

THE LONG-BILLED LARK COMPLEX: A SPECIES MOSAIC IN SOUTHWESTERN AFRICA

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ABSTRACT.—The Long-billed Lark (*Certhilauda curvirostris*) is a geographically variable species. Thirteen subspecies have been described, and at least three phenotypically well-defined groups exist. We use concordant patterns of genotypic and phenotypic variation to recognize cryptic species within this complex. Genotype information was obtained by sequencing part of the mitochondrial DNA cytochrome-*b* gene. Three taxa are genetically highly distinct, differing from each other by 6 to 9% sequence divergence. One of these taxa comprises three phenotypically distinct taxa that differ from each other by 2% sequence divergence. These values far exceed the variation within described subspecies (0.2 to 0.4%) and approach the distance to the presumed sister taxon, the Short-clawed Lark (*C. chuana*; 8 to 10%). Well-defined morphological and plumage differences exist between all taxa except *benguelensis* and northern populations of *subcoronata*. We propose that the complex consists of five species: the closely related *C. curvirostris*, *C. brevirostris*, and *C. semitorquata*, and the more distantly related *C. subcoronata* and *C. benguelensis*. Comparison of male display songs provides additional support for the recognition of five species, but sample sizes are small. The position of *C. chuana* relative to the five species noted above is not resolved. Species' ranges are allopatric, but more work is needed to elucidate the distributional limits of taxa in northern Namibia and Angola. These findings have implications for biodiversity conservation, and they suggest that considerable diversity has been overlooked in wide-ranging, sedentary lark species. Received 19 December 1997, accepted 22 June 1998.

THE LARKS (FAMILY ALAUDIDAE) are a predominantly Old World family whose affinities within the passerines are poorly understood (Sibley and Monroe 1990). Most species are found in Africa, where there are two main centers of diversity associated with the northeastern and southwestern arid zones. These regions are characterized by high levels of endemism, with many species having small ranges. Recent research suggests that superficially similar allopatric populations, which have been lumped together in polytypic species, may have been isolated for considerable periods of time (e.g. Ryan et al. 1998).

The Long-billed Lark (*Certhilauda curvirostris*) is restricted to southwestern Africa from southern Angola through western Namibia to South Africa. It forms a superspecies with the Short-clawed Lark (*C. chuana*), which replaces the Long-billed Lark in arid acacia savannas in eastern Botswana and adjacent South Africa (Dean et al. 1992, 1997; Fig. 1). Long-billed Larks occur in a wide range of habitats, including coastal dunes, open plains, rocky slopes,

deserts, and mesic montane grasslands (Dean et al. 1992, 1997). Being sedentary (Dean and Hockey 1989; Dean et al. 1992, 1997) apparently has promoted the evolution of marked geographical variation in plumage and morphology. These regional differences have been interpreted as adaptations to local conditions. For example, upperpart coloration matches the local substratum color (Macdonald 1952), and long bills and hind claws occur in birds living on soft, sandy soils (Clancey 1957).

This geographic variation has led to considerable debate about the species' taxonomy. Thirteen taxa have been described (Clancey 1980, Dean et al. 1992), which have been split into as many as four species (Roberts 1940), and even placed in separate genera (Sharpe 1904). However, the current consensus is to lump all forms into a single polytypic species (Clancey 1957, Dean et al. 1992, Maclean 1993). This is despite a recent review of the species in South Africa that concluded that the species perhaps should be viewed as a superspecies with at least three allospecies (Quickelberge 1967).

Here, we use genetic sequence data to help

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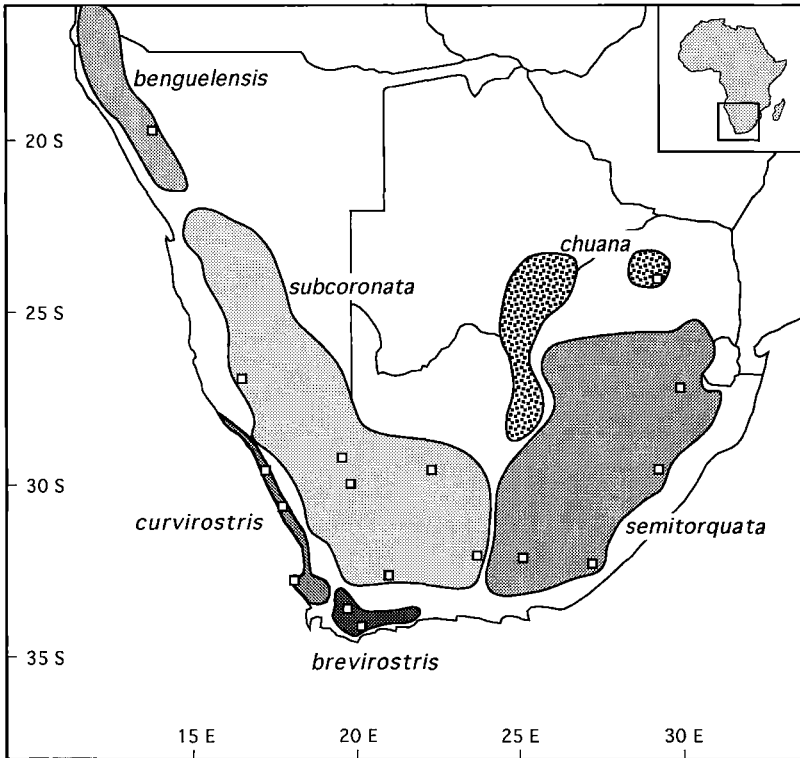


FIG. 1. The distribution of species in the Long-billed lark complex, including the presumed sister taxon, Short-clawed Lark (*Certhilauda chuana*), based on examination of specimens and atlas data from Dean et al. (1997). Open squares denote collection localities of birds whose mtDNA was sequenced.

resolve the evolutionary relationships among taxa within the Long-billed Lark complex. We sequenced part of the mitochondrial cytochrome-*b* gene, which has proved valuable in resolving relationships at the species level in larks and other birds (e.g. Shields and Helm-Bychowski 1988, Smith et al. 1991, Helbig et al. 1996, Ryan et al. 1998). We also reanalyze geographic variation in plumage and morphology in relation to the genetically defined taxa and make recommendations about the taxonomy of the complex.

METHODS

Sampling and DNA analysis.—Between October 1994 and July 1997, we collected 19 birds from 17 localities (Table 1, Fig. 1). Individuals were assigned to taxa based on plumage characters and locality (see below). We dissected out the heart, liver, and pectoral muscle tissues and preserved them in a saturated NaCl/20% DMSO solution (Amos and Hoelzel 1991).

