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PHYLOGENETIC, TAXONOMIC AND BIOGEOGRAPHICAL IMPLICATIONS OF GENETIC, MORPHOLOGICAL, AND BEHAVIORAL VARIATION IN FRANCOLINS (PHASIANIDAE: *FRANCOLINUS*)

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ABSTRACT.—We studied restriction-fragment length polymorphisms (RFLPs) in mitochondrial DNA for 13 species of African francolins (*Francolinus* spp.) and the Japanese Quail (*Coturnix c. japonica*). Phylogenetic analyses of RFLPs for these 14 species and of morphological and behavioral characters for the 41 francolin species and other perdicine taxa do not confirm the monophyly of *Francolinus* as currently recognized. Analyses of morpho-behavioral characters suggest that *Francolinus* consists of at least four major assemblages: the five Asiatic species; two groups of African quail-like species; and the African partridge-like species. Within these assemblages, analyses of RFLPs and/or morpho-behavioral characters support the monophyly of six of eight species groups attributed to *Francolinus*. Assuming the monophyly of currently recognized supraspecific groups of galliform birds, morphometric analyses of galliform skeletons correctly classified 90–99% of specimens to family, subfamily and tribe, as well as 95% of the francolin specimens to genus. Genetic distances derived from RFLP data imply that African francolins diverged from their sister taxa at or before the mid-late Miocene, and that all species studied diverged from their sister-species during the Pliocene or early Pleistocene. *Received 29 June 1990, accepted 13 July 1991.*

THE SUPRASPECIFIC phylogenetic relationships among members of the family Phasianidae (sensu Morony et al. 1975) remain poorly resolved (Verheyen 1956, Cracraft 1981, Stock and Bunch 1982, Gutiérrez et al. 1983, Sibley and Ahlquist 1985, Helm-Bychowski and Wilson 1986, Crowe 1988, Randi et al. 1991). A primary cause of this phylogenetic uncertainty is that, while the diagnostic morphological and behavioral attributes (hereafter termed morpho-behavioral characters) of phasianid supraspecific taxa tend to be highly divergent qualitatively, differences in the skeletal anatomy of these taxa tend to be subtle and continuous. For example, although Steadman (1980) was able to assign avian fossil bones to various species of turkeys (Meleagridinae) by a relatively simple morphometric approach, only a few of the more than 100 skeletal characters he employed qualitatively distinguish turkeys from other phasianids. Because osteological characters are among the more important diagnostic features used to assign species to avian genera, this marked divergence in external morphology and relatively conserved skeletal anatomy has led to a proliferation of small genera (mean phasianid species-to-genus ratio = 3.3; range = 1–41; Morony et al. 1975) of uncertain phylogenetic affinity (Olson 1985).

The most striking exception to this "small-genus rule" in the Phasianidae is the genus *Francolinus*. The francolins form the largest genus in the Galliformes (Morony et al. 1975) and one of the largest genera in the class Aves (Bock and Farrand 1980). Hall (1963:109; Fig. 1A) recognized 41 species of francolins (36 African, 5 Asian) and concluded that francolins form a single, monophyletic genus, the members of which are distinguishable from other members of the Perdicini (sensu Morony et al. 1975) by a long, hooked bill, a short tail of 14 feathers, an upright stance and, in the majority of species, spurs at least in the males.

Hall (1963:110) proposed the monophyly of *Francolinus* and then partitioned all but four species (*F. lathami, F. pondicerianus, F. nahani,* and *F. gularis*) of this assemblage into eight monophyletic groups, seven of which have representatives in Africa (Fig. 1A). Hall (1963:170) fur-

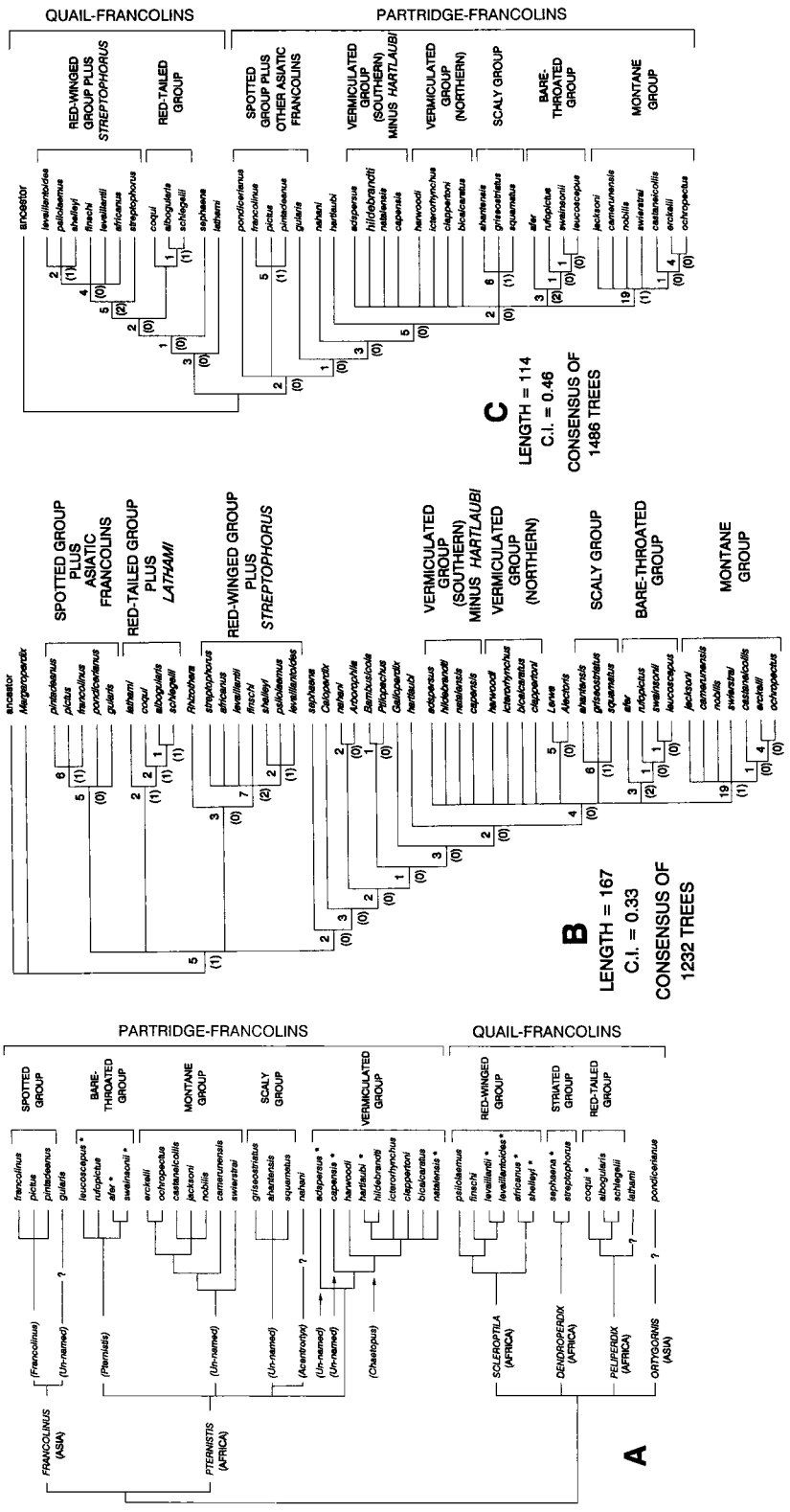

Fig. 1. (A) Phylogenetic relationships of francolins (Hall 1963). Group common names follow Hall (1963), the "partridge-francolin/quail-francolin" dichotomy follows Milstein and Wolff (1987); scientific names follow Wolters (1975). Scientific names of genera are capitalized. Names of subgenera in parentheses and in lower case, with unnamed genera designated as such. MtDNA studied from taxa signified with asterisks. Nodes marked with question mark reflect Hall's (1963) phylogenetic speculations. (B) A Nelson strict-consensus tree for a Wagner-parsimony analysis of 50 perdicine species, including the 41 *Francolinus* species. Numbers at clade nodes indicate number of character steps, and (in parentheses) number of unique and unreversed synapomorphies supporting each clade. (C) A Nelson strict-consensus tree for a Wagner-parsimony analysis of the 41 *Francolinus* species.

ther suggested that the genus may have originated in Asia during the Oligocene (ca. 25–35 × 10^6 y.b.p.), and that extant species of African francolins diverged from their sister species perhaps as recently as the last 10,000 to 100,000 years.

Milstein and Wolff (1987) argued for partitioning *Francolinus* into two major clades comprising quail-like and partridge-like birds (Fig. 1A). "Quail-francolins" (called *patryse* by Milstein and Wolff 1987) are generally small, ground-roosting birds with striped and barred rufous dorsal plumage resembling that of quails (*Coturnix* spp.); they have high-pitched, tonal calls. "Partridge-francolins" (called *fisante* by Milstein and Wolff 1987) are generally larger, tree-roosting birds with dark dorsal plumage vermiculated with white or buff; they give lower-pitched, raucous calls (Milstein and Wolff 1987). Taxonomically, following Wolters (1975), Milstein and Wolff split the southern African species into four genera (Fig. 1A).

In a preliminary phylogenetic study of francolin morphology and behavior, Crowe and Crowe (1985) failed to corroborate the monophyly of *Francolinus*. However, they confirmed the monophyly of Hall's Spotted, Red-winged, Red-tailed, Bare-throated and Montane groups, as well as that of Milstein and Wolff's (1987) partridge-francolins (Fig. 1A). Crowe and Crowe (1985) also concluded that quail-francolins are a paraphyletic assemblage. Based primarily on ontogenetic information, Crowe and Crowe (1985) hypothesized that the ancestor of the francolins was a small, quail-like phasianid, because plumage and other integumentary features (e.g. bill and tarsus color) of immature francolins are remarkably quail-like (Crowe et al. 1986). Taxonomically, on the strength of overall morphometric osteological similarities among francolins, Crowe and Crowe (1985) provisionally kept the francolins in one genus, but proposed a system of subgenera similar to that of Wolters (1975).

In this paper, we discuss studies of: (1) the mitochondrial DNA (mtDNA) of 13 species of African francolins and of the Japanese Quail (*Coturnix coturnix japonica*); (2) the morphology and behavior of the 41 species of francolins and a range of other perdicine species; and (3) the morphometrics of a representative range of galliforms (including 25 *Francolinus* species). Our aims are to: (1) reassess the monophyly of *Francolinus*, Hall's (1963) francolin species groups, and Milstein and Wolff's (1987) quail- and partridge-francolins (Fig. 1A); (2) determine the degree of genetic variation within and between certain (primarily southern) African francolins; (3) estimate the evolutionary divergence times of the genus *Francolinus* and its component taxa; (4) comment on the taxonomic and biogeographical implications of these results; and (5) assess the correlation between species groupings suggested by morphometric, morpho-behavioral, and genetic information for galliforms in general and francolins in particular.

METHODS AND MATERIALS

MtDNA data collection and analysis.—Liver tissue was excised from one specimen of the Japanese Quail and each of the 13 African francolin species (Table 1) and frozen in liquid nitrogen. Tissue from additional specimens of *F. africanus* and *F. levaillantii* was collected at sites 400–700 km from the original collection localities (Table 1) to assess geographical variation in mtDNA structure.

