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MOLECULAR SYSTEMATICS OF THE SCALED QUAIL COMPLEX (GENUS *CALLIPEPLA*)

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ABSTRACT.—We obtained 1,040 bp of sequence from the mitochondrial DNA (mtDNA) genes cytochrome *b* (cyt *b*; 736 bp) and NADH-subunit 2 (ND2; 304 bp) to address phylogenetic relationships among the four species in the Scaled Quail complex. California Quail (*Callipepla californica*) and Gambel's Quail (*C. gambelii*) were sister taxa, whereas the relationships of the Elegant Quail (*C. douglasii*) and Scaled Quail (*C. squamata*) were unclear; they might be sister species, or Elegant Quail might be the sister to California plus Gambel's quails. A third, less-likely alternative predicts a contemporaneous origin of Elegant Quail, Scaled Quail, and the ancestor of California and Gambel's quail. The latter phylogenetic hypothesis, however, matches Hubbard's (1973) biogeographic model. Irrespective of which biogeographic hypothesis is correct, calibration of mtDNA genetic distances suggests that the speciation events are much older than the late Pleistocene dates given by Hubbard. Calibration of the rate of mtDNA (cyt *b*, ND2) evolution based on dating of fossil remains of the extinct species *Cyrtonyx cooki* suggested a rate of 2% per million years. Northern Bobwhite (*Colinus virginianus*), Mountain Quail (*Oreortyx pictus*), and Montezuma Quail (*Cyrtonyx montezumae*) were successively more distantly related to the Scaled Quail complex. Phylogenetic trees derived from allozymes (Gutiérrez et al. 1983) and mtDNA sequences were topologically identical, suggesting that both types of gene trees recover the species tree. *Received 28 March 1997, accepted 9 October 1997.*

THE SCALED QUAIL COMPLEX (Hubbard 1973) includes four species: California Quail (*Callipepla californica*), Gambel's Quail (*C. gambelii*), Scaled Quail (*C. squamata*), and Elegant Quail (*C. douglasii*). These species occur throughout arid regions of the southwestern United States and Mexico north of the Isthmus of Tehuantepec (Fig. 1). Hubbard (1973) proposed an evolutionary scenario involving at least two glacial cycles to account for the evolution and biogeographic history of these quail. During the Illinoian Glacial, a widespread ancestor was thought to have been isolated into three taxa termed "pre-*californica*/*gambelii*," "pre-*douglasii*," and "pre-*squamata*." Their ranges expanded during the Sangamon interglacial, and during the Wisconsin Glacial, *californica* and *gambelii* split into distinct species, whereas *douglasii* and *squamata* did not become further subdivided. Thus, Hubbard presented an explicit and testable hypothesis for the evolution and distribution of these four species. Typical of such explanations was the assumption that the last bout of glaciation played a role in speciation (Bermingham et al. 1992, Zink and Slowinski 1995, Klicka and Zink 1997). Somewhat unusual, at least by modern standards, was the initial supposition of a basal trichotomy.

We used sequence data from the mitochondrial DNA (mtDNA) cytochrome *b* (cyt *b*) and NADH-subunit 2 (ND2) genes to test Hubbard's (1973) hypothesis. Our data confirm a close relationship between California Quail and Gambel's Quail, and a possible sister-taxon relationship between Scaled Quail and Elegant Quail. We also assessed congruence between phylogenetic hypotheses derived from mtDNA sequences and allozyme variation (Gutiérrez et al. 1983).