In the laboratory, tissue samples were digested (50

mM Tris pH 7.6, 100 mM NaCl, 1 mM NaEDTA pH 8.0, 0.5% SDS, 1 mg/mL proteinase K) overnight at 37°C. Following RNase treatment, total genomic DNA was extracted twice with phenol, once with chloroform:isoamylalcohol (24:1), and precipitated with 2M ammonium acetate and 100% ethanol. Purified mtDNA was extracted from three specimens (Table 1) following the methods of Essop et al. (1991). A 500 base-pair (bp) fragment of the mtDNA cytochrome-*b* gene was amplified using primers L14990 (L14841; Kocher et al. 1989) and H15499 (CBINT; Avise et al. 1994). Double-stranded amplifications were performed in 50- μ L volumes using 2.5mM MgCl₂, 2mM dNTPs, 25 pmol of each primer, and 1.5 units of *Taq* DNA polymerase (Promega). Reaction mixtures were subjected to 35 cycles of denaturation at 94°C (30 s), annealing at 48 to 50°C (1 min), and extension at 72°C (1 min). The first cycle was preceded by an initial denaturation of 3 min at 94°C, and the last cycle was followed by a final extension of 10 min at 72°C. PCR products were purified through 2% low-melting point agarose gels (MS8; Whitehead Scientific) and recovered using the QIAEX II gel extraction kit (Qiagen). Both light and heavy strands were sequenced by dideoxy sequencing (Sanger et al.

TABLE 1. Collection localities and subspecific designation of the 19 birds in the Long-billed Lark complex whose cytochrome-*b* gene was sequenced (one per site, except for Uniab River).

Taxon	Locality	Coordinates
<i>falcirostris</i>	Port Nolloth	29°15'S, 16°50'E
<i>falcirostris</i> ^a	Groenrivier Mouth	30°50'S, 17°35'E
<i>curvirostris</i>	Paternoster	32°48'S, 17°55'E
<i>brevirostris</i>	Roodekleigat (20 km W of Robertson)	33°50'S, 19°40'E
<i>brevirostris</i>	Bredasdorp (15 km NE)	34°25'S, 20°10'E
<i>semitorquata</i>	Cradock (25 km NW)	32°08'S, 25°24'E
<i>semitorquata</i>	Stutterheim (20 km NW)	32°23'S, 27°42'E
<i>semitorquata</i>	Nottingham Road (15 km W)	29°22'S, 29°54'E
<i>transvaalensis</i>	Wakkerstroom (10 km SE)	27°22'S, 30°12'E
<i>gilli</i>	Toorberg (35 km E of Murraysburg)	32°03'S, 24°08'E
<i>gilli</i>	Middlestevlei (40 km N of Laingsburg)	32°55'S, 20°57'E
<i>subcoronata</i> ^a	Bloubosfontein (40 km NW of Prieska)	29°24'S, 22°38'E
<i>subcoronata</i>	Dikpens (100 km NW of Brandvlei)	30°10'S, 19°32'E
<i>bradshawi</i> ^a	Pofadder	29°10'S, 19°22'E
<i>bradshawi</i>	Nieu-Tsaut (40 km S of Aus)	27°00'S, 16°12'E
<i>kaokensis</i> ^b	Uniab River (100 km W of Kamajab)	19°54'S, 13°59'E
<i>chuana</i>	Pietersburg	29°20'S, 29°25'E

^a Sequences from purified mtDNA (see Methods).

^b *n* = 3.

1977) with the Sequenase version 2 enzyme system (United States Biochemicals). The two PCR primers and two internal primers (H15 298 [Kocher et al. 1989] and L15245 [Palumbi et al. 1991]) were used for generating sequences. Sequences were aligned by eye, and no insertions or deletions were found.

A matrix of pairwise nucleotide sequence divergences for neighbor-joining analysis (Saitou and Nei 1987) was calculated in MEGA version 1.01 (Kumar et al. 1993) using the Kimura two-parameter correction (Kimura 1980). This model accounts for the higher rate of transitional substitutions in animal mtDNA and uses a 2:1 TV:TI ratio; no gamma correction was applied to correct for possible among-site rate variation. Maximum-parsimony analysis was performed using PAUP 3.1.1 (Swofford 1993). Phylogenetic signal was assessed by analyzing tree-length distributions of 1,000 random trees (Hillis and Huelsenbeck 1992). In addition to treating all phylogenetically informative characters as unordered and unweighted, different weighting schemes were used to account for the transition bias in mitochondrial DNA and to reduce homoplasy. MacClade 3.0 (Maddison and Maddison 1992) was used to calculate the transition:transversion (TI:TV) ratio by counting the average number of transition and transversion events on 1,000 random trees. Successive approximation character weighting based on mean character consistency indices across equally parsimonious trees (Farris 1969) was also used. Reliability of topologies was assessed using 1,000 bootstrap replicates (Felsenstein 1985). The Karoo Lark ("*Certhilauda*" *albescens*; Ryan et al. 1998) and the Gray-backed Finch-Lark (*Eremopterix verticalis*) were included for outgroup comparisons. Sequence data

have been deposited in GenBank under accession numbers AF033249-58.

Morphometrics and plumage.—PGR measured 414 Long-billed Larks and Short-clawed Larks; 400 were from skins housed in the Durban, East London, Namibian, South African, and Transvaal museums, and 14 were birds measured in the field. Measurement protocols follow Ryan et al. (1998). Tail length and wing length (flattened chord) were measured to the nearest 1 mm. Tarsus length, bill length (distal edge of nares to bill tip), and bill depth (depth at proximal edge of nares) were measured to the nearest 0.1 mm. Bill length from the nares was preferred to the standard measure of bill length (from the base to the tip) because molt and damage to museum skins make it difficult to consistently measure standard bill length (see Grant et al. 1985). Coefficients of variation within taxa invariably were smaller using bill length from the nares. This measure averages 68% of standard bill length in Long-billed Larks, with the proportion increasing with bill length (range 66% for *semitorquata* and 71% for *curvirostris-falcirostris*).

Sex of freshly collected specimens was determined by inspection of the gonads. The accuracy of sexes reported on museum labels was tested by estimating discriminant functions for each main taxon. Given the marked sexual dimorphism, there were very few skins whose sex could not readily be assigned. Two skins (0.5%) were found to be incorrectly sexed ($P < 0.001$) and were reassigned accordingly.

Plumage variation in the Long-billed Lark complex has two main components: (1) ground color of the upperparts and underparts; and (2) the extent, size, and intensity of dark brown feather centers or streaking. Upperpart coloration was noted but not

TABLE 2. Pairwise estimates of nucleotide sequence divergence between Long-billed Larks (*sensu lato*). Percentage sequence divergence (Kimura two-parameter distance) is above diagonal, and number of transitions/transversions is below diagonal.

