial data, or both. While the acquisition of more sequence data is an obvious way to approach improved recovery of well-supported clades, the addition of taxa may also provide better resolution of the relationships among akalats as well as among robin-chats. For example, the phylogenetic placement of taxa currently included in polytypic biological species, such as *Dryocichloides anomala*, may provide resolution to the intrageneric relationships. It is also likely that taxa related to these thrushes may be widely dispersed throughout Turdidae and may include species currently assigned to endemic African genera (such as *Cossypha, Cossyphicula, Cercotrichas*), species in genera not limited to Africa (*Saxicola, Erithacus*) or species assigned to an array of monotypic genera (e.g. *Xenocossypha*). However, the uncorrected mitochondrial genetic distances among most species of alethes and akalats exceed 10%. Because misleading effects of multiple substitutions ("saturation") may become an issue at levels of divergence greater than this, well-resolved phylogenetic relationships for these birds may have to await data from slower, nuclear markers as well as from improved taxon coverage.

The inclusion of several former *Cossypha* in the *Sheppardia* clade permit the clarification of a certain spatial pattern that would have been differently perceived if more traditional notions of the genera were used to discern evolutionary pattern. The perception of a "radiation" of akalats has been changed by the results of this study: the phylogeny recovered here does not support seeing the evolution of akalats as characterized by a nearly-simultaneous burst of morphological and ecologically similar species. This underscores the need to obtain well-supported relationships among groups of closely related species in order to proceed with comparative studies. In their revision of the forest-dwelling robins, Irwin and Clancey (1974) remarked that "no less than 16 of the 32 species involved (some 50%) have been placed in more than one genus in the last two decades or so," and Wolters (1983), Jensen (1989) and Keith et al. (1992) each suggested different arrangements of species in genera. The application in this study of a cladistic methodology to molecular data shows that much remains to be learned about the interrelationships of these birds. Although the phylogenetic relationships of forest-dwelling robins may be a particularly difficult problem, in fact many genera of African passerines are weakly diagnosed and remain untested, and much promises to be gained from generic level revisions of African birds.

Table 1. Specimens used for molecular analysis. Source of DNA indicated as tissue (ts), blood (bl) or museum study skins (sk). Localities given in decimal degrees.

Taxon	**Specimen**	**Source**	**Institution**	**Accession**	**Country**	**N/-S**	**E/-W**
Alethe poliocephala	1	ts	AMNH	CGS5199	Liberia	7.35	-8.28
	2	ts	AMNH	CGS5194	Liberia	7.35	-8.28
	3	ts	AMNH	CGS5188	Liberia	7.35	-8.28
	4	bl	UMMZ	A886	Nigeria	6.4	9.2
	5	ts	AMNH	PB204	C.A.R.	2.59	16.14
	6	ts	AMNH	PRS1987	C.A.R.	2.59	16.14
	7	ts	FMNH	389367	Gabon	-1.08	10
	8	ts	FMNH	389366	Gabon	-1.08	10
	9	ts	FMNH	357273	D.R.C.	1.25	28.35
	10	ts	FMNH	357264	D.R.C.	1.25	28.35
	11	ts	FMNH	357265	D.R.C.	1.25	28.35
	12	bl	DMZ	3201	Uganda	1.25	28.35
Alethe castanea	1	ts	AMNH	PB103	C.A.R	2.59	16.14
	2	ts	AMNH	PB111	C.A.R	2.59	16.14
	3	ts	AMNH	PB194	C.A.R	2.59	16.14
	4	ts	FMNH	357253	D.R.C.	1	28.35
	5	ts	FMNH	357260	D.R.C.	1	28.35
	6	ts	FMNH	357261	D.R.C.	1	28.35
	7	ts	FMNH	389374	Gabon	2.15	12.13
	8	ts	FMNH	389369	Gabon	2.15	12.13
	9	ts	FMNH	389371	Gabon	2.15	12.13
Alethe diademata	1	ts	AMNH	RWD21457	Liberia	7.35	-8.28
	2	ts	AMNH	MKW425	Liberia	7.35	-8.28
	3	ts	AMNH	MKW427	Liberia	7.35	-8.28
Alethe choloensis	1	ts	PFI	BD68602	Mozambique	-15.08	37
	2	ts	PFI	BD68604	Mozambique	-15.08	37
	3	ts	PFI	BD68605	Mozambique	-15.08	37
Alethe poliophrys	1	ts	FMNH	358032	Burnundi	2	29.36
	2	ts	FMNH	358037	Burnundi	2	29.36
	3	ts	FMNH	358038	Burnundi	2	29.36
Alethe fuelleborni	1	bl	DMZ	118	Tanzania	-7.45	35.42
	2	bl	DMZ	120	Tanzania	-7.45	35.42
	3	ts	DMZ	JK03	Tanzania	-5.37	37.28
Sheppardia cyornithopsis	1	ts	AMNH	PB199	C.A.R.	2.59	16.14
	2	ts	AMNH	PRS2104	C.A.R.	2.59	16.14
	3	ts	FMNH	357242	D.R.C.	1.25	28.35
	4	ts	FMNH	389356	Gabon	-1.08	10
	5	ts	AMNH	827632	Liberia	7.35	-8.28
	6	ts	AMNH	827650	Liberia	7.35	-8.28
Sheppardia aequatorialis	1	ts	FMNH	358017	Burnundi	2	29.36
	2	ts	FMNH	358018	Burnundi	2	29.36
	3	ts	FMNH	358015	Burnundi	2	29.36
Sheppardia gunningi	1	bl	DMZ	1327	Tanzania	-6.53	39.05
	2	bl	DMZ	1328	Tanzania	-6.53	39.05
	3	ts	PFI	KEN99226	Kenya	-3.29	39.5

Sheppardia lowei	1	bl	DMZ	1332	Tanzania	-7.45	35.42
	2	bl	DMZ	1330	Tanzania	-7.45	35.42
	3	bl	DMZ	1329	Tanzania	-7.45	35.42
Sheppardia sharpei	1	bl	DMZ	1335	Tanzania	-7.45	35.42
	2	bl	DMZ	1337	Tanzania	-7.45	35.42
	3	bl	DMZ	1338	Tanzania	-7.45	35.42
Sheppardia montana	1	bl	DMZ	JK3201099	Tanzania	-4.4	38.15
	2	bl	DMZ	JK5211099	Tanzania	-4.4	38.15
	3	bl	DMZ	JK14191099	Tanzania	-4.4	38.15
Sheppardia spp nov	1	bl	DMZ	JK7-240600	Tanzania	-6.2	37.1
	2	bl	DMZ	JK6-210300	Tanzania	-6.2	37.1
	3	bl	DMZ	JK6-240600	Tanzania	-6.2	37.1
Sheppardia gabela	1	sk	AMNH	800716	Angola	-10.51	14.22
	2	sk	BMNH	1959.34.1	Angola	-10.51	14.22
Sheppardia bocagei	1	sk	AMNH	707919	Angola	-12.25	15.11
	2	sk	AMNH	648200	Zambia	-11.57	29.13
Sheppardia polioptera		ts	PFI	KEN99222	Kenya	0.16	34.53
Cossypha niveicapilla		ts	AMNH	PB217	C.A.R.	2.59	16.14
Cossypha caffra		ts	PFI	KEN9977	Kenya	-1.08	34.33
Cossypha cyanocampter		ts	PFI	KEN99220	Kenya	0.16	34.53
Cossypha isabellae	1	sk	AMNH	809726	Cameroon	4.09	9.14
	2	sk	AMNH	348831	Cameroon	6.15	10.26
Cossypha archeri		ts	PFI	KEN99219	D.R.C.	1.25	28.35
Pogonocichla stellata		ts	PFI	AF48800	Malawi	-15.2	35.19
Swynnertonia swynnertoni	1	bl	DMZ	1343	Tanzania	-7.45	35.42
	2	bl	DMZ	1341	Tanzania	-7.45	35.42
Zoothera princei		ts	AMNH	PB189	C.A.R.	2.59	16.14

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. Nuclear beta-fibrinogen intron 5 primers provided by S. Hackett.