METHODS

We sequenced three California Quail (from Baja California), three Gambel's Quail (New Mexico), four Scaled Quail (New Mexico), and three Elegant Quail (Sonora, Mexico), and one each of the following outgroup species: Northern Bobwhite (*Colinus virginianus*), Montezuma Quail (*Cyrtonyx montezumae*), and Mountain Quail (*Oreortyx pictus*). Specimen voucher numbers and details on collecting localities are given with sequence information in the Genbank accession (nos. AFO28750 to 28782; see Table 2). Sequence data

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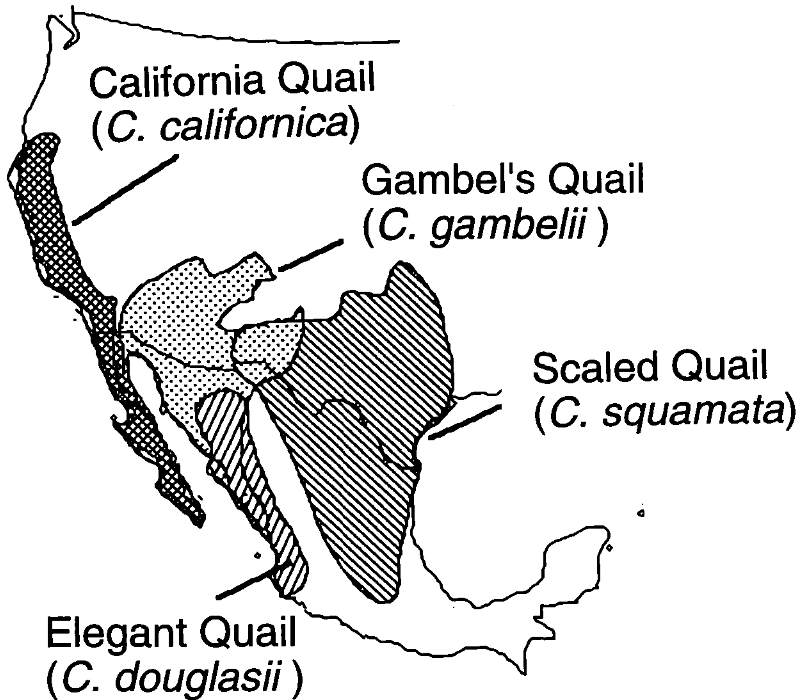

FIG. 1. Distribution of species in the Scaled Quail complex (from Hubbard 1973).

for the above ingroup and outgroup species constitute Data Set A. For comparison with allozyme data of Gutiérrez et al. (1983), we used only sequence data for a 736 bp segment of cyt *b* from Kornegay et al. (1993; Genbank accession code) for Chukar (*Alectoris chukar*; L08378), Japanese Quail (*Coturnix coturnix*; L08377), and Silver Pheasant (*Lophura nycthemera*; L08380, as a substitute for the Ring-necked Pheasant [*Phasianus colchicus*]), and we obtained sequence data of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) from J. G. Groth and G. F. Barrowclough (unpubl. data). Sequence data for these species plus those in Data Set A constitute Data Set B. We also determined the sequence for a small segment of cyt *b* and the adjoining t-RNA^{leu} from samples of study skins for two additional species, Banded Quail (*Philortyx fasciatus*; Bell Museum ornithology catalogue number 10947) and Singing Quail (*Dactylortyx thoracicus*; Bell Museum 14958), to assess their relationships to the Scaled Quail complex.

We used standard methods to extract DNA from tissue and study skins (Ellegren 1992, Hillis et al. 1996, Zink et al. 1997) and the polymerase chain reaction (PCR; Saiki et al. 1988, Palumbi 1996) to amplify mtDNA. Primers L14841 (Kocher et al. 1989) and H4a (Harshman 1996) amplified an approximately 1,100 bp segment of cyt *b*. A 400 bp portion of ND2 was amplified with L5215 and H5578 (Hackett 1996). Manual sequencing reactions (Hillis et al. 1996) were performed and run on 6% acrylamide gels. Cyt *b* was sequenced in both directions with the amplification primers and one internal primer, H15299 (Hackett 1996). ND2 was sequenced only with H5578, because L5215 did not work as a sequencing primer. Sequences were aligned with the published chicken sequence (Desjardins and Morais 1990); no gaps were detected.