Taxon	1	2	3	4	5	6	7	8	9	10	11
1 <i>falcirostris</i>	—	0.2	2.1	2.3	7.3	7.5	8.4	8.5	9.4	16.9	15.3
2 <i>curvirostris</i>	1/0	—	2.3	2.6	7.5	7.7	8.7	8.7	9.7	17.2	15.6
3 <i>brevirostris</i>	10/0	11/0	—	2.3	7.3	7.5	8.7	8.7	9.9	16.7	15.8
4 <i>semitorquata</i>	11/0	12/0	11/0	—	6.6	6.8	7.7	8.2	8.7	15.8	14.0
5 <i>subcoronata</i> A ^a	27/6	27/6	27/6	24/6	—	0.2	6.1	6.6	8.2	15.1	14.8
6 <i>subcoronata</i> B ^a	28/6	28/6	28/6	25/6	1/0	—	6.4	6.8	8.5	15.3	15.1
7 <i>kaokensis</i> A ^b	30/8	30/8	30/8	27/8	24/4	25/4	—	0.4	9.4	17.0	14.8
8 <i>kaokensis</i> B ^b	30/8	30/8	303/8	29/8	26/4	27/4	2/0	—	9.9	17.3	15.4
9 <i>chuana</i>	33/9	34/9	34/9	30/9	30/7	31/7	33/9	35/9	—	18.0	15.6
10 <i>albescens</i>	49/23	50/23	50/23	45/23	44/21	45/21	51/21	53/20	52/24	—	15.0
11 <i>Eremopterix</i>	43/23	44/23	45/23	38/23	45/19	46/19	43/21	45/21	45/22	41/24	—

^a A = five birds collected south of the Orange River, including *gilli*, *subcoronata*, and *bradshawi*; B = one bird (*bradshawi*?) collected near Aus, southern Namibia.

^b Of three birds collected near the Uniab River, two were type A and one type B.

quantified. Streaking was measured in three parts of the body. On the upperparts, streak width was estimated as a percentage of total feather width on the exposed portion of back feathers. On the flanks and belly, the extent of streaking was scored from 0 to 3 where 0 = absent and 3 = extensive. For ease of interpretation, group average scores are presented as percentages. On the breast, the extent of streaking is correlated with the size of the streaks. The length and width of breast streaks were measured to the nearest 0.5 mm, and these values were multiplied to give an index of breast streaking.

Individuals were allocated to taxa on the basis of collection locality, following published ranges (Clancey 1980). We recognized 12 putative taxa in three well-defined groups. Grayish, heavily streaked birds occur on the western coastal plain (*curvirostris* and *falcirostris*; Clancey 1957) and Agulhas Plain (*brevirostris*; Roberts 1941). Rufous, mostly unstreaked birds with buffy underparts occur in grasslands east of 25°E, with *algida* restricted to the coastal ranges in the southwest, *semitorquata* throughout most of the range, and *transvaalensis* in the north (Quickelberge 1967). Like Quickelberge (1967), we considered *daviesi* synonymous with *semitorquata*. West of 25°E, more heavily streaked birds with rufous-brown backs and whitish underparts occur in Karoo shrublands (*gilli* and *subcoronata*; Roberts 1936). Farther north, these birds become less streaked, redder, and smaller, with *bradshawi* in the Orange River basin and southern Namibia, *damarensis* in central Namibia, *kaokensis* in northern Namibia, and *benguelensis* in southern Angola (Sharpe 1904, Clancey 1980). Boundaries between the northern taxa are not well defined owing to limited and patchy collecting. We arbitrarily separated *bradshawi* from *damarensis* at 25°S, which corresponds with a large gap in collections. Atlas data (Dean et al. 1997) indicate a gap in the distribution of Long-billed Larks at 21°30'S, and

this latitude was used to separate *kaokensis* from *damarensis*. *Benguelensis* was restricted to specimens from Angola.

Variation in morphology (size and plumage pattern) was analyzed at the level of the 12 described taxa, as well as for taxa identified from the phylogenetic analysis. Univariate differences in morphology were tested using ANOVA and *t*-tests. Principal components analysis (PCA) was used to summarize phenotypic variation in size and the extent of plumage streaking. Discriminant function analysis was used to identify "incorrectly classified" individuals. Data were standardized (relative to the largest measure = 1, smallest measure = 0) for multivariate analyses.

Vocalizations.—Long-billed Larks utter an array of calls but have a relatively simple song associated with dramatic aerial displays. Males fly low over the ground before rising almost vertically 10 to 15 m in the air, the last part of the ascent being driven solely by the bird's momentum, because the wings are closed. The bird stalls at the apex of the display and plummets down, only opening its wings just before it reaches the ground. As the bird descends it utters a far-carrying, descending whistle, typically rendered "peeooooo" (Dean et al. 1992, Maclean 1993). This display apparently occurs in all *C. curvirostris* taxa and is shared with the Short-clawed Lark (Herremans et al. 1994). In Long-billed Larks, the same song also is uttered from prominent perches in the territory; flight songs do not differ from those given by perched birds.

Lark vocalizations were recorded by PGR using a TECT supercardioid shotgun microphone (model UEM-83) and a Sony cassette recorder (model TCM-17); additional recordings were supplied by Callan Cohen, John Graham, Penn Lloyd, the FitzPatrick Sound Library, and commercially available bird recordings by Guy Gibbon. Only male display songs

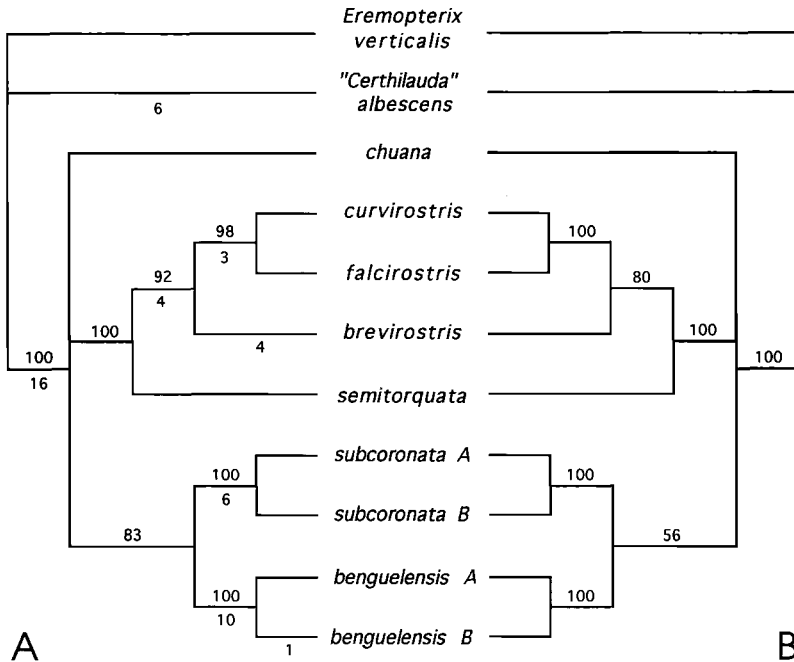


FIG. 2. Phylogeny of larks in the Long-billed Lark complex based on 483 bp of the cytochrome-*b* gene, using the Karoo Lark (*Certhilauda albescens*) and Gray-backed Finch-Lark (*Eremopterix verticalis*) as outgroups (Table 2). (A) Maximum-parsimony tree (branch and bound search) with bootstrap values above the branches and the number of unambiguous changes occurring along a branch below the branches. (B) Neighbor-joining tree based on Kimura two-parameter distances. Numbers indicate the frequency (%) with which each clade was identified in 1,000 bootstrap replicates. Branches with less than 50% bootstrap support are left unresolved.

were compared. Sonograms were produced using SoundEdit (MacRecorder, Farallon Computing Inc.) on a Power Macintosh. Because of small sample sizes, no attempt was made to quantify variation in song structure within and among taxa.