Mitochondrial cytochrome-*b*

L14838 5'-GGTCCTTCGCCCTATCCATCCTCA-3'	H15298 5'CCTCAGAATGATATCTGTCCTCA-3'
L15262 5'-CTAATAGCAACCGCCTTTGT-3'	H15560 5'-GGGTGGAATGGGATTTTATC-3'
L15289 5'-GTCCTTCCCTGAGGACAGAT-3'	H15569 5'-GAGTAGTAGGGGTGGAATGGGAT-3'
L15488 5'-CCTTCCTACATGAAACAGGCTC-3'	H15752 5'-TTTGGGATGGAGCGTAGGAT-3'
L15496 5'-CACGAAACAGGCTCTAACAACCC-3'	H16065 5'-AACGCAGTCATCTCCGGTTTACAAGAC-3'
L15511 5'-AACAACCCACTAGGCATTCCTGC-3'	H16084 5'-CAGTCTCTTGGTTTACAAGACC-3'
L15649 5'-GACCCAGAAAACTTCACACC-3'	
L15694 5'-CACATCAAACCCGAATGATA-3'	

Nuclear beta *fibrinogen* intron 5

Sense 5'-CGCCATACAGAGTATACTGTGACAT-3'	Anti-sense 5'-GCCATCCTGGCGATTCTGAA-3'

Table 3. Pairwise sequence divergeces: First data column, uncorrected distances within taxa, followed by (above diagonal) total uncorrected distaces and (below diagonal) Kimura 2 parameter distances.

Taxon	**N**	**mean (range) within**	*poliocephala*	*choloensis*	*poliophrys*	*fuelleborni*	*castanea*	*diademata*	*sharpei*	*cyornithopsis*	*aequatorialis*	*gabela*	*lowei*	*montana*	*spp nov*
Alethe poliocephala	12	0.04 (0.001-0.073)		0.106	0.088	0.101	0.132	0.138	0.127	0.12	0.118	0.118	0.12	0.115	0.113
Alethe choloensis	3	0.004 (0.002-0.006)	0.116		0.102	0.075	0.16	0.156	0.127	0.122	0.12	0.138	0.121	0.107	0.116
Alethe poliophrys	3	0.001 (0-0.001)	0.094	0.112		0.09	0.145	0.155	0.119	0.11	0.113	0.109	0.118	0.116	0.107
Alethe fuelleborni	3	0.005 (0.001-0.007)	0.11	0.089	0.098		0.152	0.155	0.013	0.118	0.12	0.12	0.11	0.117	0.113
Alethe castanea	9	0.013 (0-0.022)	0.147	0.142	0.13	0.136		0.065	0.154	0.13	0.139	0.143	0.102	0.12	0.127
Alethe diademata	3	0.004 (0-0.006)	0.155	0.138	0.137	0.138	0.068		0.144	0.125	0.137	0.141	0.111	0.124	0.126
Sheppardia sharpei	3	0.004 (0.002-0.006)	0.142	0.144	0.133	0.142	0.152	0.163		0.098	0.102	0.113	0.124	0.115	0.114
Sheppardia cyornithopsis	6	0.037 (0-0.058)	0.134	0.136	0.122	0.132	0.146	0.139	0.11		0.076	0.078	0.11	0.103	0.091
Sheppardia aequatorialis	3	0.004 (0.002-0.005)	0.131	0.134	0.126	0.134	0.157	0.154	0.113	0.082		0.07	0.116	0.11	0.108
Sheppardia gabela	2	0.11	0.131	0.138	0.119	0.133	0.161	0.159	0.125	0.085	0.076		0.133	0.112	0.098
Sheppardia lowei	3	0.007 (0-0.010)	0.132	0.134	0.131	0.121	0.111	0.122	0.14	0.121	0.13	0.119		0.076	0.053
Sheppardia montana	3	0.001 (0.002)	0.126	0.118	0.129	0.13	0.132	0.138	0.128	0.113	0.122	0.11	0.082		0.068
Sheppardia spp nov	2	0.015	0.125	0.128	0.118	0.125	0.141	0.141	0.128	0.1	0.12	0.105	0.046	0.076	
Sheppardia bocagei	2	0.22	0.137	0.134	0.127	0.127	0.156	0.141	0.108	0.114	0.112	0.126	0.125	0.116	0.12
Sheppardia polioptera	1		0.126	0.123	0.125	0.127	0.141	0.133	0.107	0.101	0.097	0.115	0.118	0.118	0.111
Cossypha isabellae	2	0.052	0.151	0.147	0.161	0.135	0.172	0.172	0.172	0.147	0.17	0.16	0.163	0.139	0.163
Cossypha niveicapilla	1		0.145	0.142	0.121	0.135	0.16	0.154	0.149	0.137	0.141	0.13	0.139	0.133	0.131
Cossypha caffra	1		0.133	0.144	0.136	0.138	0.164	0.157	0.133	0.123	0.122	0.13	0.137	0.122	0.13
Cossypha cyanocampter	1		0.134	0.135	0.125	0.137	0.16	0.165	0.15	0.13	0.126	0.14	0.135	0.129	0.123
Cossypha archeri	1		0.137	0.153	0.135	0.146	0.171	0.163	0.148	0.12	0.129	0.133	0.126	0.132	0.122
Pogonocichla stellata	1		0.152	0.157	0.14	0.138	0.168	0.168	0.143	0.14	0.143	0.148	0.134	0.128	0.129
Swynnertonia swynnertoni	2	0.009	0.143	0.148	0.133	0.15	0.152	0.162	0.139	0.127	0.136	0.142	0.136	0.114	0.132
Stiphrornis xanthogaster	1		0.12	0.128	0.117	0.127	0.139	0.135	0.138	0.125	0.125	0.121	0.114	0.12	0.114
Stiphrornis erythrothorax	1		0.119	0.129	0.121	0.124	0.141	0.132	0.119	0.118	0.119	0.116	0.115	0.112	0.11
Stiphrornis sanghensis	1		0.123	0.123	0.118	0.123	0.138	0.136	0.14	0.125	0.119	0.118	0.122	0.123	0.118
Stiphrornis gabonensis	1		0.125	0.121	0.115	0.115	0.138	0.14	0.134	0.122	0.12	0.119	0.122	0.114	0.114
Zoothera princei	1		0.157	0.153	0.144	0.157	0.173	0.167	0.161	0.147	0.15	0.137	0.153	0.142	0.152