MtDNA from each specimen was extracted from about 4 g of whole tissue (Brown 1980, as modified by Densmore et al. 1985). We used 14 restriction endonucleases: *Eco*RI, *Sca*I, *Sac*I, *Sac*II, *Pvu*II, *Stu*I, *Hin*dIII, *Nco*I, *Bam*HI, *Bcl*I, *Pst*I, *Eco*RV, *Asp* 718, and *Xba*I. Conditions for restriction-endonuclease digestions were those suggested by the suppliers (Amersham International, Boehringer Mannheim, New England Biolabs). We end-labeled mtDNA fragments with ^{32}P-dCTP by incubation with the Klenow fragment of DNA polymerase I at 25°C for 10 min to expose additional nucleotides from fragments with blunt ends or 3′ overhangs. The fragments were incubated for an additional 10 min after addition of unlabeled DTTP, dATP and dGTP plus ^{32}P-dCTP. The labeled fragments were separated by electrophoresis through 1.2% horizontal agarose gels in 1× TAE buffer that included 0.05% pyrophosphate. Gels were visualized by autoradiography. Lambda phage DNA digested with *Hin*dIII was used as a molecular-weight marker.

We assessed restriction-fragment length polymorphism (RFLP) in mtDNA from restriction-endonuclease fragment patterns, assuming that fragments with the same electrophoretic mobility are homologous between haplotypes. The percentage overall nucleotide divergence (δ) between haplotypes was estimated in a pairwise manner by the iterative method of Nei (1987).

Due to the large number of francolin species examined, it was not feasible to map restriction sites. Therefore, we used RFLPs as characters. We realize that this involves a potential loss of phylogenetic information (Swofford and Olsen 1990), but RFLPs are also legitimate synapomorphies in phylogenetic analysis (Zink and Avise 1990). Therefore, phylogeneti-

TABLE 1. Species and sources of specimens used in mtDNA analysis.

Species	Locality
Coturnix c. japonica	Domestic bird.
Francolinus	
leucoscepus	Athi River District, Kenya.
levaillantii	Sabie District, Transvaal, and Giants Castle Nature Reserve, Natal.
levaillantoides	Balfour District, Transvaal.
natalensis	Sabie District, Transvaal.
adspersus	Omaruru District, Namibia.
sephaena	Nylstroom District, Transvaal.
afer	Uitenhage District, Cape Province.
shelleyi	Nylstroom District, Transvaal.
africanus	Ceres and Molteno Districts, Cape Province.
swainsonii	Nylstroom District, Transvaal.
capensis	Cape Town District, Cape Province.
coqui	Nylstroom District, Transvaal.
hartlaubi	Omaruru District, Namibia.

cally informative mtDNA RFLPs (i.e. excluding autapomorphies and universally shared fragments) for the Japanese Quail and the 13 African francolin species were scored as present or absent for each taxon, and polarized by using the Japanese Quail as an outgroup.

Morpho-behavioral characters and polarity decisions.—We analyzed 34 morpho-behavioral characters (Appendix 1 and Table 2) for the 41 francolin species and 9 species of perdicines (*Margaroperdix madagarensis, Rhizothera longirostris, Caloperdix oculea, Galloperdix spadicea, Lerwa lerwa, Alectoris graeca, Ptilopachus petrosus, Bambusicola thoracica* and *Arborophila torqueola*) that possess some or all of the diagnostic characters offered for the genus *Francolinus* by Hall (1963). Morpho-behavioral character information was obtained from Hall (1963), Schönwetter (1967), Crowe and Crowe (1985), Crowe et al. (1986), Milstein and Wolff (1987), Johnsgard (1988), G. E. S. Robbins (unpubl. data), P. le S. Milstein (unpubl. data), and D. Marais (unpubl. data). Unless otherwise stated in Appendix 1, character polarity was determined using ontogenetic criteria. Our assumption was that quail-like features are plesiomorphic for nonquail perdicines.

Phylogenetic methods.—We analyzed character sets using Wagner parsimony (Farris 1970) with the program Hennig86 (version 1.5; Farris 1988). For analyses of morpho-behavioral characters for the 41 *Francolinus* species and the 9 other perdicine species mentioned above, we employed the *"mhennig* bb*"* tree-searching commands. Although this strategy is not guaranteed to find the tree(s) of minimal length, it constructs several trees, adding terminal taxa in different sequences, and applies branch-swapping to each of the initial trees, saving as many equally-parsimonious trees as the available tree space can hold (Farris 1988). In all analyses of the 13 African *Francolinus* species, the shortest-possible tree(s) was found by implicit enumeration (Farris 1988). In all analyses that produced multiple equally-parsimonious trees, we calculated a Nelson strict-consensus tree. The RFLP-based genetic distances also were analyzed phylogenetically following the approach of Fitch and Margoliash (1967) using the FITCH program in Felsenstein's (1987) PHYLIP (version 3.1). In this analysis, the Japanese Quail was the outgroup and the global search option (G) was invoked to ensure that the minimum-length tree was found.

In the analysis of the combined RFLP and morpho-behavioral character data for the 13 African francolins, we measured the congruence between the two character sets with the Mickevich-Farris incongruence metric (i_{MF}; Mickevich and Farris 1981; Kluge 1989), which is calculated as:

$$i_{MF} = \frac{ES_c - (ES_1 + \ldots + ES_n)}{ES_c} \times 100,$$

where the values of ES_1 to ES_n are the number of extra steps for the data sets when analyzed separately, and ES_c is the number of extra steps for the analysis of the combined data set, with extra steps being the length of the calculated tree minus the minimum length (i.e. with no homoplasy) of the tree for the data set in question. The i_{MF} is the percentage of the total incongruence that results from a lack of congruence between the data sets. We chose this approach to assess character-set congruence because others (e.g. Simberloff 1987) do not provide measures of incongruence that result from combining character sets.

We assessed the robustness of trees for the RFLP, morpho-behavioral character, and combined data in three ways. First, the character support of each node leading to at least two taxa in each tree (or the Nelson strict-consensus tree if more than one tree was found) was determined by collapsing that node into a polyfurcation using the "\\x;" command in *"Dos Equis*-mode" within Hennig86. Second, we examined the same nodes for each tree and determined the number of unique and unreversed synapomorphies that sup-

TABLE 2. Phylogenetically informative morpho-behavioral characters.

Taxon	Character no.																																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Margaroperdix madagarensis	1	0	0	0	1	0	0	2	0	0	0	1	0	0	1	0	0	1	3	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Rhizothera longirostris	2	0	1	0	2	1	0	0	0	0	0	1	0	0	0	0	0	0	2	2	0	1	0	0	1	0	0	1	0	0	0	1	0	—
Lerwa lerwa	2	0	0	0	1	1	2	1	0	0	0	1	0	0	1	0	0	0	3	3	0	0	0	1	0	0	0	—	0	1	0	1	—	0
Alectoris graeca	2	1	1	0	2	1	2	1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	1	0	0	0	0	0	1	0	1	1	0
Arborophila torqueola	1	0	0	0	0	0	1	1	1	0	0	2	0	0	2	0	0	1	2	2	0	0	0	0	1	0	0	—	1	1	0	1	1	0
Caloperdix oculea	1	0	1	0	1	0	0	1	1	0	0	2	0	0	0	0	0	0	2	2	0	1	0	0	1	0	0	1	1	1	0	1	—	—
Ptilopachus petrosus	1	0	0	0	1	1	2	1	1	0	0	2	0	0	2	0	0	0	1	4	1	0	0	0	1	0	0	1	0	1	1	1	—	—
Bambusicola thoracica	1	0	1	0	1	1	1	1	1	0	0	2	0	0	2	0	0	0	1	0	0	0	0	0	1	0	0	—	1	1	1	1	—	0
Galloperdix spadicea	1	0	4	1	1	1	1	1	1	0	0	1	0	0	2	0	0	0	2	0	1	0	0	1	0	0	0	1	1	1	1	1	—	0
Francolinus																																		
francolinus	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	3	1	0	0	0	1	0	0	0	—	1	1	0	1	0	0
pictus	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	3	0	0	0	0	1	0	0	0	—	1	1	0	1	—	0
pintadeanus	1	0	1	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	3	0	0	0	0	1	0	0	0	—	1	1	0	1	—	0
gularis	2	0	1	0	0	0	0	1	0	0	0	1	0	0	2	0	0	0	2	0	0	0	—	1	0	0	0	—	1	1	0	1	—	0
pondicerianus	1	0	1	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	2	0	0	0	0	1	0	0	0	—	1	1	0	1	—	0
sephaena	1	0	1	0	1	0	0	1	0	0	0	1	0	0	1	0	0	0	2	1	0	0	1	0	1	0	0	1	1	1	0	1	1	1
lathami	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	2	1	0	0	0	0	1	1	0	—	1	1	0	1	—	1
coqui	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	1	0	0	1	0	1	2	0	1	0	1	0	1	0	1
albogularis	1	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	—	0	1	3	0	1	0	1	0	1	—	—
schlegelii	1	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	1	0	0	—	0	1	3	0	1	0	1	0	1	—	—
streptophorus	2	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	0	2	2	2	0	0	—	0	1	0	1	—	0	1	0	1	—	—
finschi	2	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	2	0	0	—	0	1	0	1	—	0	1	0	1	—	—
levaillantii	2	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	2	0	2	0	0	2	0	1	0	2	1	0	1	0	1	—	0
africanus	2	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	2	1	2	0	0	2	0	1	0	2	1	0	1	0	1	0	0
shelleyi	2	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	2	0	2	0	0	2	0	1	0	3	1	0	1	0	1	0	—
psilolaemus	2	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	2	0	2	0	0	2	0	1	0	3	—	0	1	0	1	—	—
levaillantoides	2	0	1	1	0	1	0	0	0	0	0	1	0	0	1	0	0	2	0	2	0	0	2	0	1	0	3	1	0	1	0	1	0	0
nahani	1	0	0	0	0	0	1	1	1	0	0	2	0	0	2	1	0	0	2	4	0	0	—	—	—	0	0	—	—	1	0	1	—	—
hartlaubi	1	0	2	1	2	1	0	0	0	0	0	2	0	0	2	0	0	0	3	2	0	0	0	1	0	0	0	1	0	1	0	1	1	—
ahantensis	2	1	2	0	2	1	1	1	1	0	0	2	0	0	2	1	1	0	2	3	0	0	—	1	0	0	0	—	1	1	0	1	—	—
griseostriatus	2	1	1	0	2	1	1	1	1	0	0	2	0	0	2	1	1	0	2	3	0	0	—	1	0	0	0	—	1	1	0	1	—	—
squamatus	2	1	2	0	2	1	1	1	1	0	0	2	0	0	2	1	1	0	2	3	0	0	0	1	0	0	0	—	1	1	0	1	—	1
adspersus	2	1	2	0	2	1	2	1	1	0	0	2	0	0	1	0	0	0	3	2	0	0	0	1	0	0	0	0	1	1	0	1	1	0
hildebrandti	2	1	2	0	2	1	1	1	0	0	0	2	0	0	2	0	0	0	2	2	0	0	0	1	0	0	0	0	1	1	0	1	—	0
natalensis	2	1	2	0	2	1	1	1	0	0	0	2	0	0	2	0	0	0	3	2	0	0	0	1	0	0	0	0	1	1	0	1	1	—
capensis	2	1	2	0	2	1	1	1	0	0	0	2	0	0	2	0	0	0	3	3	0	0	—	1	0	0	0	0	1	1	0	1	1	0
harwoodi	2	1	2	0	2	1	2	1	1	0	0	2	0	0	2	0	0	0	3	3	0	0	—	1	0	0	0	—	1	1	0	1	—	—

TABLE 2. Continued.