RESULTS

Genotypic variation.—We sequenced 483 bp of the cytochrome-*b* gene from 18 birds in the Long-billed Lark complex (Appendix). Including Short-clawed Lark and the two outgroups, there were 129 variable sites. As expected, most variable sites were at third-codon positions (105 sites, 82%), with first-position (21 sites, 16%) and second-position sites (3 sites, 2%) more conserved. Most were silent substitutions, with only 20 variable amino acid sites recorded. Including the outgroups, the ratio of transitions (TI) to transversions (TV) was 2.9:1, whereas the ingroup (Long-billed Larks and Short-clawed Lark) showed a bias of 4.3:1. Pairwise estimates of nucleotide sequence diver-

gence and the TI:TV ratio for each comparison are given in Table 2.

Eight haplotypes were found among the Long-billed Larks (Table 2). Identical sequences were found among *falcirostris* (*n* = 2), *brevirostris* (*n* = 2), *semitorquata-transvaalensis* (*n* = 4), *subcoronata-gilli-bradshawi* (excluding the sole Namibian specimen, *n* = 5), and two of the three *kaokensis*. Three taxa were genetically highly distinct (6 to 9% sequence divergence), similar to the distance to the Short-clawed Lark (Table 2): (1) a northern Namibia group (*kaokensis*), (2) a Karoo-southern Namibia group (*gilli*, *subcoronata* and *bradshawi*), and (3) a group comprising the coastal and grassland taxa. Within this last group, three taxa differed from each other by at least 2% sequence divergence: birds from the west coast (*curvirostris* and *falcirostris*), the Agulhas Plain (*brevirostris*), and the eastern grassland (*semitorquata* and *transvaalensis*). These values contrast with the variation within described subspecies (0.2 to

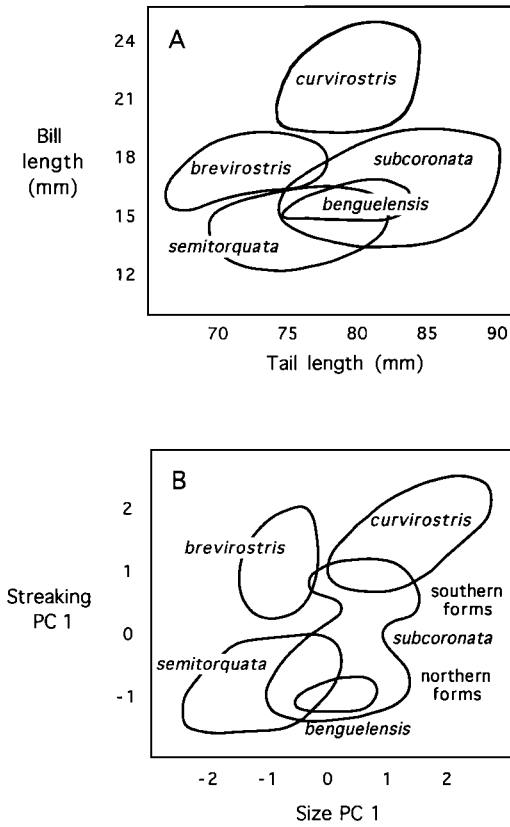


FIG. 3. Biplots of male Long-billed Lark morphology. (A) Univariate comparison of tail length versus bill length. (B) Multivariate comparison of size (PC 1 accounts for 54% of variance in five measurements of morphology) versus plumage streaking (PC1 accounts for 84% of variance in the three streaking indices). Polygons encompass >95% of individuals measured ($n = 289$).

0.4% for *kaokensis* and *bradshawi*) or between taxa within groups (0.2% for *curvirostris-falcirostris*).

The sequence differences are also reflected at the amino acid level, with three to six amino acid differences among the three distinct Long-billed Lark taxa and four to seven differences between the Long-billed and Short-clawed larks. There was only one amino acid difference within the *curvirostris-brevirostris-semitorquata* group, with *brevirostris* distinct from *curvirostris* and *semitorquata*. There were no amino acid differences within or between subspecies.

The unweighted cladistic analysis of the 71 phylogenetically informative characters yielded two equally parsimonious trees (length =

TABLE 3. Morphological measurements of males in the Long-billed Lark complex. Values are $\bar{x} \pm SD$ (mm), with degree of sexual dimorphism in size in parentheses (% that males are larger than females). Within columns, values with the same superscript are not significantly different.

Taxa (M, F) ^a	Wing length	Tail length	Tarsus length	Bill length	Bill depth
<i>curvirostris</i> (45, 22)	111.4 \pm 3.21 ^A (13.4)	77.7 \pm 2.96 ^B (15.2)	30.7 \pm 1.21 ^A (12.1)	21.7 \pm 1.96 ^A (19.2)	6.7 \pm 0.38 ^A (17.3)
<i>brevirostris</i> (15, 0)	106.7 \pm 2.96 ^{B,C}	70.3 \pm 3.01 ^D	29.8 \pm 0.79 ^B	16.9 \pm 1.15 ^B	5.6 \pm 0.25 ^D
<i>semitorquata</i> (72, 30)	107.8 \pm 2.96 ^C (13.3)	74.3 \pm 3.26 ^C (11.6)	28.5 \pm 1.10 ^C (9.5)	15.0 \pm 0.83 ^C (26.6)	5.9 \pm 0.26 ^C (12.2)
<i>subcoronata</i> (143, 56)	111.2 \pm 2.79 ^A (13.6)	80.5 \pm 3.03 ^A (12.0)	29.6 \pm 1.02 ^B (11.9)	16.7 \pm 0.98 ^B (28.0)	6.1 \pm 0.26 ^B (18.3)
<i>benguelsis</i> (14, 11)	111.5 \pm 4.03 ^A (14.3)	79.6 \pm 2.82 ^A (13.4)	29.6 \pm 0.88 ^B (12.3)	16.0 \pm 0.60 ^B (27.6)	6.1 \pm 0.26 ^B (17.5)
<i>chuwana</i> (5, 1) ^b	106.2 \pm 2.17	73.8 \pm 1.48	29.4 \pm 0.93	12.4 \pm 0.44	5.9 \pm 0.19
Overall F (5 and 288 df) ^c	20.1	62.0	23.6	212.1	51.9

^a Number of males, females in parentheses.

^b Excluded from analyses because of small sample sizes.

^c $P < 0.001$ in all cases.

TABLE 4. Indices of plumage streaking ($\bar{x} \pm SD$) among taxa in the Long-billed Lark complex (sexes combined). Back and belly streaking are expressed as percentages; breast streaking is a measure of streak size (see Methods). Within columns, values with the same superscript are not significantly different.