	bocagei	*polioptera*	*isabellae*	*niveicapilla*	*cyanocampter*	*archeri*	*stellata*	*swynnertoni*	*xanthogaster*	*erythrothorax*	*sanghensis*	*gabonensis*	*princei*
Alethe poliocephala	0.122	0.114	0.135	0.13	0.121	0.123	0.135	0.128	0.109	0.108	0.111	0.112	0.137
Alethe choloensis	0.119	0.111	0.131	0.126	0.121	0.136	0.138	0.131	0.115	0.115	0.112	0.11	0.136
Alethe poliophrys	0.114	0.113	0.142	0.11	0.122	0.122	0.125	0.12	0.107	0.11	0.108	0.105	0.13
Alethe fuelleborni	0.114	0.114	0.122	0.122	0.122	0.13	0.123	0.134	0.115	0.112	0.112	0.107	0.14
Sheppardia gunningi													
Alethe castanea	0.138	0.127	0.15	0.143	0.142	0.15	0.148	0.136	0.126	0.125	0.125	0.126	0.153
Alethe diademata	0.127	0.12	0.15	0.137	0.147	0.144	0.148	0.143	0.122	0.122	0.123	0.126	0.149
Sheppardia sharpei	0.098	0.098	0.149	0.132	0.133	0.146	0.127	0.124	0.123	0.108	0.126	0.121	0.143
Sheppardia cyornithopsis	0.103	0.092	0.13	0.123	0.117	0.12	0.124	0.14	0.115	0.108	0.114	0.111	0.132
Sheppardia aequatorialis	0.102	0.089	0.148	0.127	0.114	0.108	0.127	0.122	0.114	0.108	0.108	0.109	0.135
Sheppardia gabela	0.114	0.106	0.15	0.121	0.125	0.12	0.132	0.126	0.111	0.112	0.111	0.112	0.124
Sheppardia lowei	0.113	0.107	0.143	0.125	0.122	0.115	0.12	0.124	0.104	0.105	0.112	0.111	0.137
Sheppardia montana	0.105	0.101	0.125	0.12	0.116	0.119	0.114	0.104	0.109	0.102	0.112	0.105	0.129
Sheppardia spp nov	0.108	0.101	0.142	0.119	0.112	0.111	0.116	0.113	0.109	0.111	0.11	0.104	0.135
Sheppardia bocagei		0.081	0.108	0.118	0.118	0.13	0.133	0.117	0.113	0.114	0.124	0.119	0.141
Sheppardia polioptera	0.087		0.118	0.124	0.123	0.122	0.124	0.11	0.117	0.101	0.113	0.104	0.135
Cossypha isabellae	0.119	0.131		0.135	0.157	0.107	0.115	0.126	0.122	0.111	0.124	0.114	0.153
Cossypha niveicapilla	0.131	0.138	0.147		0.118	0.138	0.132	0.123	0.117	0.111	0.121	0.12	0.136
Cossypha caffra	0.136	0.124	0.13	0.151	0.129	0.087	0.124	0.124	0.116	0.108	0.115	0.109	0.132
Cossypha cyanocampter	0.135	0.138	0.182	0.13		0.118	0.128	0.123	0.127	0.113	0.125	0.118	0.147
Cossypha archeri	0.145	0.135	0.117	0.156	0.151		0.128	0.13	0.124	0.118	0.122	0.114	0.139
Pogonocichla stellata	0.152	0.139	0.128	0.148	0.146	0.143		0.126	0.128	0.121	0.131	0.117	0.135
Swynnertonia swynnertoni	0.13	0.087	0.141	0.137	0.124	0.146	0.141		0.114	0.111	0.115	0.112	0.132
Stiphrornis xanthogaster	0.124	0.13	0.138	0.129	0.142	0.138	0.143	0.126		0.062	0.03	0.057	0.136
Stiphrornis erythrothorax	0.126	0.111	0.123	0.122	0.124	0.13	0.134	0.122	0.065		0.06	0.053	0.129
Stiphrornis sanghensis	0.138	0.124	0.14	0.134	0.139	0.134	0.148	0.128	0.029	0.064		0.061	0.131
Stiphrornis gabonensis	0.132	0.113	0.118	0.133	0.131	0.125	0.13	0.124	0.061	0.056	0.065		0.13
Zoothera princei	0.158	0.15	0.172	0.151	0.165	0.156	0.15	0.147	0.151	0.142	0.145	0.144	

Table 4. Revised classification of alethes and akalats; following third column, only different names are shown.

Revised	**Original designations**	**Jensen 1989**	**Sibley and Monroe 1990**	**Dowsett & Forbes-Watson 1993**
Alethe Cassin 1859				
Alethe castanea	*Napothera castanea* Cassin 1857	*Alethe castanea*	*Alethe castanea*	*Alethe diademata*
Alethe diademata	*Bessonornis diademata* Bonaparte 1851	*Alethe diademata*	*Alethe diademata*	*Alethe diademata*
New genus ***Psuedalethe*** *nomen novum*				
Type *Trichophorus poliocephalus* Bonaparte 1850				
Pseudalethe poliocephala	*Trichophorus poliocephalus* Bonaparte 1850	*Alethe poliocephala*		
Pseudalethe fuelleborni	*Alethe fuelleborni* Reichenow 1900	*Alethe fuelleborni*		
Pseudalethe poliophrys	*Alethe poliophrys* Sharpe 1902	*Alethe poliophrys*		
Pseudalethe choloensis	*Alethe choloensis* Sclater 1927	*Alethe choloensis*		
Sheppardia Haagner 1909				
Sheppardia gunningi	*Sheppardia gunningi* Haagner 1909	*Sheppardia gunningi*		
Sheppardia bocagei	*Cossypha bocagei* Fisnch and Hartlaub 1870	*Sheppardia bocagei*	*Sheppardia bocagei*	
	Cossypha poensis Alexander 1903	*Sheppardia bocagei*	*Sheppardia poensis*	
Sheppardia isabellae	*Cossypha isabellae* Gray 1862	*Cossypha isabellae*		
Sheppardia polioptera	*Cossypha polioptera* Reichenow 1892	*Sheppardia polioptera*	*Cossypha polioptera*	*Cossypha polioptera*
Sheppardia cyornithopsis	*Callene cyornithopsis* Sharpe 1901	*Sheppardia cyornithopsis*		
Sheppardia sharpei	*Callene sharpei* Shelley 1903	*Sheppardia sharpei*		
Sheppardia aequatorialis	*Callene aequatorialis* Jackson 1906	*Sheppardia aequatorialis*		
Sheppardia gabela	*Muscicapa gabela* Rand 1957	*Sheppardia gabela*		
Dryocichloides Irwin & Clancey 1974 *incertae sedis*				
Dyrocichloides anomala	*Callene anomala* Shelley 1893	*Cossypha anomala*		
Dryocichloides montana	*Alethe montana* Reichenow 1906	*Sheppardia montana*		
Dryocichloides lowei	*Alethe lowei* Grant and Mackworth-Praed 1941	*Sheppardia lowei*		
Dryocichloides spp nov	[Beresford et al. in prep.]	*n/a*		

FIGURE CAPTIONS

Figure 1. A: One of 6 MP phylograms obtained for 1143bps mt cyt *b*, length 1957, C.I. 0.356. B: One of two MP phylograms obtained for 550bps nu *fibint*5, length 166, C.I. 0.910. Bootstrap values (x1000 replicates) above and decay indices below nodes recovered in bootstrap majority-rule consensus tree with greater than 70% support. Exemplars numbered according to Table 1.

Figure 2. A: Stict consensus of 2 MP combined mt cyt *b* and nu *fibint*5 trees (1693 bps); length 1567, CI 0.486. B: Single MP tree(length 1836, C.I. 0.459) of combined data including taxa with missing data. Bootstrap values (x1000 replicates) above and decay indices below nodes recovered in bootstrap majority-rule consensus tree with greater than 70% support.

Figure 3. A: Single MP network (length 234, C.I. 0.821) obtained for mt cyt *b* data for widespread *Alethe poliocephala*. B: MP network for *Sheppardia cyornithopsis*, length 151, C.I. 0.970. C: MP network for *Alethe castanea*, length 102, C.I. 0.902. Arrows indicate placement of outgroups (A, *A. poliophrys*; B, *S. aequatorialis* and C, *A. diademata*). Exemplars numbered according to Table 1. Dark symbols indicate museum specimens studied, shaded symbols indicate localities of molecular exemplars.