We computed basic sequence statistics, Kimura's (1980) two-parameter distances (K2P), and neighbor-joining (NJ) trees with MEGA (Kumar et al. 1993). We used PAUP (Swofford 1993) to conduct maximum parsimony searches (branch and bound) of the data, with weights of 1:1 and 1:2 for transitions and tranversions, to bootstrap (Felsenstein 1985) the unweighted characters 1,000 times, and to compute *g*-values as measures of phylogenetic signal (Hillis 1991, Hillis and Huelsenbeck 1992, Kallersjo et al. 1992). PAUP* (Swofford pers. comm.) was used to compute log-determinant distances (log-det), a conservative estimate of mtDNA genetic distances (Swofford et al. 1996). Maximum-likelihood trees were estimated with PHYLIP (Felsenstein 1993). Competing tree topologies were tested with the Kishino-Hasegawa (1989) maximum likelihood test. MacClade (Maddison and Maddison 1992) was used to evaluate the lengths of alternative topologies. We used Mantel's (1967) test as implemented in NTSYS (Rohlf 1992) to compare matrices of Rogers' (1972)

TABLE 1. Distribution of variation at nucleotide sites for cytochrome *b* (Cyt *b*) and NADH-subunit 2 (ND2); TS = transition, TV = transversion.

Gene region	First		Second		Third	
	TS	TV	TS	TV	TS	TV
Cyt *b*	30	7	8	0	92	33
ND2	6	3	7	2	42	11

genetic distances derived from allozyme comparisons (Gutiérrez et al. 1983) and log-det distances; significance values were based on 9,999 random matrix permutations. The absolute numbers of transitions and transversions at first and third positions of codons were plotted against log-det distance to evaluate saturation. To assess molecular-rate heterogeneity, we compared the log likelihoods of maximum-likelihood trees computed with and without the assumption of a molecular clock (PHYLIP routines DNAMLK and DNAML, respectively) by doubling the difference between the two likelihood estimates and determining its chi-square probability (df = $n - 2$, where n = number of species; Felsenstein 1993).

RESULTS

Data Set A.—We obtained 1,040 bp of mtDNA sequence for the Scaled Quail complex and outgroups, including 304 bp from ND2 and 736 bp from cyt *b*. From the 17 individuals sequenced, we identified 11 haplotypes. Percentage base composition was biased in a manner typical of birds and other vertebrates where guanine residues are uncommon, especially at third positions. Overall base percentages (cyt *b*, ND2, respectively) were: Adenine (27.1%, 34.0%), Thymine (25.2%, 22.8%), Cytosine (33.7%, 32.2%), and Guanine (14.0%, 11.0%). Of the 1,040 aligned bases, 241 were variable, and 135 were potentially phylogenetically informative; variable sites were mostly third position transitions (Table 1). A total of 33 amino acids was variable (11 were parsimony informative).

Sequence divergence (K2P distances; Table 2) ranged from 0.0019 (within California Quail and Gambel's Quail) to 0.1635 (Montezuma Quail vs. Mountain Quail). Among the four species of the Scaled Quail complex, sequence divergence averaged 0.054 ± SD of 0.016, and ranged from 0.022 (California vs. Gambel's quail) to 0.069 (Scaled vs. Gambel's quail). The Northern Bobwhite was closer to the Scaled Quail complex (average K2P distance = 0.085 ± 0.002) than was the Mountain Quail (0.115 ± 0.004) or the Montezuma Quail (0.151 ± 0.004).

Saturation was not evident at first and third positions (Fig. 2), nor at the nearly invariant second position (not shown). Log likelihoods derived from analyses with and without the assumption of a molecular clock did not differ significantly ($P > 0.10$), indicating an absence of molecular-rate heterogeneity among taxa.

A significant g_1-value of −0.63 suggested signal in the data (Kallersjo et al. 1992). The shortest tree among 1,000 random trees, 460 steps, was significantly longer than those inferred from maximum-parsimony analysis, which produced two equally parsimonious trees (Fig. 3) of length 348 with sites unweighted, and one

TABLE 2. Kimura (1980) two-parameter distance values among taxa. Distances are in the upper right matrix, and standard errors are in the lower left matrix.