Taxa (n)	Back streaking	Breast streaking	Belly streaking
<i>curvirostris</i> (67)	48.2 \pm 7.4 ^A	21.0 \pm 4.8 ^A	71.3 \pm 13.9 ^A
<i>brevirostris</i> (15)	44.3 \pm 4.9 ^A	17.0 \pm 4.7 ^B	69.1 \pm 17.0 ^A
<i>semitorquata</i> (102)	14.3 \pm 7.6 ^B	8.3 \pm 4.1 ^C	7.8 \pm 8.2 ^C
<i>subcoronata</i> (199)	16.2 \pm 10.1 ^B	13.3 \pm 6.1 ^B	22.6 \pm 24.2 ^B
<i>benguelensis</i> (25)	10.7 \pm 5.1 ^B	8.5 \pm 2.2 ^C	2.3 \pm 4.1 ^C
<i>chuana</i> (6) ^a	49.2 \pm 10.2	6.2 \pm 1.2	0.0 \pm 0.0
Overall F (5 and 408 df) ^b	190.4	56.2	126.7

^a Excluded from analyses because of small sample sizes.

^b $P < 0.001$ in all cases.

124 steps; CI = 0.710; RI = 0.752; $g1 = -0.886$). Similar topologies were obtained when placing greater emphasis on transversions relative to transitions (TV:TI weight = 3:1 or 5:1), or weighting characters according to their mean consistency indices. The latter analysis produced a single most-parsimonious tree after one round of successive weighting (Fig. 2A; length = 89 steps; CI = 0.795; RI = 0.828; $g1 = -1.146$). The neighbor-joining analysis yielded an identical topology (Fig. 2B), and in both trees the five Long-billed Lark species were supported by high bootstrap values (Fig. 2). The position of the Short-clawed Lark remains unresolved. Most analyses yielded a trichotomy between *chuana*, *curvirostris-brevirostris-semitorquata*, and *subcoronata-benguelensis*. With a 5:1 TV:TI weighting, *chuana* fell outside the Long-billed Lark group (bootstrap value only 51%), but based on the amino acid sequence, both parsimony and neighbor-joining analyses placed *chuana* with the *curvirostris-brevirostris-semitorquata* group (80% and 78% bootstrap values, respectively).

Our results suggest that the Long-billed Lark complex comprises five species: *curvirostris*, *brevirostris*, *semitorquata*, *subcoronata* and *benguelensis* (Fig. 1). We use *benguelensis* for the northern Namibian species because, to be conservative, we presume it is the same as *kaokensis* and has precedence (Sharpe 1904). The status of *damarensis* is unresolved (but see below). *Falcirostris* is considered to be a regional variant, because its degree of sequence divergence from *curvirostris* (0.2%) is typical of intraspecific variation (see Helbig et al. 1996, Ryan and Bloomer 1997, Ryan et al. 1998).

Phenotypic variation.—There was a strong male bias among collections of Long-billed Larks (71% of specimens examined were male).

This bias presumably reflects the greater detectability of males, which are more vocal and tend to sit in exposed sites more than do females. Plumage characters do not differ between the sexes, but males are much larger than females (Table 3), so morphological comparisons were restricted to same-sex groups. Males averaged at least 10% larger than females in all characters, with size dimorphism greatest in bill length, which was more than 25% larger in males in all taxa except for *curvirostris* (Table 3).

Significant morphological differences existed among the taxa identified by genetic analysis (Table 3). The west coast *curvirostris* was the largest taxon in all characters except tail length, whereas the eastern grassland *semitorquata* generally was the smallest. The Agulhas Plain population (*brevirostris*) has a short tail and a short, slender bill, and the western interior forms (*subcoronata* and *benguelensis*) have the longest tails and relatively long wings. The same trends occurred among females. However, overlap existed between individuals from different taxa, especially among *benguelensis*, *subcoronata*, and *semitorquata* (Fig. 3A).

Streaking indices on the back, breast, and belly were strongly positively correlated, with significant differences among taxa (Table 4). Combining streaking indices with morphology increased the separation between taxa, but considerable overlap remained, especially between *benguelensis* and the northern populations of *subcoronata* (Fig. 3B). Discriminant functions correctly identified only 78% of male birds on the basis of morphology and plumage, with most misclassifications being between *benguelensis* and *subcoronata*. The major factor confounding correct classification was the significant variation within genetically defined taxa in terms of morphology and, especially, plum-

