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EVOLUTIONARY PATTERNS OF MORPHOMETRICS, ALLOZYMES, AND MITOCHONDRIAL DNA IN THRASHERS (GENUS *TOXOSTOMA*)

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ABSTRACT.—We examined patterns of variation in skeletal morphometrics (29 characters), allozymes (34 loci), mitochondrial DNA (mtDNA) restriction sites (n = 74) and fragments (n = 395), and mtDNA sequences (1,739 bp from cytochrome *b*, ND2, ND6, and the control region) among all species of *Toxostoma*. The phenetic pattern of variation in skeletal morphometrics generally matched traditional taxonomic groupings (based on plumage patterns) with the exceptions of *T. redivivum*, which because of its large size clusters outside of its proper evolutionary group (*lecontei*), and *T. occelatum*, which did not cluster with *T. curvirostre*. Skull characters contributed highly to species discrimination, suggesting that unique feeding adaptations arose in different species groups. Although genetic variation was detected at isozyme loci (average heterozygosity = 3.6%), these data yielded little phylogenetic resolution. Similarly, mtDNA restriction sites were relatively uninformative; hence, phylogenetic conclusions were based on sequence data. Phylogenetic analyses confirmed the monophyly of these traditionally recognized assemblages: *rufum* group (*T. rufum*, *T. longirostre*, and *T. guttatum*), *lecontei* group (*T. lecontei*, *T. crissale*, and *T. redivivum*), and *cinereum* group (*T. bendirei* and *T. cinereum*). The *cinereum* and *lecontei* groups appear to be sister lineages. Monophyly of the *curvirostre* group (which also includes *T. occelatum*) was not confirmed. Sequence data suggest that *T. occelatum* and *T. curvirostre*, which differ by 7.7% sequence divergence, are probably most closely related to the *rufum* group. *Toxostoma rufum* and *T. longirostre* have similar external appearances and differ by 5.0%. *Toxostoma guttatum* is restricted to Cozumel Island and often is considered a subspecies of *T. longirostre*; it differs by more than 5% from the other two members of the *rufum* group and is a distinct species constituting the basal member of this group. The phenotypically distinctive *T. bendirei* and *T. cinereum* differ in sequence divergence by only 1.6%. Overall, mtDNA distances computed from coding genes (mean 8.5%) exceeded distances computed from the control region (mean 7.6%), contrary to expectation. Because neither allozymes nor mtDNA could unambiguously resolve the placement of *T. occelatum* and *T. curvirostre*, a scenario involving contemporaneous speciation is suggested. Application of a molecular clock suggested that most speciation occurred in the late Pliocene or early Pleistocene. *Received 12 June 1998, accepted 17 February 1999.*

THE AVIAN GENUS *Toxostoma* (thrashers) includes 10 formally recognized species distributed throughout much of North America (Fig. 1). Species' distributional areas vary in extent from eastern North America (*T. rufum*) to Cozumel Island (*T. guttatum*). Most species inhabit arid or semiarid regions. Engels (1940) evaluated patterns of bill shape and plumage pattern (especially presence and shape of ventral spots) and recognized four species groups: (1) the *rufum* group (*T. rufum* [Brown Thrasher], *T. guttatum* [Cozumel Thrasher], and *T. longirostre* [Long-billed Thrasher]); (2) the *cinereum* group (*T. cinereum* [Gray Thrasher] and *T. bendirei* [Bendire's Thrasher]); (3) the *occelatum* group (*T. occelatum* [Occelated Thrasher] and *T. curvirostre* [Curve-billed Thrasher]); and (4) the *lecontei* group (also known as the sickle-billed group; *T. lecontei* [Le Conte's Thrasher], *T. crissale* [Crissal Thrasher], and *T. redivivum* [California Thrasher]). *Toxostoma rufum* and *T. bendirei* are migratory, whereas the other species are thought to be generally sedentary. All species tend to be secretive and terrestrial; many run rather than fly when startled.