Taxon	Character no.																																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
icterorhynchus	2	1	2	0	2	1	0	1	1	0	0	2	0	0	2	0	0	0	3	3	0	0	0	1	0	0	0	—	1	1	0	1	—	—
clappertoni	2	1	2	0	2	1	1	1	1	0	0	2	0	0	2	0	0	0	4	3	0	0	0	1	0	0	0	—	1	1	0	1	—	0
bicalcaratus	2	1	2	0	2	1	0	2	0	0	0	2	0	0	2	0	0	0	3	3	0	0	0	1	0	0	0	—	1	1	0	1	—	1
afer	2	1	2	0	2	1	2	1	1	1	2	2	0	0	2	0	0	0	2	3	0	0	0	1	0	0	0	0	1	1	0	1	1	1
swainsonii	2	1	2	0	2	1	1	2	1	1	2	2	0	0	2	0	0	0	2	2	0	0	0	1	0	0	0	0	1	1	0	1	1	0
rufopictus	2	1	2	0	2	1	2	2	1	1	2	2	0	0	2	0	0	0	3	3	0	0	0	1	0	0	0	—	1	1	0	1	—	0
leucoscepus	2	1	2	0	2	1	1	2	1	1	1	2	0	0	2	0	0	0	4	2	0	0	0	1	0	0	0	0	1	1	0	1	—	0
castaneicollis	2	1	3	0	2	1	1	1	0	0	0	1	0	0	2	0	0	0	2	3	0	0	—	1	0	0	0	—	1	1	0	1	—	0
erckelii	2	1	4	0	2	1	0	0	0	0	0	1	0	0	2	0	0	0	2	3	0	0	0	1	0	0	0	—	1	1	0	1	1	0
ochropectus	2	1	4	0	2	1	0	0	0	0	0	0	1	0	2	0	0	0	2	3	0	0	—	1	0	0	0	—	1	1	0	1	—	—
jacksoni	2	1	2	0	2	1	2	1	0	0	0	0	1	0	2	0	0	0	2	0	0	0	—	1	0	0	0	—	1	1	0	1	—	—
nobilis	2	1	2	0	2	1	2	1	1	0	0	0	1	0	2	0	0	0	2	4	0	0	0	1	0	0	0	—	1	1	0	1	—	—
camerunensis	2	0	2	0	2	1	2	1	1	0	0	0	1	0	2	0	0	0	2	2	0	0	—	0	1	0	0	—	1	1	0	1	—	—
swierstrai	2	0	2	0	2	1	2	1	0	0	0	0	1	0	2	0	0	0	2	3	0	0	—	1	0	0	0	—	1	1	0	1	—	—

ported each node. Third, for analyses of African francolins and the Japanese Quail only, we used the bootstrapping program BOOT (with 100 replicates) in PHYLIP. BOOT repeatedly resamples characters randomly with replacement (Felsenstein 1985) and then performs a parsimony analysis on each pseudoreplicate data set, ultimately identifying the frequency with which the topological results agree with that produced by a majority-rule consensus tree. In BOOT analyses, all multistate characters were recoded in an additive binary fashion to preserve polarity information. We did not attempt to analyze the 42- and 51-taxon data sets using this method, because of the prohibitively large number of taxa involved.

Morphometric analyses of extant francolins.—To assess the utility of the "nearest-neighbor" morphometric approach employed by Crowe and Crowe (1985) in assigning galliform skeletons to monophyletic groups and to determine the correlation between morphometric and phylogenetic relationships in galliform birds, we made 73 measurements (Fig. 2; Appendix 2) on 146 skeletons of galliforms, including 99 species (25 francolins) and 67 genera (18 perdicine; Appendix 3). We included skeletons from both males and females. Unstandardized mensural data were $\log_{10}$-transformed and analyzed using BMDP2M, a cluster-analysis program (Dixon 1985), to determine the morphometric "nearest neighbor" of each skeleton. By morphometric nearest neighbor, we mean the specimen with the shortest Euclidian distance to the skeleton under study as indicated by the distance matrix output by BMDP2M prior to dendrogram construction. If this approach has utility in identifying natural groups, members of highly corroborated monophyletic groups should have members of the same groups as nearest neighbors (i.e. quails should have quails as nearest neighbors, turkeys should link with turkeys, grouse with grouse, and francolins with francolins).

RESULTS

MtDNA results.—A total of 211 distinct restriction fragments was produced by the 14 restriction enzyme digests of francolin and Japanese Quail mtDNAs. Fragment raw data are available from EHH on request. Ninety-nine of these fragments were phylogenetically informative (Table 3).

The δ values (Table 4) for two intraspecific comparisons (0.3 between two *F. africanus* and 0.1 between two *F. levaillantii* collected hundreds of kilometers apart) were an order of magnitude lower than those for nearly all the interspecific comparisons. Therefore, birds from only one locality for each species (Ceres for *africanus* and Sabie for *levaillantii*; Table 1) were

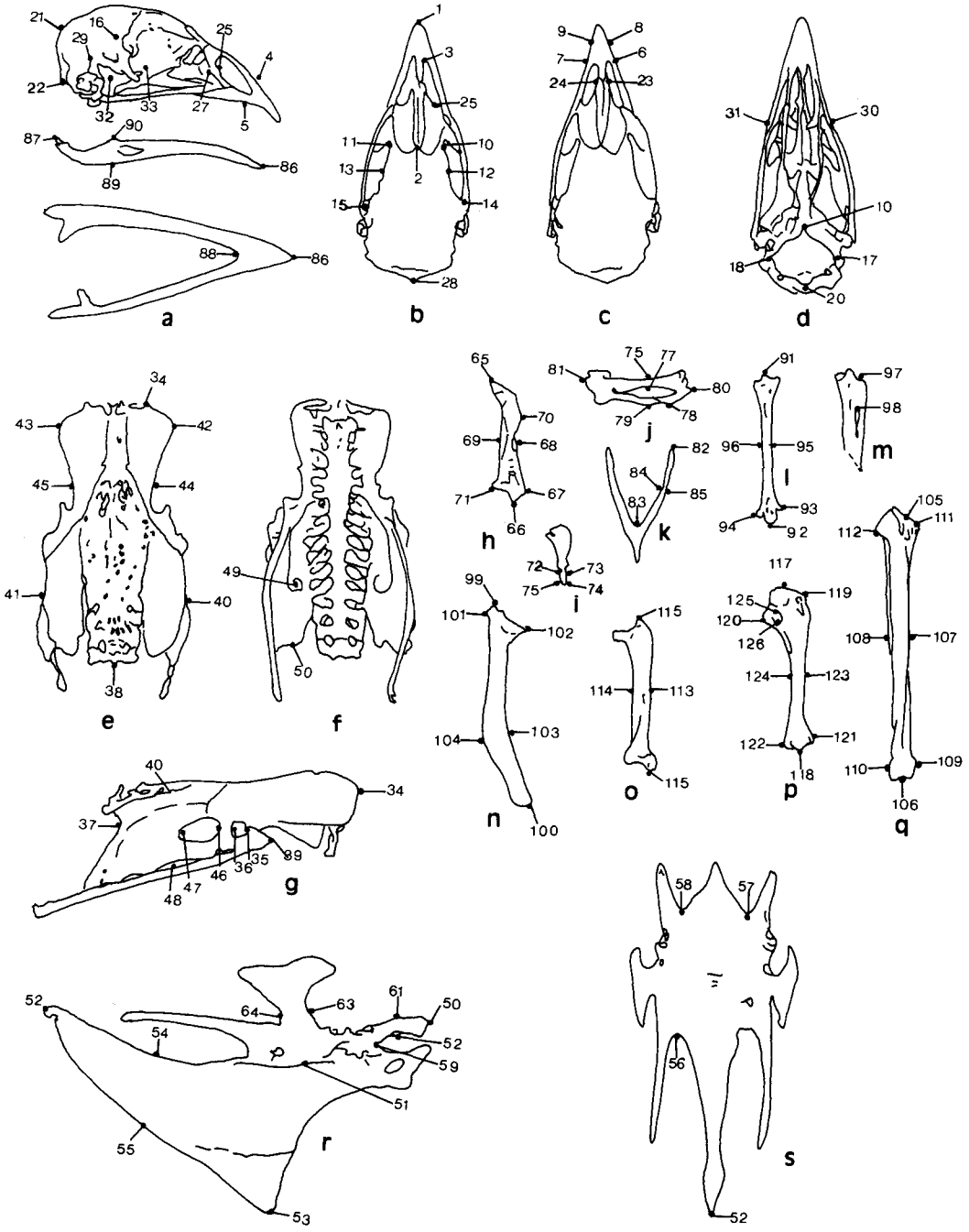

Fig. 2. Bones measured in morphometric studies. Reference points for measurements discussed in Appendix 2.

used in phylogenetic analyses. The δ values between pairs of francolin species ranged from 2.0 (between *F. capensis* and *F. natalensis*) to 14.9 (between *F. africanus* and *F. hartlaubi*). The lowest δ between a quail-francolin and partridge-francolin was 6.4 (between *F. levaillantii* and *F. natalensis*). The mean δ values between the Japanese Quail and quail- and partridge-francolins were 9.5 and 8.9, respectively.

Phylogenetic analyses.—The Hennig86 analy-

TABLE 3. Phylogenetically informative mtDNA fragment characters.

	Restriction enzyme and character no.													
	*Eco*RI	*Eco*RV	*Sac*II	*Nco*I	*Bcl*I	*Pst*I	*Stu*I	*Xba*I	*Bam*HI	*Hin*dIII	*Sca*I	*Sac*I	*Pvu*II	*Asp*718
	1234567	1111 890123	111 456	1112 7890	222222 123456	22233 78901	333333334444444444 234567890123456789	555 012	555555 345678	5666666 9012345	6666777777 6789012345	7777888 6789012	88888889999 34567890123	999999 456789
Outgroup														
Coturnix	0000001	000000	001	0000	100000	01000	100000000010000100	000	100000	1011010	0000000000	0001100	00100000000	000000
Quail-francolins														
sephaena	0100000	000000	001	0000	110100	10100	001100010010001000	000	000110	0001000	0010101000	0000000	10110100010	100000
coqui	0100000	000000	001	0001	100000	00100	000000010010010011	000	000110	0001000	0000001000	0000100	00000100000	000000
africanus	0000010	000000	001	0001	100110	10000	010000000110010100	000	001000	0000001	0011100100	0000000	10110100010	110110
shelleyi	1000010	000000	001	0000	100110	10000	011000010010010000	000	000000	0000101	0100100000	0100001	00000101000	110000
levaillantoides	1000010	000000	001	0001	000010	10010	001010001010011100	100	110000	0000101	0101100100	0100001	00000101000	110110
levaillantii	1100000	000000	001	0000	000000	00010	100110000010000000	000	010001	0011010	0000010010	0000000	01000000000	100000
Partridge-francolins														
hartlaubi	1000001	000000	001	0000	010000	00000	100000000000100000	000	010001	1011000	0000000000	1000000	00000110001	000000
adspersus	1011100	100011	001	1110	011000	01000	100010001001000001	000	000000	0011000	1000000011	0010100	00001110100	001001
natalensis	1011100	100011	110	0000	111000	01000	100011000101000001	111	010001	0111000	1000000011	1010100	01001110000	001001
capensis	1011100	100000	110	0000	111000	00000	100001000001100010	111	000000	1111000	1000000011	0001100	00001110100	001001
afer	1001100	111000	001	1110	100001	01001	000000100010010010	111	000000	0011000	0000010010	0010010	10001110000	000000
leucoscepus	1001100	100100	001	0010	100001	01001	100000100001000100	111	001000	0011000	0000010010	0010010	00000110000	000000
swainsonii	1000000	011100	001	1010	000000	01001	000000000001000000	110	000000	0101000	0000010010	0000000	00000110001	000000

TABLE 4. Matrix of estimates of percent nucleotide divergence (δ; lower half matrix) and proportion of shared mtDNA restriction fragments (upper half matrix; Nei 1987) for *Francolinus* species.