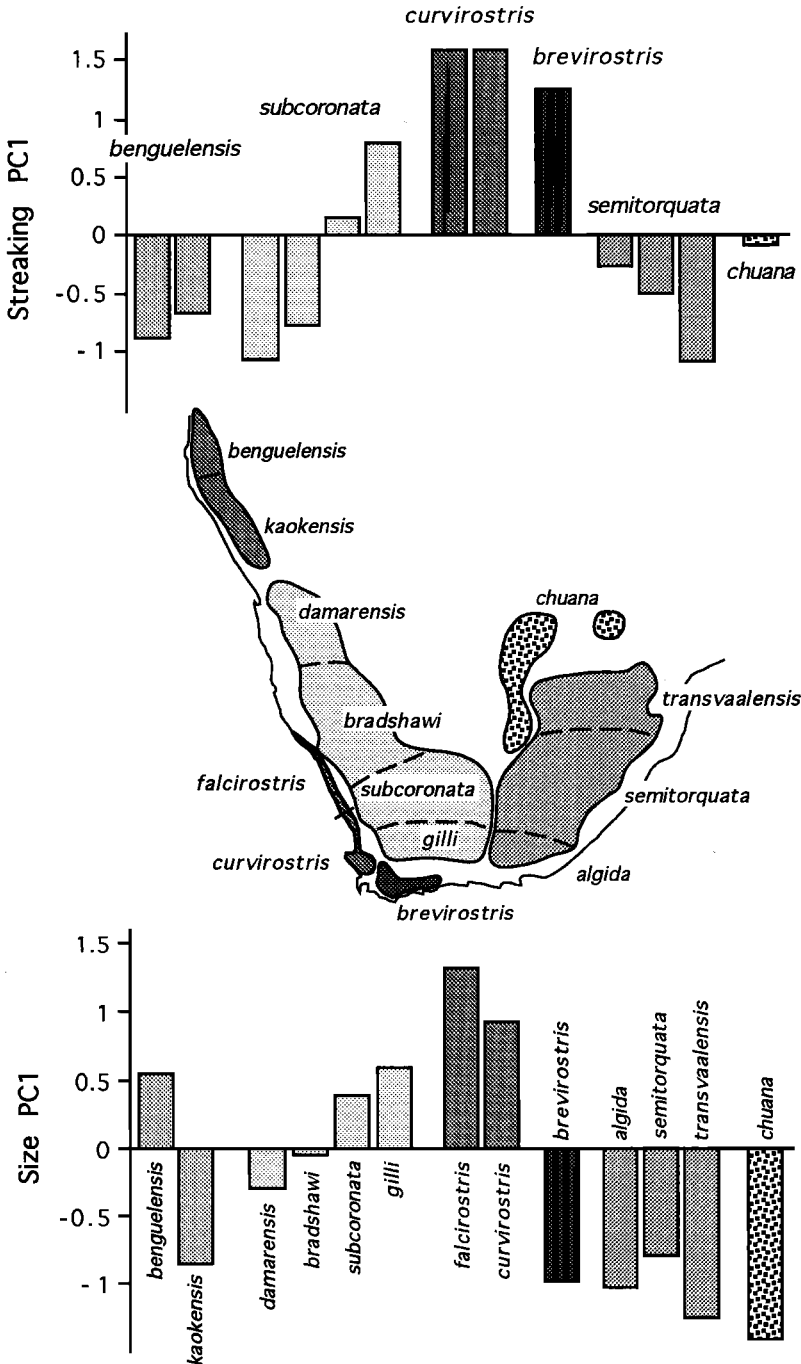
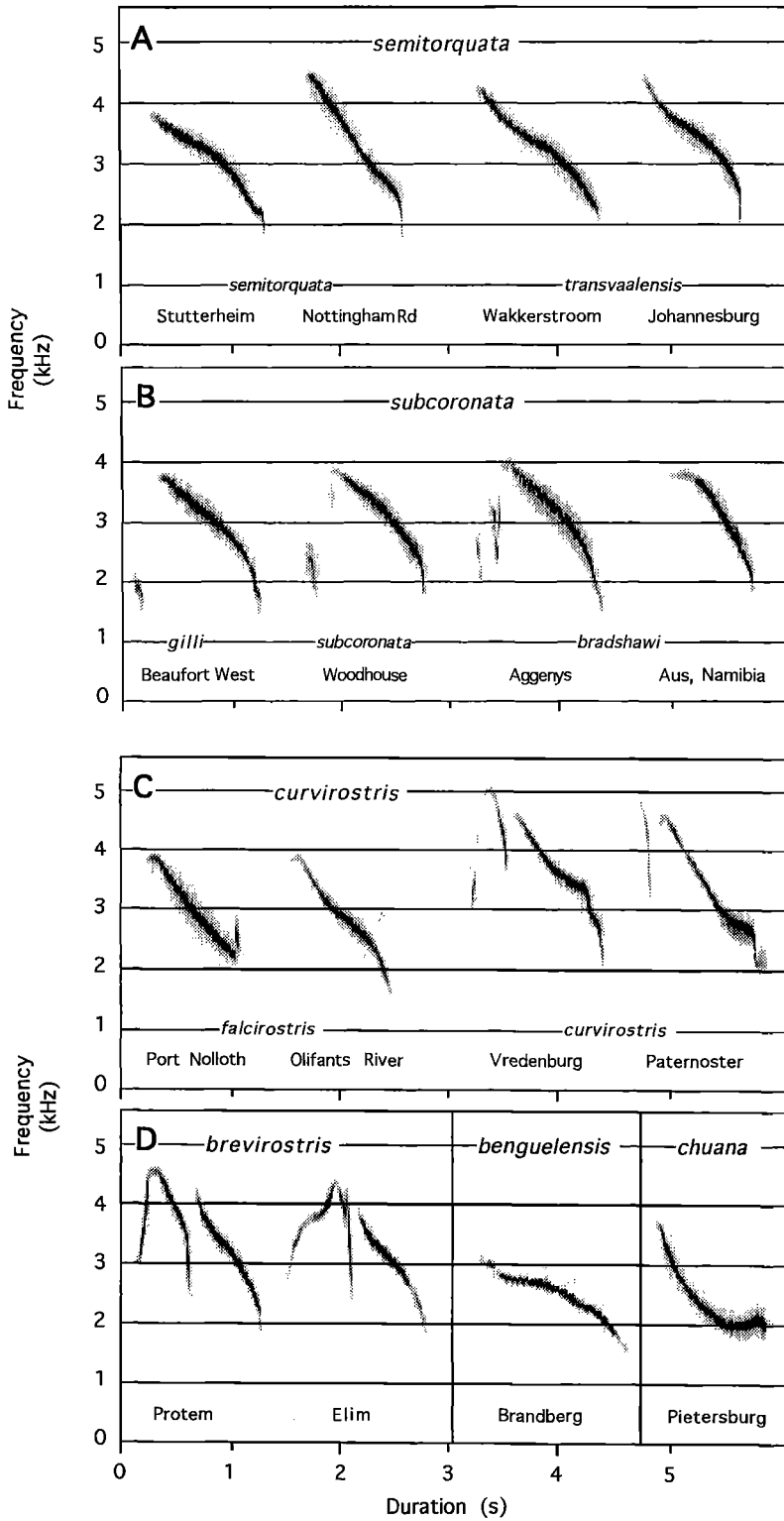


FIG. 4. Variation in plumage streaking (both sexes) and size (males only) among described subspecies in the Long-billed Lark complex, showing clinal variation within *subcoronata* and *semitorquata*. Approximate ranges of subspecies are depicted on the map. Principal components are derived from the same measurements as those in Figure 3.



age (Fig. 4). This variation appears to be clinal: body size and streaking decrease from south to north in both *semitorquata* and *subcoronata* (Fig. 4). This is especially marked in the amount of streaking within the *subcoronata* group, which is bimodal (Fig. 3B), suggesting a stepped cline. The abrupt change in these clinal trends between *damarensis* and *kaokensis* (Fig. 4) supports our contention, based in part on atlas data, that birds from central Namibia (*damarensis*) are part of the *subcoronata* group rather than the northern *benguelensis-kaokensis* group.

Only 25 male songs were available from 19 localities. There is little structure to the display song, with that of Short-clawed Lark being similar to most Long-billed Lark taxa (Fig. 5A–E). Most data are available for the eastern *semitorquata*, where variation among four individuals within a single locality is equivalent to that among six widely spaced localities. Song differences appear to be consistent between some taxa. The most distinctive feature is the presence or absence of an initial note preceding the descending whistle. This initial note is developed most fully in *brevirostris* and, to a lesser extent, *curvirostris* from the southern part of the range (nominate *curvirostris* from near Vredenburg; Fig. 5C, D). However, a reduced initial note also occurs in *subcoronata* from south of the Orange River that is absent from *semitorquata* (Fig. 5B). Two *subcoronata* recorded in southern Namibia lacked the initial note, but this difference did not coincide with the change in plumage from *subcoronata* to *bradshawi*. The only species that appears to exhibit significant variation in its display song is the west coast *curvirostris* (Fig. 5C).

DISCUSSION

The large mtDNA sequence differences among taxa suggest that the Long-billed Lark complex comprises five species. Given the small sample sizes, the possibility of intraspecific polymorphism in mtDNA cannot be ruled out, but the consistent morphological and vocal

differences coinciding with species boundaries defined by mtDNA increase confidence in the validity of the five species. Further work is needed, especially in Namibia, but it is prudent to recognize five species from a conservation perspective. The cytochrome-*b* divergence values between the species (2 to 9%) are similar to those reported for other bird species (Shields and Helm-Bychowski 1988, Helbig et al. 1996), including larks (Ryan et al. 1998).

At least in the south, the Long-billed Lark species are allopatric or narrowly parapatric, with clear gaps (or at least areas of low reported occurrence) between species' ranges (Dean et al. 1997; Fig. 1). The only area where two species are known to co-occur is where the Richtersveld abuts the coastal plain near the Orange River mouth, where *curvirostris* (*falcirostris*) and *subcoronata* have been collected together with no evidence of interbreeding (Quickelberge 1967). Interestingly, this is the same area where the newly described Barlow's Lark (*C. barlowi*) replaces the Karoo Lark (Ryan et al. 1998). Further work is required in Namibia to elucidate the boundary between *subcoronata* and *benguelensis*, which is problematic because the two are morphologically the most similar species pair. However, the clear gap in reported range at 21°30'S (Dean et al. 1997), coupled with the stepped shift in phenotypes at this latitude, suggest this as the boundary. If this is the case, Roberts' (1936, 1940) *damarensis* merely forms the northern limit of *subcoronata*, hence our use of *benguelensis* for the northern species.