Figure 4. A: Distributions of surveyed specimens of *Pseudoalethe* group with cladogram from Figure 2A. B: Distributions of surveyed specimens of *Sheppardia cyornithopsis*

group with cladogram from Figure 2B. C: Distributions of surveyed specimens of *Sheppardia bocagei* group with cladogram from Figure 2B. Solid symbols represent collecting localities of museum study skins; hollow symbols represent those of molecular exemplars.

Figure 5. Above, distributions of surveyed specimens of *Alethe castanea* and *A. diademata* species; below, *Dryocichloides montana* group. Cladograms based on Figure 2; solid symbols represent collecting localities of museum study skins and hollow symbols represent those of molecular exemplars.

Figure 1

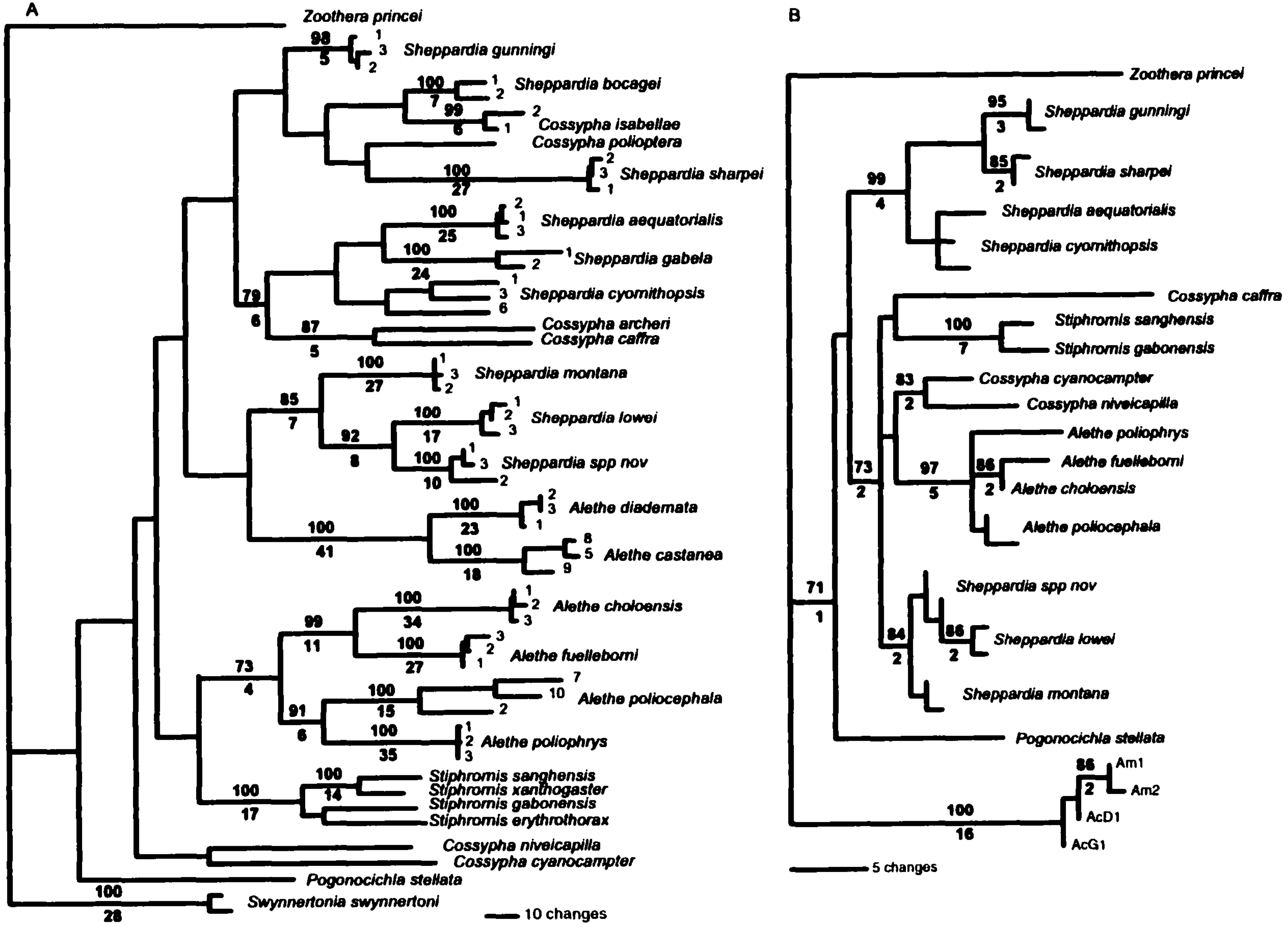

A
Zoothera princei
Sheppardia gunningi
Sheppardia bocagei
Cossypha isabellae
Cossypha polioptera
Sheppardia sharpei
Sheppardia aequatorialis
Sheppardia gabela
Sheppardia cyornithopsis
Cossypha archeri
Cossypha caffra
Sheppardia montana
Sheppardia lowei
Sheppardia spp nov
Alethe diademata
Alethe castanea
Alethe choloensis
Alethe fuelleborni
Alethe poliocephala
Alethe poliophrys
Stiphromis sanghensis
Stiphromis xanthogaster
Stiphromis gabonensis
Stiphromis erythrothorax
Cossypha niveicapilla
Cossypha cyanocampter
Pogonocichla stellata
Swynnertonia swynnertoni
10 changes
B
Zoothera princei
Sheppardia gunningi
Sheppardia sharpei
Sheppardia aequatorialis
Sheppardia cyornithopsis
Cossypha caffra
Stiphromis sanghensis
Stiphromis gabonensis
Cossypha cyanocampter
Cossypha niveicapilla
Alethe poliophrys
Alethe fuelleborni
Alethe choloensis
Alethe poliocephala
Sheppardia spp nov
Sheppardia lowei
Sheppardia montana
Pogonocichla stellata
Am1
Am2
AcD1
AcG1
5 changes