	Quail-francolins						Partridge-francolins							
	afr	levo	she	coq	sep	levi	har	nat	ads	cap	afer	swa	leu	cot
Quail-francolins														
africanus		.521	.508	.225	.448	.154	.097	.123	.105	.113	.211	.123	.206	.212
levaillantoides	3.8		.606	.189	.257	.265	.123	.167	.177	.135	.203	.176	.197	.203
shelleyi	4.0	2.9		.250	.400	.207	.109	.135	.145	.156	.232	.172	.197	.169
coqui	9.2	10.3	8.5		.382	.212	.127	.171	.182	.194	.234	.152	.174	.239
sephaena	4.7	8.3	5.4	5.7		.258	.169	.128	.184	.176	.219	.161	.185	.222
levaillantii	11.7	8.1	9.7	9.6	8.3		.316	.342	.310	.212	.282	.233	.317	.262
Partridge-francolins														
hartlaubi	14.9	13.3	14.1	13.0	11.1	6.9		.247	.235	.286	.206	.140	.200	.276
natalensis	13.3	11.2	12.6	11.0	13.0	6.4	8.5		.621	.707	.414	.316	.481	.208
adspersus	14.4	10.8	12.1	10.6	11.3	7.1	8.9	2.7		.597	.439	.338	.459	.250
capensis	13.8	12.6	11.6	10.1	10.8	9.6	7.6	2.0	3.0		.442	.333	.493	.269
afer	9.6	9.8	9.0	8.9	9.3	7.7	9.7	5.2	4.9	4.8		.479	.649	.222
swainsonii	13.3	10.8	11.0	11.8	11.4	8.9	12.4	6.9	6.5	6.6	4.3		.508	.164
leucoscepus	9.7	10.0	10.0	10.9	10.5	6.9	9.9	4.3	4.6	4.1	2.5	4.0		.281
Coturnix c. japonica	9.6	9.8	11.1	8.8	9.2	8.2	7.8	9.7	8.5	8.0	9.2	11.3	7.7	

sis of morpho-behavioral character data for the 41 *Francolinus* species and 9 other perdicine taxa "overflowed" after producing 1,232 equally-parsimonious trees. The Nelson strict-consensus tree is shown in Figure 1B. A similar analysis restricted to francolins overflowed after producing 1,486 trees (consensus tree in Fig. 1C). A third morpho-behavioral analysis restricted to the 13 African *Francolinus* species (from which RFLP data were obtained) produced four trees (consensus tree in Fig. 3A). Analysis of the 99 phylogenetically informative mtDNA fragments for the Japanese Quail and the 13 *Francolinus* species produced three equally-parsimonious trees (consensus tree in Fig. 3B). The analysis of the combined mtDNA and morpho-behavioral character data set for the 13 African francolins produced one tree (Fig. 3C) with an i_{MF} of 3.5%.

The FITCH analysis of the genetic-distance results (Fig. 4) examined 554 trees and differs from the Wagner-parsimony analysis (Fig. 3B) in three respects. First, FITCH grouped *F. swainsonii* with the other two members of Hall's Bare-throated Group. Second, it linked the quail-francolin *F. levaillantii* with *F. hartlaubi*, a partridge-francolin. Third, it placed *F. sephaena* with the three members of Hall's Red-winged Group, and not with *F. coqui*.

Morphometric analyses.—The raw galliform mensural data are available from TMC. In the BMDP2M nearest-neighbor analysis (Appendix 3), all but 2 of the 99 species (98%) examined had morphometric nearest neighbors from the same family; all phasianids had phasianids as their nearest neighbors. Within the Phasianidae, skeletons from 81 of the 86 (94%) species examined had nearest neighbors from the same subfamily. Within the Phasianinae, skeletons of 56 of 62 (90%) species had nearest neighbors from the same subfamily. Within the Perdicini, all but one of the 83 (99%) skeletons from 43 species (98%) had a perdicine nearest neighbor.

Among francolins, 61 of the 64 (95%) skeletons and 22 of the 25 (88%) francolin species studied had francolin nearest neighbors. The mean nearest-neighbor morphometric distance among the 25 francolin species (0.34, SD = 0.06, range 0.26–0.52), was significantly lower ($P < 0.0001$, Mann-Whitney U-test) than that for comparisons of francolins and the 10 perdicines which had francolins as their nearest neighbors (0.46, SD = 0.07, range 0.38–0.57). Among monophyletic species groups of francolins (Figs. 1 and 3), 41 of 46 (89%) skeletons from partridge-francolins (including all five species of Asiatic francolins) had partridge-francolins as their nearest neighbors, but only 11 of 18 (61%) quail-francolins had quail-francolins as their nearest neighbors. In Hall's (1963) species groups, the classification success rate for skeletons was 6 of 9 (66%) for Asiatic francolins, 10 of 15 (66%) for skeletons from members of the Bare-throated Group, 4 of 16 (25%) skeletons

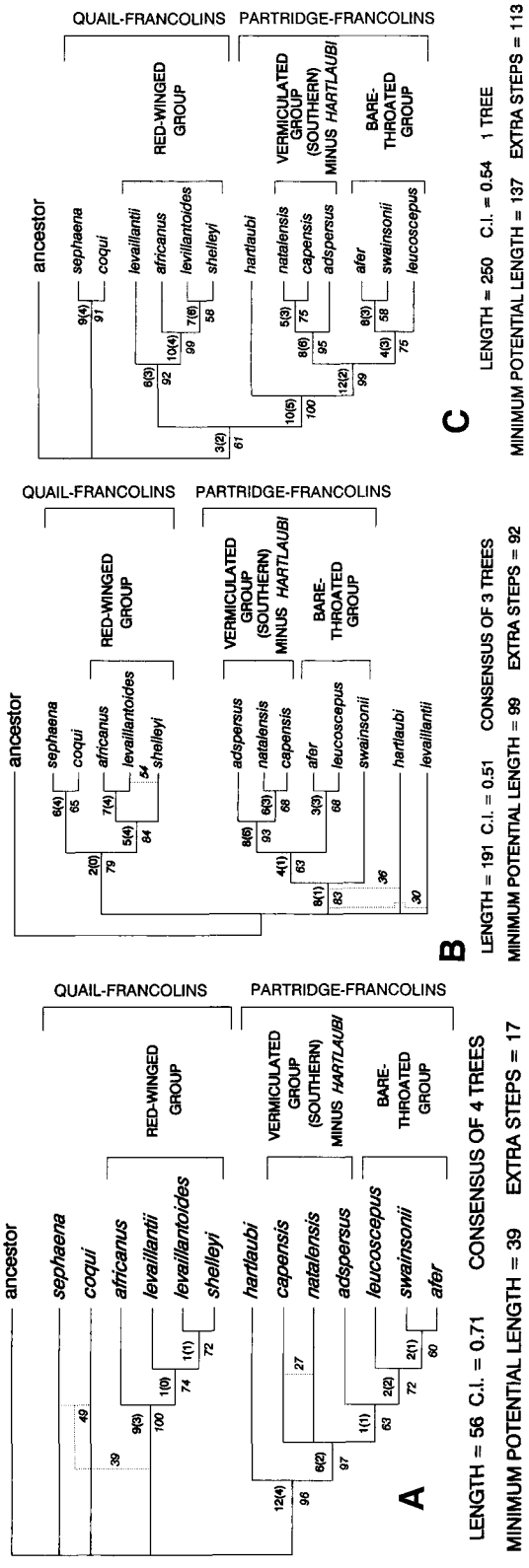

Fig. 3. Most-parsimonious (or strict-consensus) trees for 13 African *Francolinus* species and a quail-like ancestor suggested by: (A) morpho-behavioral character data; (B) mtDNA structure; and (C) combined mtDNA and morpho-behavioral data. Italicized numbers below clade nodes are percentage of times that topology occurred in a 100-replicate PHYLIP bootstrap analysis. Numbers of steps supporting a clade node indicated above node (with numbers of unique and unreversed synapomorphies in parentheses). Group names from Figure 1. Dotted lines indicate topological differences suggested by PHYLIP-BOOT majority-rule consensus tree.

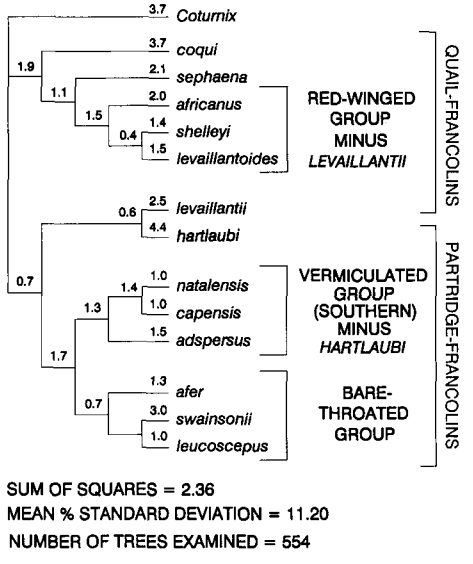

Fig. 4. Tree (rooted on Japanese Quail) based on Fitch-Margoliash algorithm applied to matrix of mtDNA δ values in Table 4. Numbers above nodes are branch lengths.

from members of the Vermiculated Group, and 6 of 6 for skeletons from members of the Red-winged Group. At the species level, in 69 instances for which more than one individual of the same species were analyzed, 57 (83%) of the nearest neighbors were conspecifics and the nearest neighbors of the remaining 12 were congeners.

DISCUSSION

Francolins as a monophyletic group.—Phylogenetic analyses of a range of morpho-behavioral characters, including those traditionally used to distinguish francolins from other perdicines (Appendix 1, Fig. 1B), do not confirm the monophyly of *Francolinus*. If Figure 1B is modified minimally to support the monophyly of *Francolinus* (i.e. if nonfrancolins that cluster within the francolin assemblage are shifted out to form a basal polytomy), the resulting tree is 19 steps longer. Moreover, if the francolins are analyzed alone, two major clades emerge (Fig. 1C), one comprised of quail-francolins (minus *pondicerianus*) and the other of partridge-francolins. Thus, should *Francolinus* prove to be a monophyletic assemblage, Milstein and Wolff's (1987) quail-francolins (*patryse*) and partridge-francolins (*fisante*) would emerge as monophyletic groups.