Hubbard (1973) noted parallels in the distri-

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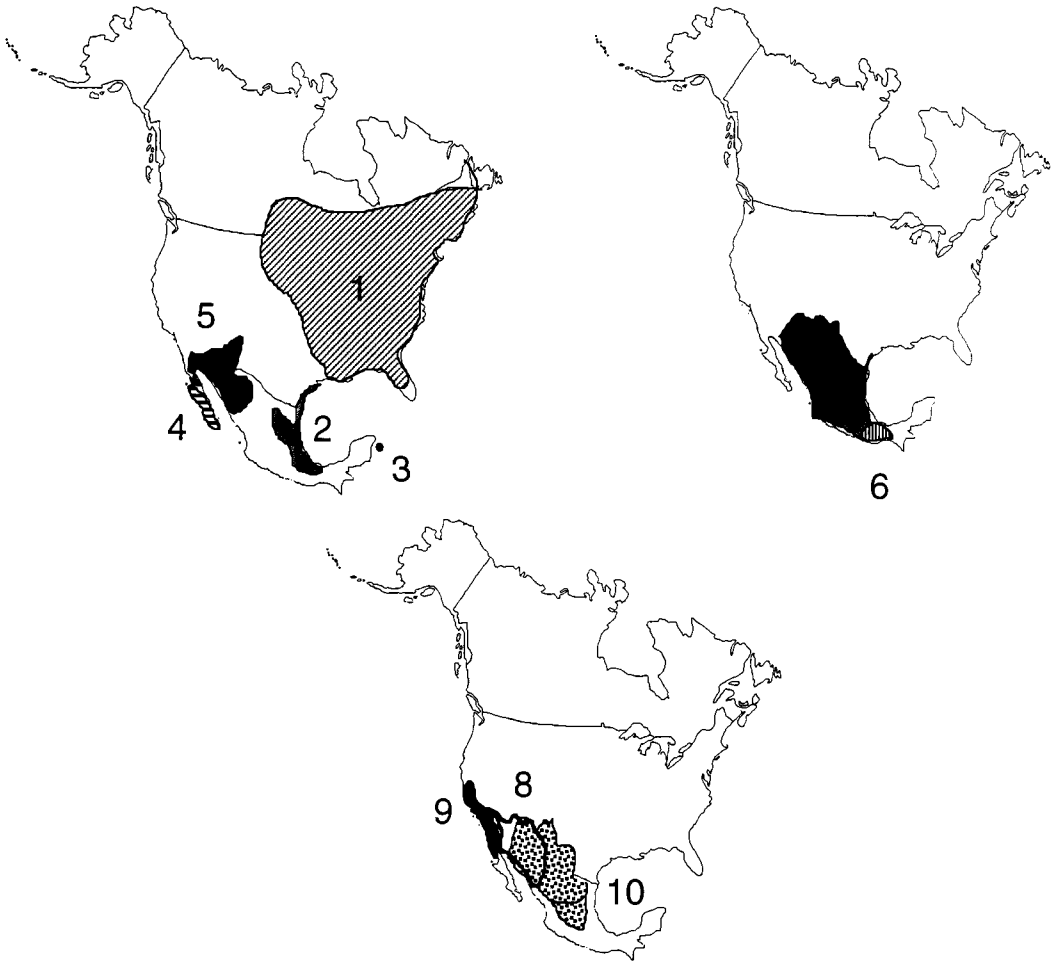

FIG. 1. Breeding distribution of species in *Toxostoma*. 1 = *T. rufum*, 2 = *T. longirostre*, 3 = *T. guttatum*, 4 = *T. cinereum*, 5 = *T. bendirei*, 6 = *T. occelatum*, 7 = *T. curvirostre*, 8 = *T. lecontei* (note Baja California distribution, termed *T. arenicola* by Zink et al. [1997]), 9 = *T. redivivum*, and 10 = *T. crissale*.