Taxon[a]	1	2	3	4	5	6	7	8	9	10	11
1	—	0.0029	0.0555	0.0644	0.0661	0.0607	0.0608	0.0608	0.0808	0.1499	0.1189
2	0.0017	—	0.0587	0.0677	0.0694	0.0640	0.0640	0.0641	0.0819	0.1537	0.1213
3	0.0077	0.0079	—	0.0643	0.0630	0.0575	0.0576	0.0576	0.0864	0.1598	0.1155
4	0.0083	0.0086	0.0083	—	0.0019	0.0217	0.0217	0.0217	0.0848	0.1533	0.1150
5	0.0084	0.0087	0.0082	0.0014	—	0.0216	0.0216	0.0216	0.0865	0.1536	0.1157
6	0.0080	0.0083	0.0078	0.0047	0.0046	—	0.0019	0.0019	0.0865	0.1477	0.1112
7	0.0081	0.0083	0.0078	0.0047	0.0047	0.0014	—	0.0019	0.0866	0.1463	0.1123
8	0.0081	0.0083	0.0078	0.0047	0.0046	0.0014	0.0014	—	0.0845	0.1489	0.1101
9	0.0094	0.0095	0.0098	0.0097	0.0098	0.0098	0.0098	0.0097	—	0.1463	0.1147
10	0.0134	0.0137	0.0140	0.0137	0.0136	0.0133	0.0132	0.0134	0.0132	—	0.1635
11	0.0116	0.0118	0.0115	0.0114	0.0115	0.0112	0.0113	0.0112	0.0115	0.0145	—

[a] Species, with Genbank numbers in parentheses: 1, Scaled Quail 1 (AFO28753–55); 2, Scaled Quail 2 (AFO28756–58); 3, Elegant Quail (AFO28750–52); 4, Gambel's Quail 4 (AFO28759–61); 5, Gambel's Quail 6 (AFO28762–64); 6, California Quail 3 (AFO28765–67); 7, California Quail 5 (AFO28768–70); 8, California Quail (AFO28771–73); 9, Northern Bobwhite (AFO28774–76); 10, Montezuma Quail (AFO28777–79); 11, Mountain Quail (AFO28780–82).

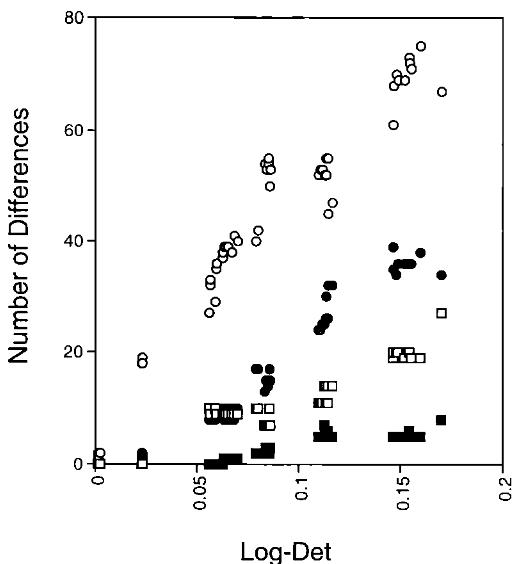

FIG. 2. Plot of the numbers of transitions and transversions at first and third positions versus log-det. Cyt *b* and ND2 data combined. Open squares are first-position transitions, closed squares are first-position transversions, open circles are third-position transitions, and closed circles are third-position transversions.

tree (l = 692) identical to that in Figure 3A with the 2:1 weighting scheme. Maximum likelihood and NJ (distance = log-det or K2P) analyses supported the topology in Figure 3A; however, the topology in Figure 3B (weighted l = 700) did not have a significantly worse log-likelihood ratio ($P = 0.62$; Kishino and Hasegawa [1989] test). Within the Scaled Quail complex, the sister-species relationship between California Quail and Gambel's Quail is highly supported (bootstrap percentage = 100%) regardless of analytical approach. Scaled Quail and Elegant Quail were supported as sister species in 51% of the bootstrap maximum-parsimony trees and 62% of the bootstrap NJ trees.