Morpho-behavioral character data also support the monophyly of at least four major monophyletic groups among the francolins (Figs. 1B and 1C): (1) Hall's (1963) Spotted Group of francolins, plus the two other Asiatic francolins (*pondicerianus* and *gularis*); (2) Hall's Red-tailed Group plus *F. lathami*; (3) Hall's Red-winged Group plus *F. streptophorus*; and (4) a large assemblage of partridge-francolins, including at least three monophyletic groups that correspond to Hall's Scaly, Bare-throated and Montane groups. RFLP analysis (Figs. 3B and 4) supports the monophyly of three of the five southern African members of Hall's Vermiculated Group (*adspersus, natalensis* and *capensis*). We provisionally accept the monophyly of these three species, plus *F. hildebrandti*, which (in male adults) closely resembles and is distributed parapatrically with *natalensis* (Crowe et al. 1986). Furthermore, although there as yet are no synapomorphies to unite the four remaining members of Hall's Vermiculated Group from northern and eastern Africa (*bicalcaratus, clappertoni, icterorhynchus, harwoodi*), their strong overall similarity and parapatric distributions (Crowe et al. 1986) suggest that they also form a monophyletic group within the partridge-francolin assemblage.

Two francolins (*F. sephaena* and *F. nahani*) fall outside the major francolin clades, grouping paraphyletically with an assemblage of primarily Indo-Malaysian perdicines (Fig. 1B). RFLP data (Fig. 3B) and measures of genetic distance for the 13 species of African francolins (Table 4, Fig. 4) suggest that *F. sephaena* has affinities with *F. coqui* and other quail-francolins (e.g. *F. africanus*) of Hall's Red-winged Group. Furthermore, if all 41 francolin species are analyzed with the RFLP data included for the 13 African species, *sephaena* joins the Red-tailed/*lathami* Group.

The affinities of *F. nahani*, which is virtually unknown biologically, remain obscure. We agree with Hall (1963) that its small size, dark coloration and spotted plumage are probably not indicative of affinities with *F. lathami*, because all three attributes are common adaptations to living in tropical-forest conditions. One possibility is that *nahani* is not a francolin and, perhaps like several other Afrotropical forest taxa (e.g. *Afropavo, Tigriornis, Pseudocalyptomena,*

Phodilus and *Himantornis*), it is a relictual form most closely related to an Indo-Malaysian taxon (Olson 1973). However, we agree with Hall (1963:166–167) that a combination of features (e.g. lack of sexual dimorphism, red tarsi, white-streaked belly, crimson-based bill, and bare skin below and behind the eye) place *nahani* with the partridge-francolin clade, possibly with Hall's Scaly Group.

Genetic variation.—In two species for which RFLPs of individuals from widely separated localities were available, we found intraspecific divergence values of an order of magnitude lower than the δ values between even the least divergent pairs of francolins ($\delta = 0.3$ between two *F. africanus* and $\delta = 0.1$ between two *F. levaillantii*). This level of mtDNA divergence is similar to that found within other bird species (Shields and Helm-Bychowski 1988) and mammals (Wilson et al. 1985).

At the interspecific level, 11 of the 13 francolins form four clusters (*coqui/sephaena; levaillantoides/shelleyi/africanus; adspersus/natalensis/capensis;* and *leucoscepus/afer/swainsonii*) of genetically similar species ($\delta = 2$–5.7; $\bar{x} = 3.4$). The genetic distances between members of different clusters tend to be much larger ($\delta = 8.9$–14.4; $\bar{x} = 9.4$), about the same magnitude as differences between francolins and the Japanese Quail.

The two remaining francolin species, *hartlaubi* and *levaillantii*, appear to be relatively distantly related to the other francolins studied ($\delta = 6.4$–14.9). The remote placement of one of these two "outsiders," *F. hartlaubi*, is not surprising given that, in many other ways, it is the most divergent francolin included in this study. It is the most distinct francolin morphometrically (Appendix 3), with a Euclidian distance (0.52) to the nearest francolin much greater than the next largest nearest-neighbor distance (0.46) between pairs of francolins. From a morpho-behavioral perspective, it is a basal taxon in the partridge-francolin assemblage (Figs. 1B, 1C, and 3A). Unlike other francolins, it is found in a highly specific habitat (isolated, rocky outcrops surrounded by subdesert steppe) and has an extremely complex, antiphonal advertisement call (Komen 1987). Osteologically, its morphometric nearest neighbor is the quail-like (Frost 1975) Madagascar Partridge (*Margaroperdix madagarensis;* Appendix 3). Like *Coturnix* spp., males of *F. hartlaubi* have extremely large, ovoid testes two to three times the size of those of any other francolin we have examined (T. M. Crowe and J. Komen, unpubl. data). The genetic, morphometric and morpho-behavioral data suggest that, if it is a francolin, Hartlaub's Francolin is a product of an early divergence within the *Francolinus* lineage.

The relatively isolated genetic position of the Redwing Francolin (*F. levaillantii*) is much more difficult to explain. Its unresolved or basal position within the African francolins (Fig. 3B) and its apparent genetic affinities to partridge-francolins (Fig. 4, Table 4) were unexpected given that Hall (1963) named her Red-winged Group (Fig. 1A) after the common name of this typical quail-francolin. Nevertheless, the Redwing Francolin's first five genetic nearest neighbors are partridge-francolins (Table 4). This genetic similarity between a quail-francolin and the morphologically, behaviorally and ecologically distinct partridge-francolins can be explained by three hypotheses. First, the δ value between the Redwing Francolin and its nearest genetic neighbor, *F. natalensis*, is 6.4; *F. natalensis* is a partridge-francolin and, perhaps as recently as 3×10^6 y.b.p., there was gene flow between quail- and partridge-francolins such that *levaillantii* males hybridized successfully with female partridge-francolins, and "partridge" mtDNA introgressed into the *levaillantii* lineage through subsequent back-crossing of fertile hybrid females with *levaillantii* males. Alternatively, *levaillantii* represents a stem species that possesses an ancestral quail-like phenotype and mtDNA haplotype. Finally, *levaillantii* is either a partridge-francolin that convergently acquired quail-francolin morphology and behavior, or a quail-francolin that convergently acquired partridge-francolin RFLPs. These hypotheses can be tested through further study of mtDNA by restriction-site mapping and sequencing, as well as by study of the nuclear genome (e.g. using DNA-DNA hybridization, restriction-fragment/site analysis, or protein electrophoresis) and other character systems (e.g. the syrinx).

Our RFLP results tend to favor the stem-species hypothesis. Of the 11 RFLPs in *F. levaillantii* not shared with *Coturnix*, three are shared with both quail- and partridge-francolins, and four each with only quail-francolins and and partridge-francolins. Furthermore, *levaillantii* lacks most of the RFLPs that are synapomorphies for

the Red-winged Group (e.g. characters 6, 25, and 95 in Table 3).

Divergence times.—Applying the estimate of a mean rate of divergence of 2 δ units per 10^6 years (Brown et al. 1982, Shields and Wilson 1987, Shields and Helm-Bychowski 1988), which is based on fossil-calibrated studies of primates and a range of avian taxa (including galliforms), the francolins appear to have diverged from the quail lineage at least 3.8×10^6 y.b.p. The most recent speciation event was at least 10^6 years ago. These divergence times agree with those suggested by Helm-Bychowski and Wilson (1986) for other groups of phasianids. Our minimum estimate for the age of the genus is supported by the existence of a well-differentiated francolin in southern Africa nearly 5×10^6 y.b.p. (Crowe 1992). Thus, our results are consistent with Hall's hypotheses of an ancient origin for *Francolinus*. However, if mid-Miocene fossil humeri from Arrisdrift, Namibia, prove to be from a primitive francolin (Crowe 1992), this divergence might not have been as long ago as the Oligocene (Hall 1963, Sibley and Ahlquist 1985). At the interspecific level, our results do not support Hall's hypothesis that there may have been a major bout of speciation in African francolins during the late Pleistocene, or Sibley and Ahlquist's (1985) suggestion that *F. capensis* and *F. natalensis* diverged from one another 9×10^6 y.b.p.

Biogeography.—Should *Francolinus* prove to be a monophyletic assemblage, our results (Fig. 1B) do not support Hall's hypothesis that the genus evolved first in Asia. A more likely scenario is that the genus evolved in Africa, with an early offshoot of the partridge-francolin lineage secondarily dispersing into and, subsequently, diverging within Asia. With regard to intra-African francolin biogeography, a comparison of δ values for francolins and African mole-rats (Honeycutt et al. 1987) suggests that vicariance events that promoted speciation in these groups were not contemporaneous. For example, the δ values between the endemic east African mole-rats (*Heterocephalus glaber* and *Heliophobius argentocinereus*) and their endemic southern African sister taxa range from 14 to 28 (i.e. $7–14 \times 10^6$ y.b.p.), whereas that between east African endemic *F. leucoscepus* and the southern African endemics (*F. afer* and *swainsonii*) are 2.5 and 4.0, respectively. This implies a much more recent divergence. Furthermore, *F. afer*, the geographically intermediate species in this bare-throated trio, is much closer to *leucoscepus* than to *swainsonii*. Perhaps *F. afer* evolved even more recently in central Africa from a relictual population of proto-*leucoscepus*. Assuming that *F. hartlaubi*, one of the many bird species endemic to southwestern Africa (Crowe and Crowe 1982), evolved *in situ*, its relatively remote genetic distance from other partridge-francolins suggests that there was at least a third, much more ancient, bout of francolin speciation in arid southern Africa. Thus, the opening of the "arid corridor" between east and southern Africa (Winterbottom 1967) was the vicariance event that led to the speciation of these bare-throated francolins (Crowe et al. 1986). It occurred much more recently than the closure of the "corridor," which may have promoted speciation within the mole-rats and of *F. hartlaubi*. Hall (1963) has already commented on the importance of the corridor as the common boundary between the "black-and-white" and "vermiculated" subspecies groups within *F. afer*.

Among the more quail-like members of Hall's Red-winged Group, our results suggest a biogeographical scenario similar to one Hall (1963: 158–160) proposed. Assuming that *F. levaillantii* is a member of the Red-winged Group, the ancestral quail-like francolin could have been a widespread taxon, and present-day extant taxa that are more localized could have speciated *in situ* when isolated during periods of long-term, climatic fluctuations. During such periods, members of the Red-winged Group, most of which seem to be generally adapted to cooler climatic conditions (Crowe et al. 1986), may have been isolated (and subsequently speciated) within relatively cool, disjunctly distributed highlands. If Hall (1963) was correct in assuming that *F. levaillantoides* evolved in east Africa, its low δ value (2.9) to its sister-species (*F. shelleyi*) suggests that it only recently spread to, and became secondarily isolated in, southwestern Africa.