Figure 2

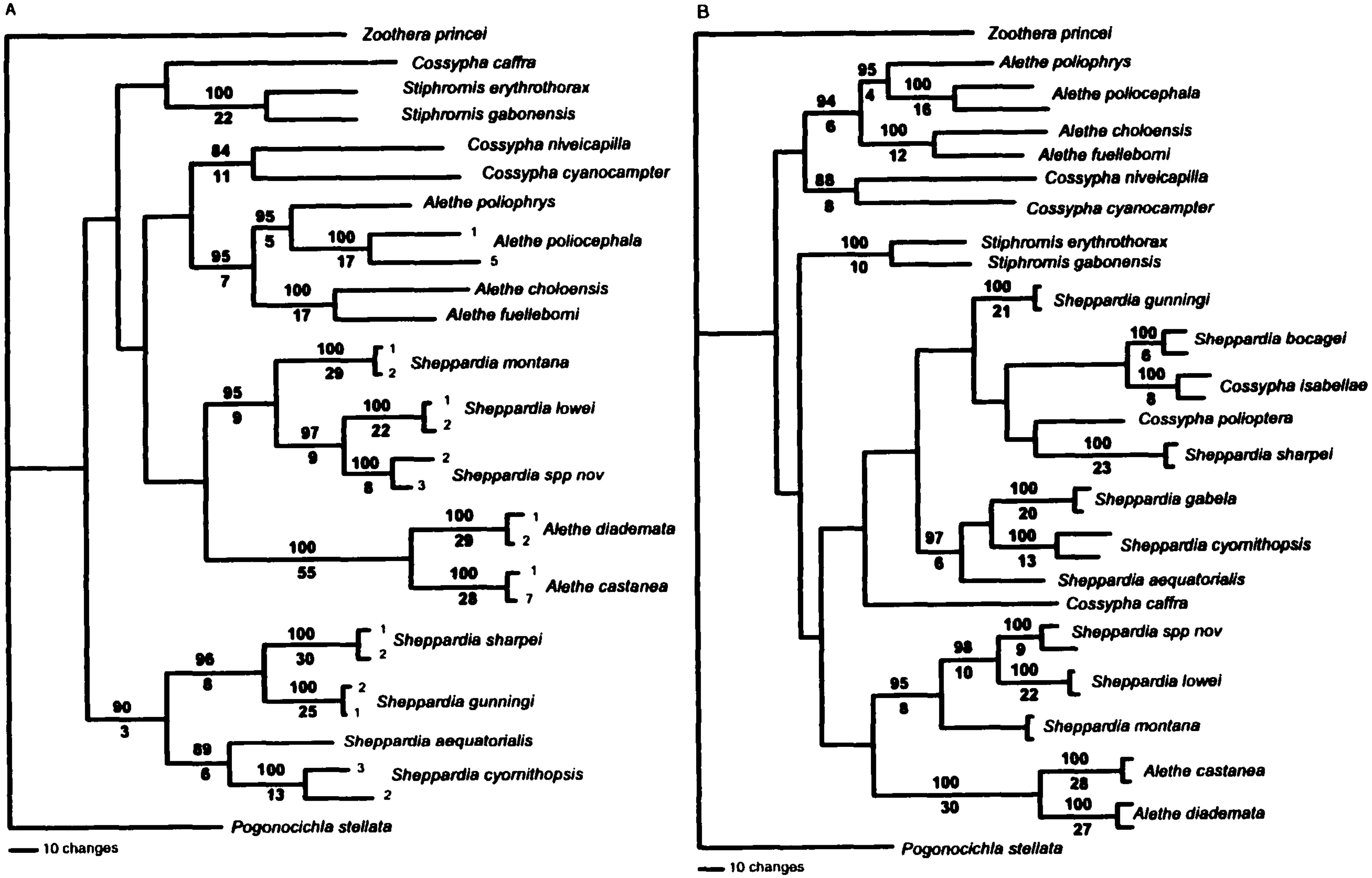

A
Zoothera princei
Cossypha caffra
Stiphromis erythrothorax
Stiphromis gabonensis
Cossypha niveicapilla
Cossypha cyanocampter
Alethe poliophrys
Alethe poliocephala
Alethe choloensis
Alethe fuellebomi
Sheppardia montana
Sheppardia lowei
Sheppardia spp nov
Alethe diademata
Alethe castanea
Sheppardia sharpei
Sheppardia gunningi
Sheppardia aequatorialis
Sheppardia cyornithopsis
Pogonocichla stellata
10 changes
B
Zoothera princei
Alethe poliophrys
Alethe poliocephala
Alethe choloensis
Alethe fuellebomi
Cossypha niveicapilla
Cossypha cyanocampter
Stiphromis erythrothorax
Stiphromis gabonensis
Sheppardia gunningi
Sheppardia bocagei
Cossypha isabellae
Cossypha polioptera
Sheppardia sharpei
Sheppardia gabela
Sheppardia cyornithopsis
Sheppardia aequatorialis
Cossypha caffra
Sheppardia spp nov
Sheppardia lowei
Sheppardia montana
Alethe castanea
Alethe diademata
Pogonocichla stellata
10 changes