bution of members of *Toxostoma* with many other avian lineages distributed in arid regions of North America, including towhees (*Pipilo*), gnatcatchers (*Polioptila*), and quail (*Callipepla*). Hubbard proposed that cycles of late Pleistocene glaciations led to speciation in these clades and that parallels in distribution among groups resulted from independent evolutionary responses to a common set of isolating events. If each lineage responded to the same sequential series of vicariant barriers, they should exhibit congruent area cladograms. However, phylogenetic analyses of these groups were not explicit. To facilitate biogeographic analysis and understanding of avian evolution in the aridlands, we undertook phylogenetic studies of these lineages (Zink and Blackwell 1998a, b; Zink et al. 1998). We report here on *Toxostoma*, for which we obtained multiple data sets, including skeletal morphometrics, allozymes, and both restriction fragments/sites and sequences of mitochondrial DNA (mtDNA); only sequence data were available for *T. guttatum*.

METHODS

Specimens.—The numbers of geographic localities and specimens used for each of the following analyses differed and are given below. The Sage Thrasher (*Oreoscoptes montanus*) is more closely related to mockingbirds (*Mimus*) than to species of *Toxostoma* (Sibley and Ahlquist 1990: figure 379) and was used

TABLE 1. Loadings of skeletal characters of thrashers on principal components (loadings were similar irrespective of whether only species means or all individuals were used).

Character	PC I	PC II	PC III
1 Premaxillary length	0.32	−0.16	0.02
2 Premaxillary length to nasal opening	0.51	−0.31	−0.25
3 Premaxillary depth	0.15	0.12	−0.22
4 Nasal bone width	0.10	0.12	−0.01
5 Interorbital width	0.17	0.33	−0.36
6 Postorbital width	0.08	0.10	−0.04
7 Skull width	0.06	0.14	−0.07
8 Skull length	0.20	−0.04	−0.01
9 Mandible length	0.21	0.02	−0.02
10 Minimum mandible length	0.48	−0.29	−0.03
11 Mandible depth	0.07	0.46	−0.53
12 Coracoid length	0.09	0.13	0.11
13 Scapula head width	0.05	0.14	0.11
14 Sternum length	0.07	0.12	0.19
15 Sternum width	0.08	0.17	0.13
16 Sternum depth	−0.02	0.26	0.16
17 Posterior synsacrum length	0.22	0.15	0.22
18 Length of fused vertebrae	0.13	0.13	0.32
19 Anterior synsacrum length	0.13	0.15	0.20
20 Synsacrum width	0.13	0.07	0.23
21 Synsacrum minimum width	0.06	0.18	0.20
22 Femur distal end width	0.24	0.07	0.11
23 Femur length	0.17	0.06	0.18
24 Tibiotarsus length	0.11	0.09	0.15
25 Tarsus length	0.09	0.13	0.13
26 Humerus trochanter length	0.09	0.18	0.05
27 Humerus length	0.09	0.16	0.01
28 Ulna length	0.03	0.21	0.01
29 Carpal length	0.01	0.20	−0.03

as an outgroup for all analyses; we also used the Northern Mockingbird (*Mimus polyglottos*) as an outgroup for some data sets.

Morphometrics.—We (RMZ) measured 29 skeletal characters (Table 1) to the nearest 0.01 mm. These characters represented major body regions and were scored on a total of 174 specimens (Table 2). Means, variances, pairwise Mahalanobis distances, and taxonomic distances (Sneath and Sokal 1973) were computed with SAS (SAS 1982) and NTSYS (Rohlf 1992). Principal components analysis (PCA) was used to summarize broad patterns of overall skeletal similarity; measurements were $\log_{10}$ transformed, and components were extracted from the covariance matrix using SAS. PCAs were done on species' character means to mitigate the effects of differing sample sizes and different variance-covariance structures, and also on all individuals. Using NTSYS, a minimum-spanning tree (MST) was computed from taxonomic distances derived from log-transformed character means and superimposed on the principal components plots to reveal distortion resulting from collapsing all variation into two or three axes (Sneath and Sokal 1973). Canonical discriminant function analysis (DFA) was used to classify specimens to species and to investigate patterns of differentiation in multivariate skeletal space. Generalized squared distances (Sneath and Sokal 1973) resulting from discriminant analysis were clustered using KITSCH, FITCH, and NEIGHBOR (neighbor-joining [NJ]) routines in PHYLIP (Felsenstein 1993).