Taxonomy.—Previous researchers (e.g. Ogilvie-Grant 1896, Hall 1963, Crowe and Crowe 1985) have lumped the francolins into one or, at most, two genera because there are "linking taxa" that form a "graded series" (Chapin 1926) between otherwise distinct subgroupings (i.e. Hall's groups in Fig. 1). For example, *F. sephaena* is the key taxon that links the quail- and partridge-francolins from a morpho-behavioral perspective (Figs. 1B and C), because it has a quail-francolin bill and plumage. However, it

also has red tarsi and roosts in trees like many partridge-francolins. Nevertheless, in the light of the additional morpho-behavioral and RFLP character data, this francolin falls decisively with the quail-francolins and probably with those of Hall's Red-tailed Group. Therefore, we feel that, independent of the question of monophyly of the francolins, *Francolinus* should be partitioned into at least four genera:

Genus *Francolinus* Stephens 1819
[Subgenus *Francolinus* Stephens 1819]
pictus, francolinus, pintadeanus
[Subgenus *Ortygornis* Reichenbach 1853]
pondicerianus
[Subgenus **nov.** *Limnocolinus*]
gularis

Genus *Peliperdix* Bonaparte 1856
[Subgenus *Peliperdix* Bonaparte 1856]
coqui, albogularis, schlegelii, lathami
[Subgenus *Dendroperdix* Roberts 1922]
sephaena

Genus *Scleroptila* Blythe 1849
streptophorus, finschi, levaillantii, africanus, psilolaemus, shelleyi, levaillantoides

Genus *Pternistis* Wagler 1832
[Subgenus *Acentrortyx* Chapin 1926]
nahani
[Subgenus *Chapinortyx* Roberts 1928]
hartlaubi
[Subgenus *Chaetopus* Swainson 1837]
bicalcaratus, icterorhynchus, clappertoni, harwoodi
[Subgenus **nov.** *Notocolinus*]
adspersus, capensis, natalensis, hildebrandti
[Subgenus **nov.** *Squamatocolinus*]
squamatus, ahantensis, griseostriatus
[Subgenus *Pternistis* Wagler 1832]
leucoscepus, rufopictus, afer, swainsonii
[Subgenus **nov.** *Oreocolinus*]
jacksoni, nobilis, camerunensis, swierstrai, castaneicollis, erckelii, ochropectus

The new subgenus *Limnocolinus* differs from the other subgenera in *Francolinus* in having: long toes (Hall 1963); large-bodied males (morpho-behavioral character 1 in Appendix 1 and Table 2); streaked belly plumage (character 15); uniform brownish-grey primaries (character 19). Three of the members of the subgenus *Notocolinus* (mtDNA unavailable from *F. hildebrandti*) are distinguished by four synapomorphic RFLPs (characters 3, 23, 66, and 96 in Table 3). The members of the subgenus *Squamatocolinus* differ from other *Pternistis* species in having dark edging to their belly plumage (17), which gives them a scaly appearance (Hall 1963). Members of *Oreocolinus* differ from those of other subgenera in *Pternistis* by the uniform brown crown, back, primaries, and tails of the males (character 13; Hall 1963).

Morphometrics and phylogenetics.—Assuming the correctness of the morpho-behavioral phylogenies (Figs. 1B and 1C) and the highly congruent phylogeny based on morpho-behavioral and RFLP characters (Fig. 3C), our results (Appendix 3) suggest that a morphometric approach can correctly assign galliform osteological material to independently derived monophyletic taxa. This finding is in marked contrast to those from other morphometric and phylogenetic studies (e.g. Zink and Avise 1990). Our empirical results could be useful for studies of fossil galliforms for which there are few reliable osteological synapomorphies below the family level (Cracraft 1981). For example, Crowe and Short (1992) and T. M. Crowe (unpubl. manuscript) have shown that both morphometric and synapomorphic characters place a fossil humerus from the Oligocene of Nebraska and *Gallinuloides wyomingensis* (a fossil galliform from the Eocene of Wyoming) within the Gallinuloididae, the sister group of the Phasianidae. This challenges Tordoff and Macdonald's (1957) hypothesis that *Gallinuloides* was a cracid and eliminates the need to hypothesize that the Cracidae originated in the Nearctic and, subsequently, dispersed and diversified within the Neotropics (Vuilleumier 1965).

At the genus level, we suggest that the francolins form a relatively homogeneous morphometric assemblage within the Perdicini (Appendix 3). Indeed, the phylogenetically most distinct francolins (e.g. *hartlaubi, sephaena, coqui,* and *lathami*) also are the most morphometrically distinct francolins (Appendix 3). However, at the species-group level (=subgenus), the nearest-neighbor morphometric approach had much poorer success in correctly placing skeletons. In our study, 93% of the skeletons from partridge-francolins (e.g. members of *Francolinus* and *Pternistis*) had partridge-francolins as their nearest neighbors, and all six skeletons of *Scleroptila* spp. had congeners as nearest neighbors. No more than two-thirds of the skeletons from any of the other francolin genera or subgenera had nearest neighbors from the same supra-

specific taxon. Thus, the congruence between morphometric and qualitative morpho-behavioral characters appears to break down below the level of the genus.

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LITERATURE CITED

BOCK, W. J., AND J. FARRAND, JR. 1980. The number of species and genera of Recent birds. Am. Mus. Novit. No. 2703:1-29.

BROWN, W. M. 1980. Polymorphism of mitochondrial DNA of humans as revealed by restriction endonuclease analysis. Proc. Natl. Acad. Sci. USA 77:3605-3609.

BROWN, W. M., E. M. PRAGER, A. WANG, AND A. C. WILSON. 1982. Mitochondrial DNA sequences of primates: Tempo and mode of evolution. J. Mol. Evol. 18:225-239.

CHAPIN, J. P. 1926. A new genus *Acentrortyx* proposed for *Francolinus nahani* Dubois. Auk 43:235.

CRACRAFT, J. 1981. Toward a phylogenetic classification of the Recent birds of the world (class Aves). Auk 98:681-714.

CROWE, T. M. 1988. Molecules vs morphology in phylogenetics: A non-controversy. Trans. R. Soc. S. Afr. 46:317-334.

CROWE, T. M. 1992. Morphometric research on Miocene and Pliocene fossil phasianids from the west coast of southern Africa: Some preliminary taxonomic and phylogenetic conclusions. Proc. 7th Pan African Ornithol. Congr. In press.

CROWE, T. M., AND A. A. CROWE. 1982. Patterns of distribution, diversity and endemism in Afrotropical birds. J. Zool. (Lond.) 198:417-442.

CROWE, T. M., AND A. A. CROWE. 1985. The genus *Francolinus* as a model for avian evolution and biogeography in Africa: I. Relationships among species. Pages 207-231 *in* Proceedings of the International Symposium on African Vertebrates (K.-L. Schuchmann, Ed.). Museum Alexander Koenig, Bonn.

CROWE, T. M., G. S. KEITH, AND L. H. BROWN. 1986. Galliformes. Pages 1-75 *in* Birds of Africa, vol. 2 (E. K. Urban, C. H. Fry, and G. S. Keith, Eds.). Academic Press, London.

CROWE, T. M., AND L. L. SHORT. 1992. A new gallinaceous bird from the Oligocene of Nebraska with comments on the phylogenetic position of the Gallinuloididae. Science Series, Los Angeles County Natural History Museum. No. 36.

DENSMORE, L. D., J. W. WRIGHT, AND W. M. BROWN. 1985. Length variation and heteroplasmy are frequent in the mitochondrial DNA from parthenogenetic and bisexual lizards (genus *Cnemidophorus*). Genetics 110:689-707.

DIXON, W. J. (ED.) 1985. BMDP statistical software. Univ. California Press, Los Angeles.

FARRIS, J. S. 1970. Methods for computing Wagner trees. Syst. Zool. 19:83-92.

FARRIS, J. S. 1988. Reference manual for Hennig86 version 1.5. Published by the author. Port Jefferson Station, New York.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. Evolution 39:783-791.

FELSENSTEIN, J. 1987. PHYLIP (phylogeny inference package), version 3.0. Univ. Washington, Seattle.

FITCH, W. M., AND E. MARGOLIASH. 1967. Construction of phylogenetic trees. Science 155:279-284.

FROST, P. G. H. 1975. The systematic position of the Madagascar Partridge *Margaroperdix madagascariensis* (Scopoli). Bull. Br. Ornithol. Club 95:64-68.

GUTIÉRREZ, R. J., R. M. ZINK, AND S. Y. YANG. 1983. Genic variation, systematic, and biogeographic relationships of some galliform birds. Auk 100: 33–47.

HALL, B. P. 1963. The francolins, a study in speciation. Bull. Br. Mus. (Nat. Hist.) 10:8–204.

HELM-BYCHOWSKI, K. M., AND A. C. WILSON. 1986. Rates of nuclear DNA evolution in pheasant-like birds: Evidence from restriction maps. Proc. Natl. Acad. Sci. USA. 83:688–692.

HONEYCUTT, R. L., S. V. EDWARDS, K. NELSON, AND E. NEVO. 1987. Mitochondrial DNA variation and the phylogeny of African mole rats (Rodentia: Bathyergidae). Syst. Zool. 36:280–292.

JOHNSGARD, P. A. 1988. The quails, partridges, and francolins of the world. Oxford Univ. Press, Oxford.

KLUGE, A. G. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among *Epicrates* (Boidae, Serpentes). Syst. Zool. 38:7–25.

KOMEN, J. 1987. Preliminary observations of the social pattern, behaviour and vocalization of Hartlaub's Francolin. S. Afr. J. Wildl. Res. Suppl. 1: 82–86.

MICKEVICH, M. F., AND J. S. FARRIS. 1981. The implications of congruence in *Menidia*. Syst. Zool. 30:351–370.

MILSTEIN, P. LE S., AND S. W. WOLFF. 1987. The oversimplification of our "francolins." S. Afr. J. Wildl. Res. Suppl. 1:58–65.

MORONY, J. J., W. J. BOCK, AND J. FARRAND. 1975. Reference list of the birds of the world. American Museum of Natural History, New York.

NEI, M. 1987. Molecular evolutionary genetics. Columbia Univ. Press, New York.

OGILVIE-GRANT, W. R. 1896. A hand-book to the gamebirds. Edward Lloyd, Ltd., London.

OLSON, S. L. 1973. A classification of the Rallidae. Wilson Bull. 85:381–416.

OLSON, S. L. 1985. The fossil record of birds. Pages 80–238 *in* Avian biology, vol. 8 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.

RANDI, E., G. FUSCO, R. LORENZINI, AND T. M. CROWE. 1991. Phylogenetic relationships and rates of allozyme evolution in the Phasianoidea. Biochem. Syst. Ecol. 19:213–221.

SCHÖNWETTER, M. 1967. Handbuch der Oologie, Lieferung 8. Berlin, Akademie-Verlag.

SHIELDS, G. F., AND K. HELM-BYCHOWSKI. 1988. Mitochondrial DNA of birds. Curr. Ornithol. 5:273–295.

SHIELDS, G. F., AND A. C. WILSON. 1987. Calibration of mitochondrial DNA evolution in geese. J. Mol. Evol. 24:212–217.

SIBLEY, C. G., AND J. E. AHLQUIST. 1985. The relationships of some groups of African birds, based on comparisons of the genetic material, DNA. Pages 115–161 *in* Proceedings of the International Symposium on African Vertebrates (K.-L. Schuchmann, Ed.). Museum Alexander Koenig, Bonn.

SIMBERLOFF, D. 1987. Calculating probabilities that cladograms match. A method of biogeographic inference. Syst. Zool. 36:175–195.

STEADMAN, D. W. 1980. A review of the osteology and paleontology of turkeys (Aves: Meleagridinae). Contrib. Sci. Nat. Hist. Mus. Los Angeles County 330:131–207.

STOCK, A. D., AND T. D. BUNCH. 1982. The evolutionary implications of chromosome banding pattern homologies in the bird order Galliformes. Cytogenet. Cell Genet. 34:136–148.

SWOFFORD, D. L., AND G. J. OLSEN. 1990. Pages 411–501 *in* Molecular systematics (D. M. Hillis and C. Moritz, Eds.). Sinauer Associates, Sunderland, Massachusetts.