Our recommendation that five species be recognized concurs with Roberts' (1936, 1940) treatment of the Long-billed Lark complex, with the addition of *brevirostris* (which Roberts described in 1941). Roberts (1940) used the English names: Cape Long-billed Lark (*curvirostris*), Eastern Long-billed Lark (*semitorquata*), Karoo Long-billed Lark (*subcoronata*), and Damaraland Long-billed Lark (*damarensis*). Given the confusion regarding the status of *damarensis* as a possible subspecies of *subcoronata*, we suggest

←

FIG. 5. Sonograms of male display songs in the Long-billed Lark complex. Each song represents a separate individual. (A) Variation within *semitorquata* (note similarity between subspecies). (B) Variation within *subcoronata* (subspecies in South Africa are similar, but Namibian *bradshawi* lack the initial note). (C) Variation within *curvirostris* (note marked difference between subspecies). (D) *brevirostris*, *benguelensis* and *C. chuana*.

that Benguela Long-billed Lark is more appropriate for *benguelensis*, and that Agulhas Long-billed Lark be used for *brevirostris*, given that it is virtually restricted to the Agulhas Plain.

Intraspecific variation.—Distinct regional variants occur within at least three of the Long-billed Lark species. The widespread species *subcoronata* and *semitorquata* exhibit marked clinal variation in plumage streaking and, to a lesser extent, size. It is intriguing that these clines run in the same direction in both species. The decrease in streaking from south to north among *subcoronata* parallels that found in other larks in the region (e.g. Macdonald 1953, Lawson 1961, Ryan et al. 1998) and corresponds with a decrease in shrub cover. Streaking may thus be adaptive, providing camouflage in areas of dappled shade in the south, and being replaced with uniform plumage in more arid open habitats farther north. This explanation is less plausible for variation within *semitorquata*, which occurs in primarily grassy habitats throughout its range (although the southwestern areas contain more shrubs). The variation within *semitorquata* appears to be gradual, with little need to recognize well-defined subspecies. However, variation within *subcoronata* is bimodal (Fig. 3B), and we advocate the use of subspecific names, if only as convenient labels, for *subcoronata* for the southern, large, heavily streaked birds, and *bradshawi* for the northern, smaller, plain birds.

Sample sizes available for this study were too small to assess the status of forms within *benguelensis* and the other Namibian taxa. This is a priority for further study. There were also too few specimens of *curvirostris* (sensu stricto) to fully assess its status relative to *falcirostris*. Atlas data (Dean et al. 1997) indicate a gap between the ranges of the two forms south of the Olifants River, suggesting that they are rather discrete. The southern species, *brevirostris*, has the smallest range, and no regional variation was detected among the small series of specimens available. However, further work is required to elucidate the relationships among *brevirostris*, *curvirostris*, and *falcirostris*, given that *curvirostris* appears to be intermediate between the two taxa in morphology, and perhaps closer to *brevirostris* in terms of song and habitat use.

Relationships within the Alaudidae.—The Long-billed Lark complex differs markedly from the Karoo Lark complex, the other putative mem-

bers of *Certhilauda* (Dean et al. 1992), in bill and body proportions, display flight, and nest structure (Herremans et al. 1994). The sequence data confirm that the Karoo and Long-billed lark complexes are not closely related, being unable to resolve the trichotomy between these two taxa and a finch-lark (*Eremopterix*). Our unpublished sequence data suggest that the Karoo Lark complex is closely allied to the Sabota Lark (*Mirafransabota*) and is rather distant from the Long-billed Lark complex (Ryan et al. 1998). Accordingly, we support Herremans et al.'s (1994) recommendation that the Karoo Lark complex be dropped from *Certhilauda*, which is now restricted to the Long-billed Lark complex, and possibly the Somali Lark (*C. somalica*), which currently is placed in *Mirafransabota* (Dean et al. 1992). The Karoo Lark complex can be included in *Mirafransabota* for the time being, although this genus is in need of revision.

Range, habitat use, and conservation.—Together with the Short-clawed Lark, the five species within the Long-billed Lark complex occupy most of southwestern Africa (Fig. 1). Based on atlas data (Dean et al. 1997), the crude (maximum) ranges of the five species vary from approximately 15,000 km² for *brevirostris* to some 400,000 km² for *subcoronata*. Habitats occupied differ among species, and atlas data suggest that differences in abundance exist among species. Most populations are patchily distributed, however, and occur at fairly low densities relative to other resident larks in southern Africa.

The northern form of *curvirostris* (*falcirostris*) is common from south of the Olifants River to extreme southern Namibia, where it is restricted to dunes and adjacent strandveld vegetation of the Namaqualand coastal plain. The southern form (n nominate *curvirostris*) occurs more sparingly on coastal dunes from St. Helena Bay to Langebaan, and inland on Malmesbury shales south and east to Tygerberg and Gouda. The latter area has largely been modified for agriculture, but the species occurs in arid wheatfields, especially on the Columbine Peninsula. It does not appear threatened, provided current land-use practices persist. Dean et al. (1997) suggest that its range increased as a result of agriculture.

The Agulhas Long-billed Lark (*C. brevirostris*) is restricted to the Agulhas Plain from Bot River to George, with an extension up the Breede River valley. It occurs primarily in

stony wheatfields and pasture lands on the Agulhas Plain but is also found in succulent Karoo vegetation in the Breede River valley. Both *brevirostris* and *curvirostris* avoid mountain fynbos, with the Cape fold mountains forming a natural barrier between the two species. Despite its limited range, *brevirostris* also appears to be secure provided current conditions persist. However, further study to assess habitat requirements for breeding is warranted, given the species' patchy distribution within its range. Very little, if any, of the species' range is conserved within protected areas.

The eastern *semitorquata* occurs sparsely throughout its large range, preferring rocky slopes and ridges in grasslands (Dean et al. 1997). Afforestation poses a threat to the species in the east of the range (the eastern escarpment and KwaZulu-Natal midlands), but it appears to be secure in the eastern Karoo and adjacent semiarid grasslands. The Karoo Long-billed Lark (*subcoronata*) is widespread and abundant, occurring in semiarid dwarf shrublands of the Nama and succulent Karoo, as well as southern Namibia. It prefers rocky or stony areas but also occurs in other habitats. It is not currently threatened, but very little of the ranges of either *semitorquata* or *subcoronata* fall within formal conservation areas (Siegfried 1989).

Atlas data suggest *benguelensis* is fairly common in the fore-Namib (Dean et al. 1997); its status in southern Angola is little known but it is apparently "not uncommon" (W. R. J. Dean pers. comm.). It occurs primarily in arid and semiarid grassland and shrubland on rocky hills. It probably faces few threats, and a substantial proportion of its Namibian range is protected within the Skeleton Coast Park.