Because distant outgroups can bias rooting (Smith 1994), we removed Mountain Quail and Montezuma Quail and used only Northern Bobwhite, the sister species of the Scaled Quail complex, as an outgroup. Maximum-parsimony analysis of unweighted sequence data recovered the topology in Figure 3A (tree length 168), and that in 3B was one step longer. Thus, use of the two more distant outgroups yielded a second tree, and therefore more ambiguity, but the trees were very similar in length.

Despite use of many primer pairs for PCR, we only succeeded in obtaining 135 bp of cyt *b* and t-RNA^{leu} sequence (Appendix) from *P. fasciatus* and *D. thoracicus,* because DNA from the 45-year-old study skins had degraded. Comparison of these 135 bp from all ingroup species revealed that *D. thoracicus* was very distant from the Scaled Quail complex (>6%), whereas *P. fasciatus* was approximately the same distance (2.7%) as the Northern Bobwhite (2.0%) from the ingroup. Thus, we found no evidence that either *P. fasciatus* or *D. thoracicus* was closer to the ingroup (or a part of it) and would therefore be more appropriate outgroups, than the Northern Bobwhite.

We noted a discrepancy in the cyt *b* sequence for Gambel's Quail between our data and that deposited in Genbank (accession L08382) by Kornegay et al. (1993). In particular, their nucleotide sequence beginning at amino acid 135, CATGAGGGC, almost certainly should be CCATGAGGG, which is consistent with most of the other galliforms that they sequenced and the three Gambel's Quail that we sequenced.

Data Set B.—Species showed considerable divergence (151 of 736 base positions were phylogenetically informative), with K2P distances of up to 20% (data not shown but can be computed from sequences in Genbank). Therefore, for this phylogenetic analysis, we weighted transversions 2:1 over transitions. Maximum-parsimony analysis of cyt *b* sequences revealed a single tree with the topology in Figure 3A for the species already discussed, with the following taxa added as successively more distant sister taxa: *A. chukar, C. coturnix,* and *L. nycthemera* (with *T. pallidicinctus* as the root).

DISCUSSION

Phylogeny and classification.—The sister-taxon relationship of California Quail and Gambel's Quail is unambiguous, with the bootstrap support at 100%; sequences of these species differ by less than 2.5% (Table 2). The morphology of these two species is similar (Holman 1961, 1964, Hudson et al. 1966), and some authors have suggested that they are conspecific or together form a superspecies (Mayr and Short 1970, AOU 1983). Sequence data do not resolve the relationships of Elegant Quail and Scaled Quail. The two alternative topologies (Fig. 3) resulted from different placements of the root