Figure 3

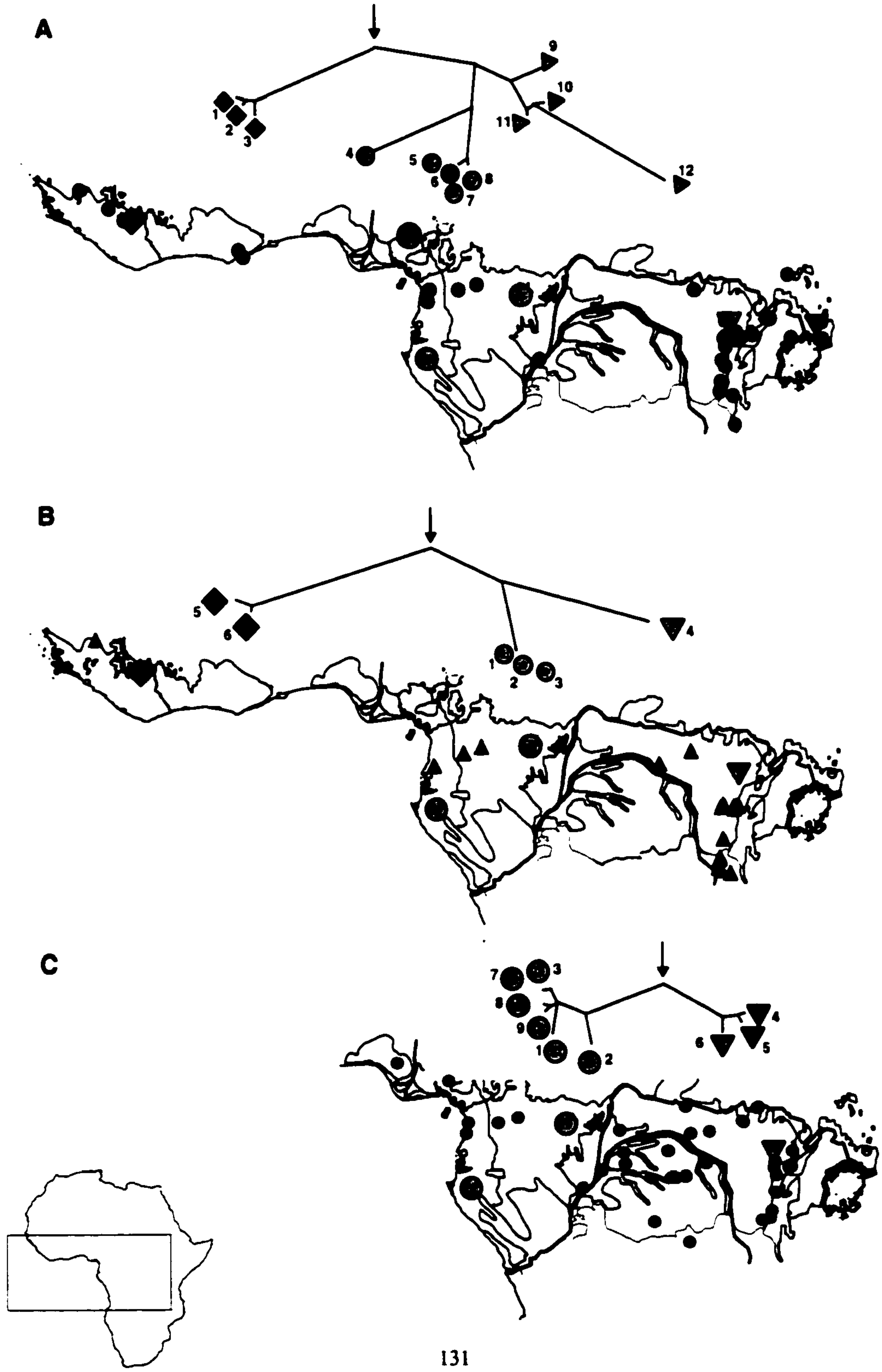


Figure 4

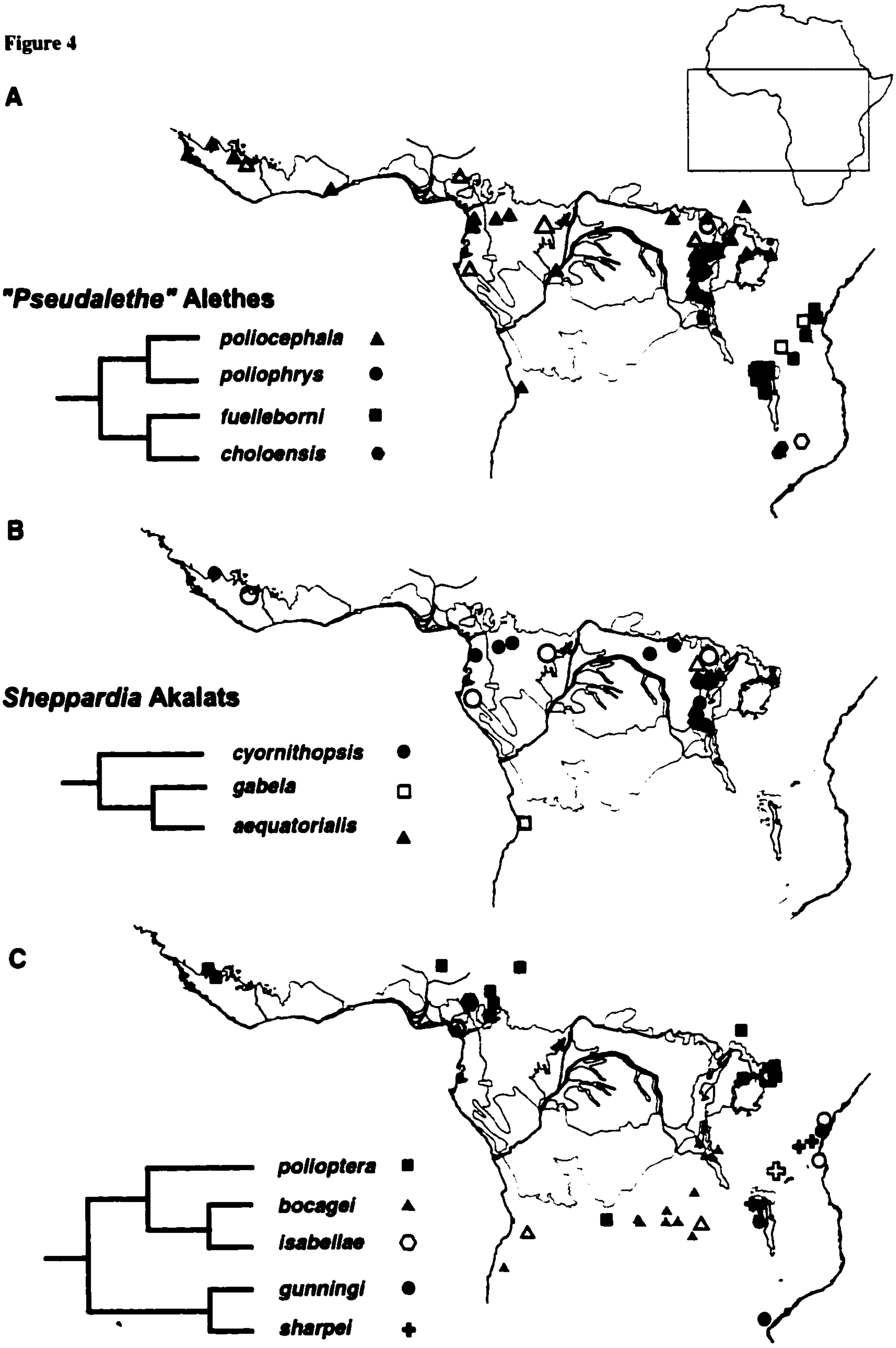
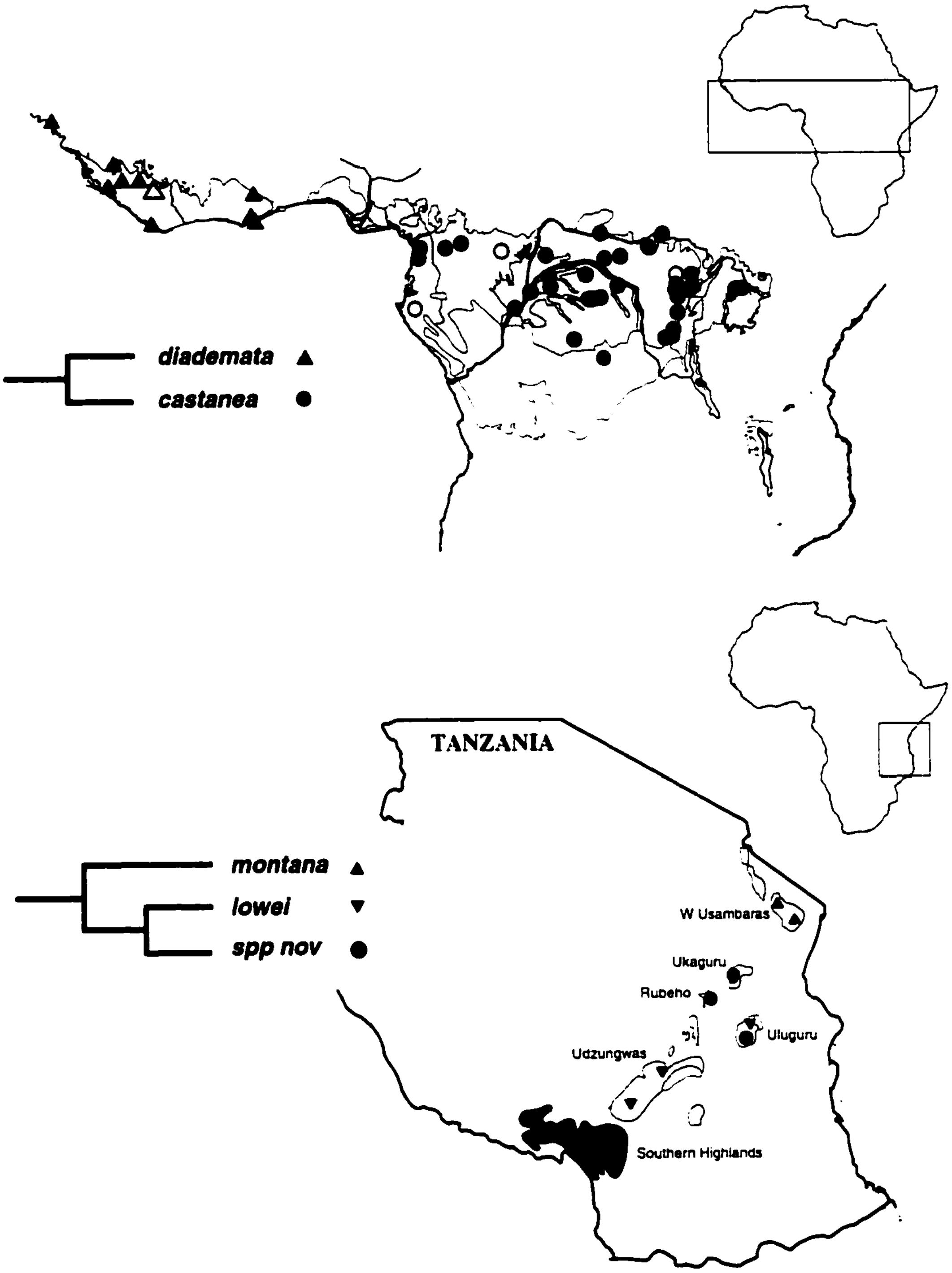

A
"Pseudalethe" Alethes
poliocephala ▲
poliophrys ●
fuelleborni ■
choloensis ●
B
Sheppardia Akalats
cyornithopsis ●
gabela □
aequatorialis ▲
C
polioptera ■
bocagei ▲
isabellae ○
gunningi ●
sharpei ✚

Figure 5


diademata ▲
castanea ●
TANZANIA
montana ▲
lowei ▼
spp nov ●
W Usambaras
Ukaguru
Rubeho
Uluguru
Udzungwas
Southern Highlands

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Conclusion

This research has a provided the first detailed phylogenetic analyses of patterns of speciation within the Guineo-Congolian avifauna and presented the first biogeographic analysis for birds within the Guineo-Congolian biome, as well as between that biome and non-forest areas. Aspects of the data and the implications of the research are discussed below.