In summary, although probably none of the newly recognized species is threatened, populations of several species do not receive adequate protection in formal conservation areas. Consequently, this type of study is important to identify cryptic species within polytypic species complexes.

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APPENDIX. Nucleotide sequences of 483 base pairs of the mitochondrial cytochrome-*b* gene of the Long-billed Lark complex aligned with that of the Karoo Lark ("Certhilauda" *albescens*) and Gray-backed Finch-Lark (*Eremopterix verticalis*). Dots indicate identity to the *falcirostris* sequence, and question marks indicate undetermined bases. These sequences correspond to positions L15 010 to 15 492 in the published chicken sequence (Desjardins and Morais 199).

							[60]
<i>falcirostris</i>	ATCTGCCTGA	TCATGCAAAT	CATCACAGGC	CTCCTACTAG	CCATGCACTA	CACTCCGGAC	
<i>curvirostris</i>	
<i>brevirostris</i>G	
<i>semitorquata</i>A.....A.....	
<i>subcoronata</i> AA.....A..T..	T..A..A..	
<i>subcoronata</i> BA.....A..T..	T..A..A..	
<i>kaokensis</i> AG.A.....	..G.....A..T..	T..A..A..	
<i>kaokensis</i> BG.A.....	..G.....A..T..	T..A..A..	
<i>chuana</i>A.....CA.....	T..A..A..	
<i>albescens</i>A.	..CA.....	...T.....CA.....	...AG.A..	
<i>Eremopterix</i>	..T.....A.	...T.....	...T.....	..A.....C.	...A.....	...AG.....	
							[120]
<i>falcirostris</i>	ACCTCCCTAG	CCTTCGCCTC	TGTCGCTCAC	ATCTGCCGAG	ATGTTCAATT	CGGCTGACTA	
<i>curvirostris</i>	
<i>brevirostris</i>	C.....C..	
<i>semitorquata</i>C..C.....	
<i>subcoronata</i> A	...T..T..	...T.....C..C..C.....	...T.....	
<i>subcoronata</i> B	..T..T..	...T.....C..C..C.....	...T.....	
<i>kaokensis</i> AT..C..C..C.....	...T.....	
<i>kaokensis</i> BT..C..T..	..C.....	...T.....?	
<i>chuana</i>TA..	...T..T..	C..T..C..C.....	
<i>albescens</i>	C.....A..	..T.....	..C..C.....	T.....C	
<i>Eremopterix</i>T.....C..	..T.....	..C..C.....	...A.....	
							[180]
<i>falcirostris</i>	ATCCGAAACC	TCCACGCAAA	CGGAGCATCC	CTCTTCTTCA	TCTGCATCTA	CCTCCACATT	
<i>curvirostris</i>	
<i>brevirostris</i>C	
<i>semitorquata</i>	
<i>subcoronata</i> A"C.....C..	..A.....	TT.....C	
<i>subcoronata</i> BC.....C..	..A.....	T.....C	
<i>kaokensis</i> AT.....C..T..	..A.....C	
<i>kaokensis</i> BT.....C..T..	..A.....C	
<i>chuana</i>G..C..	T.....	
<i>albescens</i>C..T..	..A.....C..	T.....T.....C	
<i>Eremopterix</i>A..T.....T..	..A.....GT.....	
							[240]
<i>falcirostris</i>	GGCCGAGGAC	TATACTACGG	CTCATACTTA	AACAAAGAGA	CCTGAAACGT	AGGAATCATC	
<i>curvirostris</i>	
<i>brevirostris</i>A.	
<i>semitorquata</i>G.A.	
<i>subcoronata</i> AA.T..	...G.....	
<i>subcoronata</i> BA.T..	...G.....	
<i>kaokensis</i> AA.GG.T..	
<i>kaokensis</i> BA.GG.T..	
<i>chuana</i>	..T.....	..T.....A.T.....	
<i>albescens</i>T	..C.....GAGA.	C...G..C..	
<i>Eremopterix</i>T	..T.....A.	C...G.....	
							[300]
<i>falcirostris</i>	CTCCTCCTGC	TACTCATGGC	CACTGCTTTC	GTAGGGTACG	TTCTCCCCTG	AGGACAAATA	
<i>curvirostris</i>	
<i>brevirostris</i>A.	
<i>semitorquata</i>A.C..A..	
<i>subcoronata</i> AA.A..	..C..T.....	

APPENDIX. Continued.

<i>subcoronata</i> BA.A....	.C..T....
<i>kaokensis</i> A	..T....ATA..	A.....A....	.C.....
<i>kaokensis</i> B	..T....ATA..	A.....A....	.C.....
<i>chuana</i>A.C.....A..T.	.C.....
<i>albescens</i>T..AG	CC.....A..	A.....C..A....	.C..T..A..G
<i>Eremopterix</i>A..AA	.C.....A..	A..C..A..TA....	.C.....	..C.....
[360]						
<i>falcistrostris</i>	TCATTCTGAG	GGGCTACAGT	AATCACAAAC	CTACTCTCAG	CCATCCCATA	TGTTGGTCAG
<i>curvirostris</i>
<i>brevirostris</i>A.....
<i>semitorquata</i>
<i>subcoronata</i> AT..C..
<i>subcoronata</i> BT..C..
<i>kaokensis</i> AC.....T..C.
<i>kaokensis</i> BC.....T..C.
<i>chuana</i>	..C.....	T.....T..C.	..C..C..
<i>albescens</i>A.....T..	..GT.....	.A.....	CA...A..A
<i>Eremopterix</i>C.....T..T.....C..	CA...C..
[420]						
<i>falcistrostris</i>	ACCCTGGTAG	AGTGGGCGTG	GGGGGGGTTC	TCAGTAGATA	ACCCTACTCT	CTCCCGATTC
<i>curvirostris</i>T
<i>brevirostris</i>	T..T.....
<i>semitorquata</i>	T..T.....
<i>subcoronata</i> AA....A...G..
<i>subcoronata</i> BA....A...G..
<i>kaokensis</i> AA..C..A.....
<i>kaokensis</i> BA..C..A.....
<i>chuana</i>A....	.A..A....A..C..A.....
<i>albescens</i>A....	.A..A....T..	..G.....C.	.T..C.....	.A...C..
<i>Eremopterix</i>A....	.A..A..A..	A..A..A..	..C.....C.	...C..C..	.A..T.....
[483]						
<i>falcistrostris</i>	TTCGCCCTCC	ATTTCTACT	CCCATTCCTT	ATCGCAGGCC	TCACACTAGT	TCACCTCACC CTC
<i>curvirostris</i>
<i>brevirostris</i>T.....
<i>semitorquata</i>
<i>subcoronata</i> AG..T.....T
<i>subcoronata</i> BT..C..	..T
<i>kaokensis</i> AC.....T..C.T
<i>kaokensis</i> BC.....T..C.T
<i>chuana</i>	..C.....T..T..C.	..C..C..	..T
<i>albescens</i>A.....T..	..GT.....	.A.....	CA...A..A ??
<i>Eremopterix</i>C.....T..T.....C..	CA...C..