Allozymes.—Standard starch-gel electrophoresis was used (Zink 1988), and 34 loci were scored for 111 specimens (Table 2, Appendix 1). Heterozygosity was estimated by direct count. Allelic frequencies were converted to genetic distances following Cavalli-Sforza and Edwards (1967) and Nei (1972) and analyzed with NJ to infer a phylogeny. A minimum-spanning tree was constructed from Nei (1972) distances using NTSYS (Rohlf 1992) and superimposed on the PCA plot of species' skeletal character means. CONTML in PHYLIP was used to infer a phylogeny using maximum likelihood. Alternative trees were evaluated using Kishino and Hasegawa's (1989) maximum-likelihood test as implemented in CONTML.

Restriction fragments/sites.—From crude tissue extracts, we isolated mtDNA using CsCl density-equilibrium gradients developed by ultracentrifugation (Lansman et al. 1981, Zink and Dittmann 1991). Twenty-one restriction enzymes were used to digest purified mtDNA for 40 individuals (Table 3). We scored the presence/absence of 395 restriction frag-

TABLE 2. Specimens used in morphological and allozyme study, and measures of allozyme variation.

Species	Morphology[a]	Allozymes[a]	% Heterozygosity	% Polymorphic loci
Mimus polyglottos	CA (1), TX (1), NM (1), NV (2), SO (2), BC (1)	LA (5)	3.2	5.9
Oreoscoptes montanus	NV (9), OR (1), CA (1), ID (2), AZ (2)	CA (14)	2.7	20.6
Toxostoma bendirei	AZ (25)	AZ (13)	4.6	17.6
T. cinereum	BC (12)	BC (11)	2.4	17.6
T. curvirostre	AZ (28), NM (1), OA (2), TX (1)	AZ (21)	1.9	17.6
T. occelatum	OA (3)	OA (2)	2.9	5.9
T. redivivum	CA (22)	CA (12)	2.2	20.6
T. lecontei	CA (10), AZ (5), NV (1)	CA (6), BC (2)	2.2	8.8
T. crissale	AZ (23), SO (1)	AZ (16)	7.0	23.6
T. longirostre	TX (5), TM (1)	TX (2)	2.9	5.9
T. rufum	NY (7), MI (1), KS (1), NJ (2), CT (1)	LA (11)	6.4	11.8
Totals/mean	$n = 174$	$n = 115$	$\bar{x} = 3.6$	$\bar{x} = 14.7$

[a] Entries are location, with n in parentheses. CA = California, TX = Texas, LA = Louisiana, OA = Oaxaca, BC = Baja California, AZ = Arizona, TM = Tamaulipas, KS = Kansas, NV = Nevada, NJ = New Jersey, CT = Connecticut, SO = Sonora.

ments and from these inferred the presence/absence of 74 restriction sites for 9 restriction enzymes. In the latter case, sites were easily inferred from digestion profiles and were obviously related by one or two cleavage events; hence, a sample of restriction sites could be scored without double-digestions. The fragment matrix for all haplotypes was converted to *p*-distances (Nei and Li 1979) using a computer program ("PEST") written by J. E. Neigel. The distance matrix was used to estimate a neighbor-joining tree as above. Because all conspecific haplotypes clustered together, the site matrix for a reduced set of individuals was used to compute *p*-distances (PEST), and a minimum-spanning tree was constructed and superimposed on the PCA plot of species based on means of skeletal characters. RESTML in PHYLIP provided an estimate of phylogeny using maximum likelihood. Because of small samples within species, measures of haplotype and nucleotide diversity were not computed.