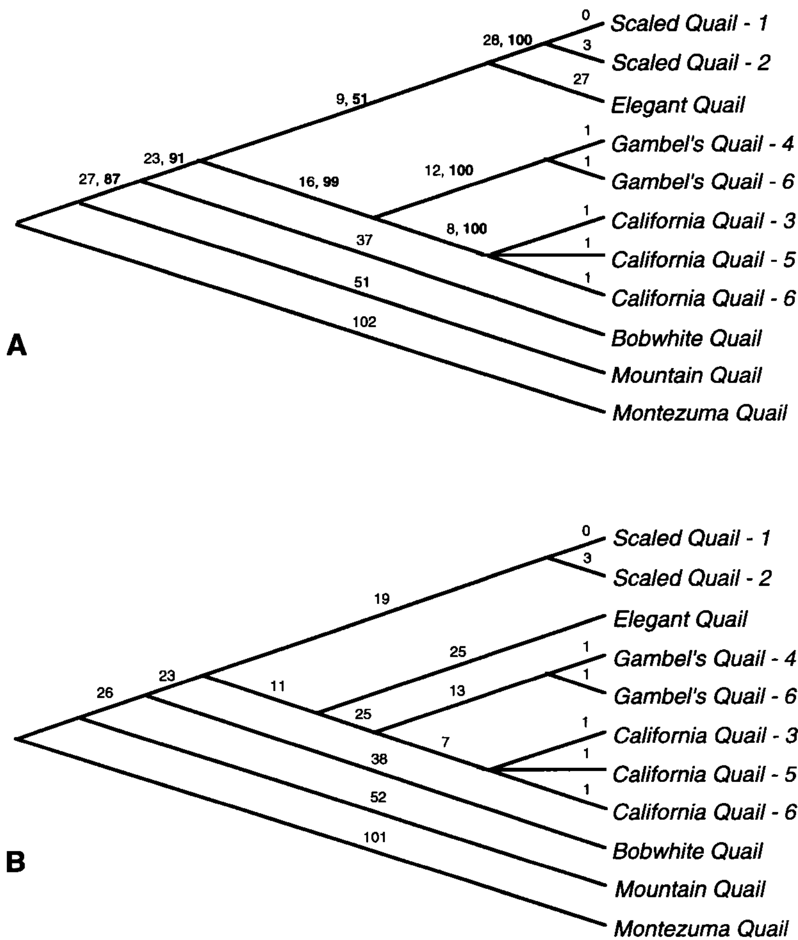

FIG. 3. Two equally parsimonious trees of length 348; ci = 77, ri = 68, and rc = 53. Using a 2:1 TV : TS ration, the log-likelihood was −3003.338 of topology A and −3005.607 of topology B. Topology A was found by NJ and the 2:1 weighted maximum parsimony analysis. Numbers represent synapomorphies and numbers in bold (topology A only) are bootstrap proportions derived from 5,000 replications.

on the ingroup (Scaled Quail complex) tree. Of the three possible unrooted trees that exist for four taxa, topology A is best supported (Fig. 4). Distant outgroups can result in the root being drawn artifactually to long branches (Smith 1994). The two rootings in Figure 4 (denoted by arrows) occur on relatively long branches. Hence, our outgroups might be inappropriate for rooting the tree because the nearest species to the Scaled Quail complex, the Northern Bobwhite, differs on average by 8.5% from the ingroup. Our analysis of short segments of sequence from *P. fasciatus* and *D. thoracicus* provides no better choices for outgroups, although the former is much closer to the ingroup. Thus, unambiguous outgroup rooting appears unlikely with extant quail, and phylogenetic placements of Elegant Quail and Scaled Quail remain uncertain.

We consider the two topologies in Figure 3 as viable hypotheses. A third hypothesis, contemporaneous speciation, is discussed below. The topologies in Figure 3 could result from speciation events being closely spaced in time, which inhibits their recovery (Lanyon 1988), or from inadequate data. One might favor closely spaced speciation events, a so-called "star phylogeny," because phylogenetic resolution occurred at both basal and terminal nodes. Such a situation suggested to Lara et al. (1996) that the genes used were capable of resolving relationships. However, no theory predicts that

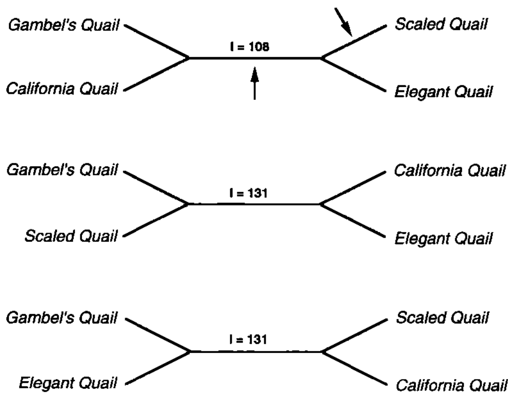

FIG. 4. Three possible trees for ingroup taxa (all conspecific haplotypes from Figure 2 were used to determine tree length [numbers] but for clarity are not shown). Topology A (top panel) is the best explanation of the data.

speciation events must be equally spaced and recoverable throughout the duration of a lineage. Lack of phylogenetic resolution for Elegant and Scaled quail likely resulted from closely spaced speciation events at an intermediate period during the evolution of New World quail. Although more sequence data might allow phylogenetic resolution, we note that these quail species are relatively differentiated, with many synapomorphies and typical levels of homoplasy (Fig. 3). Therefore, it would take a different quality (e.g. genes encoded in the nucleus) of sequence data, rather than simply more mtDNA data, to shift the balance of synapomorphies to favor significantly one topology over the other (but see Otto et al. 1995).