TORDOFF, H. B., AND J. R. MACDONALD. 1957. A new bird (family Cracidae) from the early Oligocene of South Dakota. Auk 74:174–184.

VERHEYEN, R. 1956. Contribution à l'anatomie et à la systématique de Galliformes. Inst. R. Sci. Nat. Belg. 32:1–24.

VUILLEUMIER, F. 1965. Relationships within the Cracidae. Bull. Mus. Comp. Zool. 134(1):1–27.

WILSON, A. C., R. L. CANN, S. M. CARR, M. GEORGE, U. B. GYLLENSTEIN, K. M. HELM-BYCHOWSKI, R. G. HIGUCHI, S. R. PALUMBI, E. M. PRAGER, R. D. SAGE, AND M. STONEKING. 1985. Mitochondrial DNA and two perspectives on evolutionary genetics. Biol. J. Linnaean Soc. 26:375–400.

WINTERBOTTOM, J. M. 1967. Climatological implications of avifaunal resemblances between southwestern Africa and Somaliland. Pages 77–79 *in* Paleoecology of Africa, vol. 2 (E. M. Van Zinderen Bakker, Ed.). A. A. Balkema, Amsterdam.

WOLTERS, H. E. 1975. Die Vogelarten der Erde. Paul Parey, Berlin.

ZINK, R. M., AND J. C. AVISE. 1990. Patterns of mitochondrial DNA and allozyme evolution in the avian genus *Ammodramus*. Syst. Zool. 39:148–161.

APPENDIX 1. Descriptions of 34 morpho-behavioral characters from 41 *Francolinus* species, several non-francolin perdicines, and a hypothetical quail-like ancestor. Suggested plesiomorphic character states listed first. Characters for which polarity decisions based on ontogenetic criteria marked with asterisk (*). Otherwise, polarity based on outgroup analysis.

1*. Mean male mass (g): (0) 95–110; (1) 120–370; (2) >400. **2*.** Sexual size dimorphism (based on wing and tail measurements): (0) male ≤10% larger; (1) male >10% larger. **3*.** Spur complement: (0) absent; (1) 1 spur; (2) 2 spurs, upper shorter; (3) 2 spurs of equal length; (4) 2 spurs, upper longer. **4.** Spur position: (0) absent or closer to distal end of tarsus; (1) closer to proximal end of tarsus. **5*.** Cere: (0) feathered; (1) moderately cartilaginous; (2) strongly cartilaginous. **6.** Culmen length/$\log_{10}$ wing: (0) ≤11.7; (1) >11.7. **7*.** Bill color: (0) yellow or black; (1) with at least some orange or red; (2) all red. **8*.** Leg color: (0) yellow; (1) orange or red; (2) brown or black. **9*.** Naked skin around eye: (0) absent; (1) present. **10*.** Throat: (0) feathered; (1) unfeathered. **11.** Throat color: (0) undifferentiated from surrounding skin; (1) yellow; (2) red. **12*.** Dorsal plumage 1: (0) quail-like or any of states in characters 13 and 14; (1) quail-like with buff-grey vermiculations; (2) vermiculated with barring and/or streaking, or streaked. **13.** Dorsal plumage 2: (0) any of states in characters 12 and 14; (1) uniform brownish or rufous grey in males. **14.** Dorsal plumage 3: (0) any of states in characters 12 and 13; (1) upper back spotted. **15*.** Belly plumage 1: (0) uniform buff; (1) barred; (2) streaked. **16.** Belly plumage 2: (0) states 0–2 under character 15; (1) black and streaked white with broad black shaft streak. **17.** Belly plumage 3: (0) states 0–2 under character 15 and states 0–1 under character 16; (1) feathers with very narrow dark edges giving a scaly appearance. **18.** Black and white "necklace" plumage on side of head and neck: (0) none; (1) restricted to narrow strip behind eye and bordering throat; (2) extensive strip running from behind eye to below throat. **19*.** Color of primaries: (2) uniform brownish grey; (3) grey with lighter vermiculations; 4 = grey, streaked with white or buff; (0) rufous-chestnut; (1) grey with some rufous-chestnut. **20*.** Color of under-tail coverts: (0) rufous; (1) rufous with black and white barring; (2) barred and/or barred and vermiculated with black and white; (3) barred and streaked, or streaked with black and white; (4) black. **21.** Tail shape: (0) flat; (1) vaulted. **22.** Hallux claw: (0) well developed; (1) absent or rudimentary. **23.** Chick eye stripe: (0) single stripe; (1) faint second stripe; (2) well-developed second stripe. **24.** General form of advertisement call 1: (0) quail-like "wheet whit-it"; (1) grating "kee-raack." **25.** General form of advertisement call 2: (0) states 0–2 under characters 24; (1) whistling, tonal call. **26.** Specialized tonal advertisement call 1: (0) absent; (1) 8–9 low-pitched, cooing notes, ascending and then descending in pitch; (2) same as state 1, but overall pitch much higher; (3) same as state 2, but speed of delivery doubled or trebled. **27.** Specialized tonal advertisement call 2: (0) absent; (1) quail-like "wheet whit-it"; (2) high-pitched "whee-hee-hee-hee, whee-pee-eu" or "whee-hee-hee-hee, whee-hee"; (3) high-pitched "kee-bee-tillee." **28.** Response to playback of advertisement call: (0) none or poor; (1) strong, at least seasonally. **29.** Known to perch in trees: (0) no; (1) yes. **30.** Number of tail feathers: (0) = <14; (1) = 14. **31.** Tail length/wing length: (0) ≤0.66; (1) >0.66. **32.** Stance: (0) squat; (1) upright. **33.** Incubation period: (0) ≤21 days; (1) >21 days. **34.** Shell thickness: (0) ≤0.5 mm; (1) >0.5 mm.

APPENDIX 2. Description of mensural characters of skeleton. Character number and abbreviation followed by indication of reference points in Figure 2 (in parentheses) and character description.

1. PMAXL1 (b. 1–2): premaxilla length, medially from posterior edge to anterior tip of premaxilla. **2.** PMAXL2 (b. 1–3): premaxilla length from narial opening, laterомedially from anterior edge of nares to anterior tip of premaxilla. **3.** PMAXD (a. 4–5): upper mandible depth, medially at anterior edge of nares. **4.** PMW1 (c. 6–7): premaxilla width at anterior margin of nares. **5.** PMW2 (c. 8–9): premaxilla width midway between anterior margin of nares and tip of premaxilla. **6.** FW1 (b. 10–11): width of frontals at distal end of nasal process of premaxilla. **7.** FW2 (b. 12–13): width of frontals at midorbit. **8.** FW3 (b. 14–15): width of frontals above palatine pterygoid junction. **9.** POW (a. 16 to same point on other side of skull): postorbital skull width at base of postfrontal orbital processes. **10.** BTPW (d. 17–18): basitemporal plate width. **11.** BTPL (d. 19–20): basitemporal plate length from anterior margin of occipital condyle to anterior edge of projection above basisphenoid. **12.** OD (a. 21–22): occipital depth from anterior margin of occipital condyle to dorsal edge of supraoccipital. **13.** MNPW (c. 23–24): mid-narial nasal process width. **14.** NAP (b. 3–25): nares anterior–posterior length. **15.** LNBW (a. 26–27): width of lateral nasal bar at midpoint between top of nares and jugal-nasal junction. **16.** SKAP (b. 2–28): skull anterior–posterior length from supraoccipital to posterior tip of premaxilla nasal process. **17.** MPW (a. 29 to same point on other side of skull): mid-parietal skull width, measured dorsally at junction of quadrate

APPENDIX 2. Continued.

and parietals. **18.** PPW (d. 30–31): posterior premaxilla width at origin of zygomatic maxillary process. **19.** OPQL (a. 32–33): length of orbital process of quadrate. **20.** PRAL (g. 34–35): pre-acetabular pelvis length. **21.** POAL (g. 36–37): postacetabular pelvis length. **22.** TPL (e. 34–38): total pelvic length. **23.** PPL (g. 35–39): pectineal process length. **24.** PRW (e. 40–41): pelvis rear width. **25.** PFW1 (e. 42–43): pelvis frontal width 1. **26.** PFW2 (e. 44–45): pelvis frontal width 2. **27.** IF (g. 46–47): ischiadic foramen anteroposterior diameter. **28.** PD (g. 40–48): pelvis depth. **29.** RBW (f. 49–50): renal bar width. **30.** STL (r. 51–52): sternum length. **31.** SD1 (r. 51–53): sternum depth at anterior end. **32.** SD2 (r. 54–55): sternum depth at half-way point. **33.** SND (s. 52–56): depth of internal sternal notch. **34.** SW (s. 57–58): sternum anterior width. **35.** ALPL (r. 59–60): anterior lateral sternal process length. **36.** ALPW (r. 61–62): anterior lateral sternal process width. **37.** PLPW (r. 63–64): outer posterior lateral process width. **38.** CL1 (h. 65–66): coracoid length 1. **39.** CL2 (h. 65–67): coracoid length 2. **40.** CW (h. 68–69): coracoid width half-way down shaft. **41.** CSW (h. 65–70): coracoid width from head to distal edge of scapular facet. **42.** CDTW (h. 67–71): total width of coracoid at sternal end. **43.** CDW1 (h. 66–71): coracoid sternal end width 1. **44.** CDW2 (h. 66–67): coracoid sternal end width 2. **45.** CDW3 (i. 72–73): coracoid sternal end width 3. **46.** CDW4 (i. 74–75): coracoid sternal end width 4. **47.** CPWIII (j. 76–77): width of metacarpal III at midpoint. **48.** CPWIV (j. 78–79): width of metacarpal IV at midpoint. **49.** CPWT (j. 76–79): total width of carpometacarpus. **50.** CPL (j. 80–81): carpometacarpus length. **51.** FL (k. 82–83): furcula length. **52.** FW (k. 84–85): furcula width half-way along its length. **53.** ML1 (a. 86–87): mandible length 1. **54.** ML2 (a. 86–88): mandible length 2. **55.** MD (a. 89–90): mandible depth. **56.** TMTL (l. 91–92): tarsometatarsus length. **57.** TMDW (l. 93–94): tarsometatarsus distal width. **58.** TMHW (l. 95–96): tarsometatarsus width half-way along shaft. **59.** TMHD (m. 97–98): tarsometatarsus hypotarsal depth. **60.** SCL (n. 99–100): scapula total length. **61.** SCFW (n. 101–102): scapular facet width. **62.** SCW (n. 103–104): scapular width two-thirds along its total length from coracoid. **63.** TBTL (q. 105–106): tibiotarsus length. **64.** TBW (q. 107–108): tibiotarsus width half-way down shaft. **65.** TBDW (q. 109–110): tibiotarsus distal width. **66.** TBPW (q. 111–112): tibiotarsus proximal width. **67.** FEMW (o. 113–114): femur width half-way down shaft. **68.** FEML (o. 115–116): femur length. **69.** HMTL (p. 117–118): humerus length. **70.** HMPW (p. 119–120): humerus proximal width. **71.** HMDW (p. 121–122): humerus distal width. **72.** HMHW (p. 123–124): humerus width half-way down shaft. **73.** HMFD (p. 125–126): humerus pneumatic foramen diameter.

APPENDIX 3. Scientific names of species in morphometric analyses and their morphometric "nearest neighbors." In cases in which nearest neighbor was a conspecific, the nearest species is also listed. Species not correctly assigned by nearest-neighbor method signified with an asterisk. Family or subfamily name followed by species, with nearest neighbor(s) and Euclidian distance(s) in parentheses.