Properties of the Data

This study revealed previously unknown mitochondrial diversity among closely related species and within widespread populations. The use of multiple exemplars for examining the boundaries of phylogenetic species provided a satisfactory way of establishing reciprocal monophyly with both the mitochondrial (cyt *b*) and nuclear (*fibint*5) loci. Mitochondrial cyt *b* gave a better supported phylogenetic signal among the species of *Bleda*, *Criniger* and *Stiphrornis* than it did among *Sheppardia*, which may be due to excessive homoplasy as suggested by uncorrected pairwise divergence values between species in excess of 10% in many cases. At higher taxonomic levels, the mitochondrial phylogenetic signal was weak. The nuclear intron loci was more informative at recovering intergeneric relationships among thruses, and among African and Asian bulbuls, but was less reliable for interspecific relationships among endemic African bulbuls.

The results of the sampling of widespread taxa indicate that strong geographic structure is present, which suggested the need for future studies designed to clarify the geographic nature of that phylogeograpic structure. Future intrapopulation studies designed to test refuge scenarios, or even ecotone gradient hypotheses, will have to be designed to incorporate very rapidly evolving markers. Perhaps more importantly, such studies will have to carefully consider the spatial properties of a "population." Little is known about seasonal movement, natal dispersal, effective population size, or other demographic factors in the birds studied here, and all of these can affect intrapopulation divergence measures.

Finally, this study showed that delineating species limits is critically important to understanding diversity on the African continent. The application of a biological species concept to African birds in the early 20th century (e.g. Sclater, 1930) had the effect of ranking many diagnosably distinct taxa as subspecies. "Species" are hypotheses, and most of those "polytypic species" taxa have not been investigated under a phylogenetic species concept, nor has their monophyly been tested with any kind of data. Sibley and Monroe (1990) are frequently reported (Dowsett and Dowsett-Lemaire 1993, Williams et al. 1999) to have applied a phylogenetic species concept, and those workers did split certain polytypic taxa; however, they did so with little explanation and no discussion of which characters were used. Furthermore, the distributional limits of their resulting species are difficult to understand. For example, the *Psalidoprocne prisoptera* species complex is a difficult array of (mostly black) swifts, and in some treatments (the maps in Hall and Moreau 1970, the descriptions in Fry et al. 1988) certain subspecies are sympatric. Sibley and Monroe (1990) recognized an array of named taxa that are difficult to reconcile with the named subspecies in Hall and Moreau (1970) or Fry et al. (1988), and distributions, as described briefly in the text by reference to countries or large continental areas, are often ambiguous.

Although there are arguments against excessive reliance on specimen-based data — as opposed to sight records, for example — it is only with specimens that the distribution of diagnostic characters can be verified. Although it may be important for resource managers to know whether a taxon occurs in an extremely specific area, at the species-level scale that an investigation of this continental biome entails, such specificity may not be required. However, several factors continue to confound the recovery of spatial patterns of geographic variation in Guineo-Congolian birds. The laudable effort by Hall & Moreau (1970) to map point localities for museum specimens is geographically incomplete. While no sampling (collecting effort) can be perfect, specimen records for Africa are more a function of past colonial activity than of systematic inventory efforts. Furthermore, Louette (1984) pointed out that Hall & Moreau (1970) did not consult the collection at the Musée Royale D'Afrique Centrale which exclusively contains specimen records for the former Belgian Congo, representing a significant block of the central equatorial (Lower Guinea) forest. Distributional data continue to be accumulated: Elgood (1994) records nearly 50 new records for Nigeria; new lists have emerged for previously unknown areas (e.g., Dowsett-Lemaire & Dowsett, 1997), and two collecting trips by the American Museum of Natural History (AMNH) added 34 new records to an area in the Central African Republic. Distribution maps of taxa are often depicted with large gaps (e.g., in Hall and Moreau, 1970; Keith et al. 1992; Urban et al. 1997, Fry et al. 1988), which appear to be artifacts of inadequate geographic sampling.

The University of Copenhagen has developed a distributional database that includes the AMNH expedition results as well as specimen and sight records, published and unpublished, since Hall and Moreau (1970), yet, species richness is still very low in the center of the Congolian region (Williams et al. 1999, Brooks et al. 2001). Patterns of endemism and phylogenetic hypotheses are necessary components of a biogeographical investigation, but neither of these has been available for the African lowland forest avifauna. The factors emphasize the point that specimen-based research on diagnosibly distinct taxa still needs to be undertaken.

Systematic results and spatial pattern

This study showed that species and generic level revisions of African birds can add accuracy to the delineation of terminal entities (species) and previously unavailable information to hierarchical relationships among related species. At the same time, however, it shows that we have much to learn about intergeneric relationships among bulbuls and thrushes.

The dominant spatial pattern recovered for the Guineo-Congolian biome, both within widespread taxa and among sister species, described a divergence across the Dahomey, or Togo, Gap. The persistence of this vicariant event is not predicted by the current explanatory hypotheses discussed above, nor was it expected based on discussions of the Quaternary history of the lowland forest biome. Thus, workers from Moreau (1966) to Maley (1996) expected this gap to have been repeatedly forested during warmer and/or wetter climatic periods, and Robbins (1978) even suggested that the Dahomey Gap is a recent product of anthropogenic agricultural practices. Most importantly, the Gap has probably not been perceived to be of importance because it has been obscured by an overly inclusive polytypic species concept; the assignment of similar morphotypes to the same species in the past undoubtedly led Moreau (1966:163) to perceive much "west-to-east continuity"of species across the Gap.

Within the Guineo-Congolian biome, certain patterns previously described in the older literature were corroborated with morphological and molecular data. Both *Stiphrornis gabonensis* and *Bleda notata* were endemic to an area broadly recognized as the Cameroon-Gabon center of endemism. Although few other species of birds are currently understood to be endemic to that area, it has nonetheless been prioritized in the conservation literature as an Endemic Bird Area by BirdLife International, characterized by several restricted-range species (Stattersfield et al., 1998). The eastern limits of this area must be clarified with systematic research as well as with detailed taxonomic inventories.

As has been noted in the past (e.g. Marchant, 1954), southern Nigeria is a biogeographically complex area for birds; and the results in this study reinforced that complexity. *Bleda canicapilla* and *Stiphrornis erythrothorax* have populations in southern Nigeria related to Upper Guinea (west of the Dahomey Gap). *Criniger barbatus* and *Criniger calurus* both have populations in the region that are allopatric across the Cross River, at least as understood on present knowledge of their distributions. For all other taxa, southern Nigerian populations were related to those in Lower Guinea (*Criniger calurus, Bleda syndactyla, Bleda notata, Alethe diademata, Alethe poliocephala* and *Sheppardia cyornithopsis*). The different patterns of replacement in southern Nigeria might be explored with other data. The role of a marine incursion into the Niger Delta has not been carefully considered since Moreau (1954) and Marchant (1954), yet geological research has provided information (Nwogbo 1997) that may be interpreted in the context of establishing a sequence of vicariant events. Alternatively, Nichol (1998) reinterpreted geologic and drainage data to show that dunes have occurred further south in Nigeria during past arid phases than has been suspected. Thus, several lines of evidence implicate the southern Nigeria region as incorporating one or more barriers.