Previous classifications (e.g. AOU 1957) placed California Quail, Gambel's Quail, and Elegant Quail in *Lophortyx,* with only the Scaled Quail in *Callipepla.* The topology in Figure 3B is consistent with this arrangement. A tree (not shown) in which Scaled Quail is sister to California Quail plus Gambel's Quail is four steps longer than the most parsimonious tree, although it is not significantly "worse" according to the Kishino-Hasegawa (1989) maximum-likelihood test. Yet, this topology occurred in no method of tree building, including neighbor joining, maximum parsimony (unweighted or weighted), or maximum likelihood. Therefore, we do not consider it to be a viable hypothesis.

Mayr and Short (1970) used the genus name *Callipepla* for the single species of *Oreortyx* (i.e. the Mountain Quail). Principles of phylogenetic systematics (Hennig 1966, Wiley 1981) applied to Figure 3 invalidate this nomenclature unless the Northern Bobwhite is also included in *Callipepla,* a suggestion made by Mayr and Short (1970). Our data do not rule out a genus that combines *Callipepla, Colinus,* and *Oreortyx.* Although it would be inappropriate in our opinion (Johnson and Zink 1983) to use levels of genetic distance to resolve taxonomic categories, such a combined genus would be genetically heterogeneous (pairwise distances up to 12.0%) relative to other avian genera studied to date. The other species of New World quail should be examined in depth prior to generic revision.

Rates of molecular evolution in quail.—The only calibration of allozyme distances with a relatively old New World fossil was by Gutiérrez et al. (1983) for the same galliform birds that we studied. They concluded that an extinct species, *Cyrtonyx cooki* (congeneric with *Cyrtonyx montezumae* and which was examined by Gutiérrez et al. [1983] and us), indicated that this genus had been evolving independently from other New World galliforms for at least 16 million years (MY). However, Marten and Johnson (1986) obtained unpublished information from paleontologists familiar with the depositional environments of the same specimen of *C. cooki* that suggested it could be as young as 7 to 9 MY. Thus, estimates of the age of the fossil differ by a factor of two. Marten and Johnson (1986) used the estimate of 7 to 9 MY to calibrate an allozyme clock.

Calibrations of molecular clocks assume a roughly uniform rate of nucleotide substitution, which was supported for our data. The average log-det distance from *C. montezumae* to the Scaled Quail complex is 0.154 (0.148 for cyt *b* data alone). Assuming that *C. cooki* is correctly placed in a phylogenetic context (see Gutiérrez et al. 1983), the rate of mtDNA sequence divergence (cyt *b* alone or combined with ND 2) is 1 to 2%, depending on the age of the fossil. This is consistent with estimates derived from independent calibrations of a number of other avian taxa (citations in Klicka and Zink 1997). Given the apparent convergence of such estimates on 2% per MY, this figure is perhaps more likely than the estimate of 1% per MY derived from assuming an age of 16 MY for *C. cooki.* We stress, as do others (Avise 1994), that

owing to a variety of factors, rate calibrations are best viewed as heuristic tools only.