Megapodiidae: *Megapodius freycinet** (*Agelastes meleagrides*, 0.82); *Alectura lathami* (*M. maleo*, 0.66); *Macrocephalon maleo* (*A. lathami*, 0.66). **Cracidae**: *Ortalis vetula** (*Polyplectron bicalcaratum*, 0.69); *Penelope purpurascens* (*C. globulosa*, 0.51); *Aburria pipile* (*C. unicolor*, 0.50); *Champaetes unicolor* (*A. pipile*, 0.50); *Nothocrax urumutum* (*C. globulosa*, 0.83); *Mitu mitu* (*P. pauxi*, 0.42); *Pauxi pauxi* (*M. mitu*, 0.42); *Crax rubra* (*C. alberti*, 0.55); *C. alberti* (*M. mitu*, 0.51); *C. globulosa* (*P. purpurascens*, 0.51). **Phasianidae, Meleagridinae**: *Meleagris gallopavo* (*M. gallopavo*, 0.43; *M. ocellata*, 1.02); *M. gallopavo* (*M. gallopavo*, 0.43; *M. ocellata*, 0.89); *M. ocellata** (*P. cristatus*, 0.69). **Tetraoninae**: *Lagopus mutus* (*B. umbellus*, 0.57); *Tetrao tetrix* (*T. cupido*, 0.59); *T. urogallus* (*C. urophasianus*, 0.89); *Bonasa umbellus* (*L. mutus*, 0.57); *Centrocercus urophasianus* (*T. tetrix*, 0.73); *Tympanuchus cupido* (*T. cupido*, 0.36; *T. tetrix*, 0.59); *T. cupido* (*T. cupido*, 0.36; *T. tetrix*, 0.59). **Odontophorinae**: *Dendrortyx leucophrys** (*Melanoperdix nigra*, 0.57); *Oreortyx pictus* (*C. virginianus*, 0.48); *Callipepla squamata* (*L. californicus*, 0.49); *Lophortyx californicus* (*C. virginianus*, 0.36); *Philortyx fasciatus* (*L. californicus*, 0.43); *Colinus virginianus* (*L. californicus*, 0.36); *Odontophorus guttatus** (*Melanoperdix nigra*, 0.49); *Dactylortyx thoracicus* (*C. montezumae*, 0.48); *Cyrtonyx montezumae* (*C. virginianus*, 0.46); *Rhynchortyx cinctus* (*C. montezumae*, 0.49). **Phasianinae, Perdicini**: *Lerwa lerwa* (*A. graeca*, 0.51); *Ammoperdix heyi* (*F. coqui*, 0.42); *Alectoris graeca* (*F. swainsonii*, 0.39); *Francolinus francolinus* (*F. francolinus*, 0.24; *F. harwoodi*, 0.33); *F. francolinus* (*F. francolinus*, 0.33; *F. harwoodi*, 0.36); *F. francolinus* (*F. francolinus*, 0.24; *F. pintadeanus*, 0.35); *F. pictus* (*F. coqui*, 0.37); *F. pintadeanus* (*F. pondicerianus*, 0.36); *F. pintadeanus* (*F. pintadeanus*, 0.26; *F. francolinus*, 0.35); *F. pintadeanus* (*F. pintadeanus*, 0.26; *F. francolinus*, 0.35); *F. afer* (*F. swainsonii*, 0.26); *F. afer* (*F. afer*, 0.29; *F. bicalcaratus*, 0.30); *F. afer* (*F. afer*, 0.25; *F. swainsonii*, 0.30); *F. afer* (*F. afer*, 0.25; *F. icterorhynchus*, 0.28); *F. swainsonii* (*F. swainsonii*, 0.26; *F. bicalcaratus*, 0.27); *F. swainsonii* (*F. swainsonii*, 0.23; *F. leucoscepus*, 0.26); *F. swainsonii* (*F. afer*, 0.26); *F. swainsonii* (*F. swainsonii*, 0.23; *F. leucoscepus*, 0.31); *F. swainsonii* (*F. swainsonii*, 0.23; *F. leucoscepus*, 0.33); *F. swainsonii* (*F. swainsonii*, 0.26; *F. adspersus*, 0.34); *F. leucoscepus* (*F. leucoscepus*, 0.25; *F. swainsonii*, 0.30); *F. leucoscepus* (*F. leucoscepus*, 0.25; *F. swainsonii*, 0.26); *F. leucoscepus* (*F. leucoscepus*, 0.25; *F. adspersus*, 0.31); *F. leucoscepus* (*F. leucoscepus*, 0.25; *F. afer*, 0.30); *F. leucoscepus* (*F. leucoscepus*, 0.29; *F. afer*,

APPENDIX 3. Continued.

0.30); *F. jacksoni* (*F. capensis*, 0.44); *F. squamatus* (*F. squamatus*, 0.30; *F. afer*, 0.31); *F. squamatus* (*F. natalensis*, 0.27); *F. squamatus* (*F. bicalcaratus*, 0.25); *F. squamatus* (*F. squamatus*, 0.29; *F. icterorhynchus*, 0.29); *F. bicalcaratus* (*F. bicalcaratus*, 0.32; *F. swainsonii*, 0.33); *F. bicalcaratus* (*F. swainsonii*, 0.27); *F. bicalcaratus* (*F. squamatus*, 0.25); *F. icterorhynchus* (*F. levaillantii*, 0.28); *F. clappertoni* (*F. afer*, 0.32); *F. clappertoni* (*F. harwoodi*, 0.29); *F. natalensis* (*F. natalensis*, 0.28; *F. harwoodi*, 0.30); *F. natalensis* (*F. natalensis*, 0.29; *F. squamatus*, 0.35); *F. natalensis* (*F. squamatus*, 0.27); *F. adspersus* (*F. capensis*, 0.26); *F. hartlaubi** (*Margaroperdix madagarensis*, 0.44; *F. pondicerianus*, 0.52); *F. harwoodi* (*F. squamatus*, 0.29); *F. capensis* (*F. capensis*, 0.25; *F. swainsonii*, 0.35); *F. capensis* (*F. capensis*, 0.31; *F. adspersus*, 0.37); *F. capensis* (*F. capensis*, 0.25; *F. swainsonii*, 0.40); *F. capensis* (*F. adspersus*, 0.26); *F. capensis* (*F. capensis*, 0.26; *F. swainsonii*, 0.36); *F. sephaena* (*F. sephaena*, 0.33; *F. coqui*, 0.37); *F. sephaena* (*F. sephaena*, 0.33; *Rollulus roulroul*, 0.37); *F. sephaena* (*F. sephaena*, 0.33; *F. lathami*, 0.46); *F. sephaena* (*F. sephaena*, 0.33; *F. coqui*, 0.37); *F. africanus* (*F. levaillantii*, 0.30); *F. levaillantoides* (*F. levaillantoides*, 0.28; *F. levaillantii*, 0.35); *F. levaillantoides* (*F. levaillantoides*, 0.28; *F. levaillantii*, 0.31); *F. shelleyi* (*F. levaillantoides*, 0.31); *F. levaillantii* (*F. levaillantii*, 0.25; *F. icterorhynchus*, 0.28); *F. levaillantii* (*F. levaillantii*, 0.25; *F. africanus*, 0.32); *F. coqui* (*F. coqui*, 0.22; *F. sephaena*, 0.37); *F. coqui* (*F. coqui*, 0.26; *F. pintadeanus*, 0.40); *F. coqui* (*F. coqui*, 0.22; *F. pictus*, 0.39); *F. coqui* (*F. coqui*, 0.32; *F. pictus*, 0.38); *F. coqui* (*F. coqui*, 0.34; *F. pictus*, 0.39); *F. lathami* (*F. lathami*, 0.31; *Arborophila brunneopectus*, 0.43); *F. lathami* (*F. lathami*, 0.29; *F. sephaena*, 0.45); *F. lathami* (*F. lathami*, 0.29; *F. sephaena*, 0.42); *F. pondicerianus* (*F. pintadeanus*, 0.36); *F. gularis* (*F. francolinus*, 0.39); *Perdix perdix* (*F. coqui*, 0.55); *Rhizothera longirostris* (*F. afer*, 0.43); *Margaroperdix madagarensis* (*F. pintadeanus*, 0.42); *Melanoperdix nigra* (*Rollulus roulroul*, 0.33); *Coturnix c. coturnix* (*C. c. africana*, 0.32); *C. c. africana* (*C. c. coturnix*, 0.32); *C. c. japonica* (*C. c. coturnix*, 0.41); *C. delegorguei* (*C. c. coturnix*, 0.43); *Synoicus ypsilophorus* (*C. c. africana*, 0.45); *Excalfactoria chinensis* (*P. argoondah*, 0.65); *Perdicula argoondah* (*C. delegorguei*, 0.50); *Arborophila brunneopectus* (*F. lathami*, 0.43); *Tropicoperdix charltonii* (*A. brunneopectus*, 0.46); *Rollulus roulroul* (*M. nigra*, 0.33); *Ptilopachus petrosus** (*P. petrosus*, 0.26; *Lophortyx californicus*, 0.48); *P. petrosus* (*P. petrosus*, 0.26; *A. heyi*, 0.48); *Bambusicola thoracica* (*F. sephaena*, 0.38); *Galloperdix spadicea* (*F. sephaena*, 0.43). **Phasianini**: *Ithaginis cruentus** (*Francolinus squamatus*, 0.56); *Tragopan temminckii* (*P. macrolopha*, 0.41); *Pucrasia macrolopha* (*T. temminckii*, 0.41); *Lophophorus impeyanus* (*C. mantchuricum*, 0.68); *Gallus gallus* (*G. varius*, 0.50); *G. varius* (*L. swinhoii*, 0.42); *Lophura leucomelanos** (*Francolinus adspersus*, 0.46); *L. swinhoii* (*G. varius*, 0.42); *L. ignita* (*A. argus*, 0.54); *Crossoptilon mantchuricum* (*L. impeyanus*, 0.68); *Catreus wallichii* (*P. colchicus*, 0.41); *Syrmaticus humiae** (*Francolinus capensis*, 0.44); *Phasianus colchicus* (*C. wallichii*, 0.41); *Chrysolophus pictus* (*L. leucomelanos*, 0.52); *Polyplectron bicalcaratum** (*Francolinus gularis*, 0.57); *Rheinartia ocellata* (*A. argus*, 0.62); *Argusianus argus* (*L. ignita*, 0.54); *Pavo cristatus** (*Meleagris ocellata*, 0.69). **Numidinae**: *Agelastes meleagrides* (*A. niger*, 0.35); *A. meleagrides* (*A. meleagrides*, 0.46; *A. niger*, 0.50); *A. niger* (*A. meleagrides*, 0.35); *Numida meleagris* (*N. meleagris*, 0.31; *G. pucherani*, 0.51); *N. meleagris* (*N. meleagris*, 0.38; *A. vulturinum*, 0.53); *N. meleagris* (*N. meleagris*, 0.32; *A. vulturinum*, 0.49); *N. meleagris* (*N. meleagris*, 0.31; *A. vulturinum*, 0.53); *Guttera plumifera* (*G. pucherani*, 0.45); *G. pucherani* (*G. plumifera*, 0.45); *Acryllium vulturinum* (*N. meleagris*, 0.49).