The relationships among the taxa distributed in the Cameroon highlands was complicated and included some sympatry (*Sheppardia bocagei* and *S. isabellae*) as well as sister relationships to non-montane and non-forest taxa. This pattern may have resulted from climate-induced allopatry among species in the Cameroon highlands.

Two pairs of sister species showed relationships between the lowland forest biome and the montane forests of the Western Rift mountains (*Alethe poliocephala/poliophrys, Sheppardia cyornithopsis/aequatorialis*). The inter-montane relationships among the remaining alethes, along the mountains in Tanzania and Mozambique, can not immediately be compared to any other group, but may be with future systematic work. Similarly, the relationships among the Eastern Arc mountains revealed by the *Sheppardia (Dryocichloides) montana* species group cannot yet be compared to other patterns. However, this work has revealed these spatial patterns using phylogenetic analysis and has improved understanding of the origin and evolution of the lowland forest biota.

As discussed above, the temporal domain of current models invoked to explain diversification processes in African birds is primarily the Pleistocene. Today, two conclusions argue against an exclusive focus on this time frame. The first, based on molecular clocks (applied to either DNA-DNA hybridization values by Fjeldsaa 1995 or to mitochondrial DNA sequence divergence by many workers, e.g. Klicka and Zink, 1997 and Fleischer et al., 1998) suggests that species differentiated well before the Pleistocene. The pairwise differences reported here also argue against the Pleistocene refuge hypothesis, if a molecular clock is assumed. The 2.0% per million years calibration value of Shields and Wilson (1987) puts the divergence between *Bleda notata* and *B. canicapilla* at approximately 3 million years ago, and the Kimura 2-parameter calibration value of 1.6% per million years derived by Fleisher et al. 1998 dates that divergence to roughly 6.6 million years ago (applying a gamma correction, with an empirically derived alpha value of 0.205 for the taxa in this study, adds between two and seven percent to the K2P differences, making the ages of divergences even older). Again, if a molecular clock is assumed, and if demographic processes have not biased the pairwise differences, then most of the divergences between the species of *Bleda, Criniger, Sheppardia* and *Alethe* would have had to occur in the late Miocene.

The second conclusion, derived from the research reported here, is that there is a general pattern of vicariance that requires explanation. If that pattern cannot be explained by Pleistocene-era events, other historical factors must be considered. It will be necessary to examine closely the patterns revealed here to investigate whether they represent a single vicariant event between Upper and Lower Guinea.

While both the Dahomey Gap and the region of the Cross River correspond to vicariant nodes between species of *Alethe, Stiphrornis, Bleda,* and *Criniger*, it is not immediately clear that these nodes correspond to the same abiotic event. Molecular data might be used to clarify this issue: the mean uncorrected pairwise distances between *Criniger olivaceous/ndussumensis* and *Bleda eximia/(ugandae, notata, canicapilla)* are 6.1 and 9.7%, respectively, suggesting that, under the assumption of a common rate, the times of divergences differ . Similarly, the mean uncorrected distances among *Bleda* *canicapilla/notata* and *Criniger barbatus/chloronotus* are 6.4 and 8.3%, respectively, again arguing against a single common vicariant event.

Interestingly, Fjeldsaa and Lovett (1997:334) did not find any "biogeographic relicts" in Upper Guinea forests; they suggested that taxa accumulated there from speciation centers located elsewhere. This conclusion is likely due to the application of a polytypic species concept that lumped similar taxa with different morphotypes on either side of the Dahomey Gap. The basal position of Upper Guinea endemics recovered in the rooted trees obtained in this study suggest instead that there is an older avifauna in the Upper Guinea forests. In certain western forest fragments, 6 of the 10 bulbul species studied are sympatric or nearly so (e.g. Allport et al., 1989), and combined with the presence of deep, possibly long isolated lineages evidenced by the widespread species, this study shows that the number of nodes (or phylogenetic diversity, Faith 1992) of some Upper Guinea forests is quite high. The Upper Guinea avifauna does have a number of endemics (22 under the polytypic species concept of Dowsett-Lemaire and Dowsett, 2001), and if the basal position of several Upper Guinea taxa shown here are interpreted to be older in time, then these data indicate that some historical relationships of the highly fragmented and vulnerable Upper Guinea forests may be found in the Miocene.

Although many investigators who have considered the evolution of the African avifauna have perceived the African continent to be geologically stable (Moreau, 1966; Fjeldsaa, 1995), there is much evidence for considerable geomorphological activity before and throughout the Quaternary. Recent stratigraphic and seismic reconstruction studies, for example, have shown that relatively rapid uplift of the Congo margin (Lavier et al. 2001) in the later Miocene, which affected the development of the Congo river drainage system. Subsequently, the cold Bengeula current was established (Uenzelmann-Neben et al., 1997) which continues to affect the climate of the western forests (Hayward and Oguntoyinbo, 1987). These factors may have contributed to the patterns of endemism and vicariance in the Cameroon-Gabon area of endemism. Should the basal position of Upper Guinea endemics prove to be a more general pattern, that is likely dated in the Miocene, few explanatory hypothesis are available. The current Upper Guinea landscape is characterized by several features that are thought to promote speciation, specifically, topographical heterogeneity, an extensive coast with complex offshore weather patterns, and a highly fragmented forest habitat that is home to the species in this study.

The largely allopatric distributions and phylogenetic relationships among the akalats and alethes considered here seem to be good candidates for a vicariant-based historical analysis, but this will require more systematic data. Late Tertiary to Recent eastern African history is marked by a complex series of tectonic events that have affected both the physical landscape and climatic regimes. Rifting in the Western Arc and the Gregory Rift is thought to be characterized by three bursts of activity in the from the late Miocene to the late Pleistocene (Partridge et al., 1995), and although the Eastern Arc mountains are block-faulted non-volcanic mountains of Karoo age origin (i.e. circa 250MYA), their faults are thought to have been affected by Pleistocene activity in the Gregory Rift (Griffiths, 1993). Therefore, given the repeated nature of these abiotic events, it may be difficult to assign specific periods of geomorphological activity to specific phylogenetic nodes without both evidence from additional co-distributed species groups as well as from more precise models of geological history.

In general, vicariant histories of the African avifauna have not been explored in terms of regional, as opposed to global, climate affects, yet late Neogene tectonic and volcanic activity (Partridge et al., 1995), the Tibetan plateau uplift, the closing of the Indonesian seaway (Cane and Molnar, 2001) all have potential to have effected the distribution of forest. Discriminating among these factors will be challenging, however, since they all fall within the realm of 4 to 2 million years ago, as does the major shift in the global climate regime (Denton, 1999). Older geomorphological events include the potential impacts of the Cameroon volcanic line (Meyers et al., 1998) as well as periods of rifting activity in eastern Africa and their effects on the crystalline fault mountains further south.

Plio-Pleistocene effects may still be sought within species. A necessary component of a refuge model is the actual persistence of forest fragments for lowland areas, and the persistence of such elements has begun to be corroborated by palynological research (Maley, 1996; Jahns et al., 1998) for the later Pleistocene. Increasing palynological research supports the differential persistence of forest habitat, and Cruzon and Templeton (2000) have described models that might be used to test refugial scenarios with molecular data.

In summary, this research has provided new data in terms of species-level area cladograms by which methods in analytical biogeography may be further explored (Cracraft, 1994; Humphries and Parenti, 1999). It is also hoped that these results will facilitate efforts to obtain higher-level molecular phylogenies for Pycnonotidae and Turdidae. Finally, given the threatened nature of the African lowland forest and the paucity of phylogenetic studies of its avifauna, it is hoped that these "baseline" studies will inspire further systematic research in understanding the evolution of diversity in this biome.

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