Direct sequencing.—From both purified mtDNA and crude tissue extracts, mtDNA was amplified using the polymerase chain reaction (PCR) for the following gene regions: cytochrome *b* (cyt *b*), ND2, ND6, $tRNA^{Glu}$, and the control region (CR). PCR primers (Tarr 1995, Zink and Blackwell 1998a) also were used for manual sequencing. Total genomic DNA from *T. guttatum* was extracted from feather fragments taken from museum study skins (see Klicka et al. 1999). At least two individuals of the other species were sequenced, and for *T. lecontei* and *T. curvirostre,* many individuals were sequenced from throughout their respective ranges (Zink et al. 1997, Zink and Blackwell unpubl. data).

Alignment for coding regions was unambiguous with the exception of 23 bp of ND6, which was deleted from analysis; no gaps or insertions were noted. Some gaps were required in CR sequences to facilitate alignment by eye, and two short segments were omitted because alignment was ambiguous. Basic sequence statistics and Kimura (1980) two-parameter (K2P) distances were computed with MEGA (Kumar et al. 1993) and PAUP* (Swofford 1999). Some saturation was evident at third positions (plots not shown), and various weighting schemes (see below) were used to compensate for this.

Phylogenetic trees were estimated using maximum-parsimony, neighbor-joining, and maximum-likelihood analyses, all using PAUP*. We used the partition homogeneity test (Swofford et al. 1996) with 1,000 replications to determine if the coding and noncoding regions provided different phylogenetic signals; the test was done with and without gaps in the CR. For maximum-parsimony analysis, we evaluated the data in several ways. We inferred maximum-parsimony trees with all positions weighted equally and with coding genes weighted by the 6-parameter method using ln-transformed frequencies of character state changes (estimated by

TABLE 3. Composite haplotypes found in thrashers. Letters correspond to restriction patterns resulting from digestion with *Ava* I, *Ava* II, *Bam*H I, *Bcl* I, *Bgl* I, *Bgl* II, *Eco*R I, *Hinc* II, *Hind* III, *Kpn* I, *Nci* I, *Nde* I, *Pst* I, *Pvu* II, *Sac* I, *Sma* I, *Sst* II, *Stu* I, *Xba* I, and *Spe* I.

n	Locality[a]	Composite haplotype	Haplotype number
		Toxostoma ocellatum	
2	OAX	FAAAAAAAAAAAAAAAAAA?G	1
		T. curvirostre	
		DBBHBBBBBBBBBBBBBAF	
1	OAX	DBBHBBBBBBBBBBBBBAC	2
1	OAX	DBBHBBBBBBBBBBBBBAC	3
1	AZ	DMBCBBBBBJBBBJJCBBBAF	4
2	AZ	DNBCBBBBJH??BJJCBKBAC	5
		T. bendirei	
4	AZ	ACCACCBCCCCCCCCCACCAA	6
		T. cinereum	
5	BJ, BJS	ADCADCBCCDCDCCDCADCAA	
1	BJ	ADCAKCBCCDCDCCDCADCAA	8
		T. lecontei	
2	BJ	AEDIEBBDDEDEDDECCEDCE	9
2	CA	BKJAEBBAJEEKHKECELJBB	10
1	CA	BKJAEB?AJKEKHKECELJBB	11
		T. redivivum	
1	CA	EFEDFBBAEFCFEIFCAFEAJ	12
1	CA	EFKEFBBAEFCFEIFCAFEAJ	13
2	CA	EFEEFBBAEFCFEIFCAFEAJ	14
		Oreoscoptes montaus	
1	CA	GJIAJGBFIICJCHJCAJICK	15
		T. crissalis	
1	CA	CGFBGDCAFGCGDEECAGFBD	16
3	CA, AZ	CGCBGDCAFGCGDEECAGFBD	17
2	AZ	CGCBGDCAFGCGDEECAGFBL	18
		T. rufum	
2	LA	CHGFHEDAGHCHGFGCDHGCH	19
2	LA	CLLFHEDAGHCHGFGCDHGDH	20
		T. longirostre	
2	TX	HIHGIFBEHICIGGHAAIHAI	21
1	TX	IIHGIFBEHICMGLHDAIHAI	22

[a] AZ = Arizona, BJ = Baja California, BJS = Baja California Sur, CA = California, LA = Louisiana, OAX = Oaxaca, Mexico, TX = Texas; precise localities available from senior author.