Biogeography.—The consensus of the two equally parsimonious trees (Fig. 3) yields a trichotomy (not shown), exactly as outlined in Hubbard's (1973) scenario. This consensus tree is six steps longer than the shortest trees, but it is not significantly worse than either topology in Figure 3A (Kishino-Hasegawa test, $P = 0.2$). The increased length of the consensus tree over the two equally parsimonious trees illustrates why many taxonomists do not interpret consensus trees phylogenetically (Swofford et al. 1996). That is, the consensus tree indicates uncertainty about the placements of Elegant Quail and Scaled Quail, not necessarily that a trichotomy is the best explanation of the data. Thus, Hubbard's (1983) hypothesis of a basal, three-way split of a common ancestral species is not supported by parsimony but it is not ruled out by maximum likelihood. Zink et al. (1998) have favored contemporaneous speciation for other aridland avian lineages, and we consider as a third viable (albeit less likely) hypothesis the contemporaneous origin of Elegant Quail, Scaled Quail, and the common ancestor of California Quail and Gambel's Quail. Resolution of general area relationships requires comparison of phylogenetic patterns in multiple lineages, including quail, *Polioptila* (Zink and Blackwell 1998), *Pipilo* (Zink et al. 1998), and *Toxostoma* (Zink et al. unpubl. data).

Given the preceding discussion of rates of molecular evolution, the timing of speciation events envisioned by Hubbard (1973) is too recent. It is extremely unlikely that the 2.2% divergence between California and Gambel's quail evolved in only 40,000 to 100,000 years, concomitant with the onset of the Wisconsin glacial period. A rate of 2% per MY also would alter the timing of speciation events shown in Gutiérrez et al. (1983: figure 5). The date of separation of Mountain Quail from the remaining species would be about 6 MY rather than the 12.6 MY as shown. Separation of Northern Bobwhite would date to 4.1 MY rather than 7.0 MY, and California Quail and Gambel's Quail separated from their common ancestor approximately 1 MYA. These dates are hypotheses but are consistent with other data (Zink and Slowinski 1995, Klicka and Zink 1997) that suggest that most extant avian species originated in the late Pliocene or early Pleistocene.

Phylogenetic congruence of allozyme and mtDNA data.—Mantel's test indicated that the matrices of allozyme and mtDNA distances were significantly congruent ($P < 0.0001$; matrix correlation = 0.84). In addition, Gutiérrez et al. (1983: figure 2) presented a tree that was topologically identical to that based on cyt *b* data alone. However, large distances among taxa for both mtDNA and allozymes might make phylogeny reconstruction relatively unambiguous; unfortunately, Gutiérrez et al. (1983) lacked specimens of Elegant Quail. Nonetheless, the congruence of allozymes and mtDNA for this set of taxa, as well as for many others (e.g. Zink et al. 1991, Zink and Dittmann 1991, Zink and Blackwell 1996, Zink et al. 1998), suggest that allozymes and mtDNA effectively recover phylogenetic signal; i.e. both recover the species tree.

Recent studies have noted that amplification and sequencing of nuclear copies of mitochondrial genes (Zhang and Hewitt 1996) can bias phylogenetic inference. The congruence between nuclear (allozymes) and mtDNA data sets render it less likely that we accidentally sequenced nuclear copies of cyt *b* or ND2 in quail. Alternatively, if we did sequence nuclear copies, they must have been transposed recently into the nucleus so as not to confound phylogenetic inference. The observations that our sequences contained no stop codons, and that they exhibited a typical distribution of variation at first, second, and third codon positions, provide further evidence against nuclear contamination (Zhang and Hewitt 1996).

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APPENDIX. Cyt *b* and t-RNA[leu] (beginning at base 95) sequence for selected species, obtained with PCR (and sequencing) primers H4A and LCBD (J. T. Klicka 5′ to 3′: CATCATCATYGGMCAACTAGCCTC). A dot signifies identity to the California Quail sequence.

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California Quail:
CAACTAGCCTCATTCTCATACTTCACCACCCTCCTAATCCTCTTCCCCATCATCGGAACCCTAGAAAACAAAATACTCAAC?TACTAAATACTCTAATAGTTTATAAAAAACATTGGTCTTGTAAACCGAAGACT
Gambel's Quail:
..............................A.................................................................................................A......
Scaled Quail:
............................T....T................T.............................................................................A......
Elegant Quail:
............C.A...................................T.....................................?.........??............................A......
Bobwhite Quail:
..................................................T........T...........................................................................
Banded Quail:
?.................................................T........G.................T.........................................................
Singing Quail:
............C.T..C.....T..T.TT.................T................................................................................AG.....
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