MacClade; Maddison and Maddison 1992) and a 2:1 TV:TS ratio for the CR (the empirical ratio). We bootstrapped (Felsenstein 1985) the equally weighted and weighted data 500 times. Neighbor-joining trees employed K2P distances. Maximum-likelihood options followed the gamma-HKY85 model, with the proportion of invariant sites, transversion : transition ratio, and the gamma shape distribution estimated from the data (Sullivan and Swofford 1997).

RESULTS

Morphometrics.—PCA resulted in similar patterns irrespective of whether all individuals or only character means (Appendix 2) were used. The following groupings were observed in a plot of PC I, II, and III (Fig. 2): *T. lecontei* plus *T. crissale*; *T. rufum* plus *T. longirostre*; *T. occelatum* plus *T. curvirostre*; *T. redivivum*; and *T. bendirei* plus *T. cinereum*. *Mimus polyglottos* and *O. montanus* stood apart from the other taxa on PC I. The MST suggested relatively little distortion in the PCA plot. Characters most influential were PC I (characters 1, 2, 10), PC II (characters 2, 5, 11), and PC III (characters 5, 11, 18; Table 1). PC I explained 64.8% of the variance and appeared to be a size axis in that most loadings

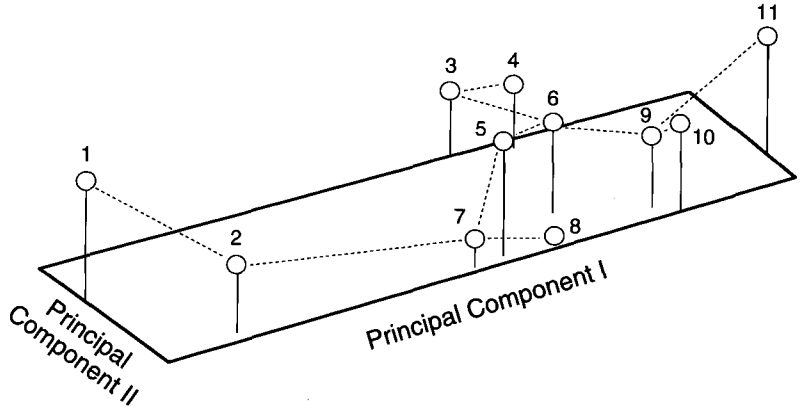

FIG. 2. Three-dimensional PCA plot derived from species' mean skeletal values (Appendix 2). Superimposed is a minimum-spanning tree (dashed line) derived from generalized squared distances resulting from discriminant analysis. 1 = *Oreoscoptes montanus*, 2 = *Mimus polyglottos*, 3 = *T. lecontei*, 4 = *T. crissale*, 5 = *T. rufum*, 6 = *T. longirostre*, 7 = *T. bendirei*, 8 = *T. cinereum*, 9 = *T. curvirostre*, 10 = *T. occelatum*, 11 = *T. redivivum*.

were positive; it was dominated by skull characters. PC II explained 17.1% of the variance and essentially was a skull-shape axis. PC III explained 5.4% of the variance and appeared to contrast skull characters with the rest of the body.

Discriminant analysis resulted in plots (not shown) similar to those from PCA and correctly classified 173 of 174 (99%) individuals; one *T. curvirostre* was misclassified as a *T. bendirei*. Hence, each of the species is distinct in morphometric space.

Different clustering algorithms revealed similar patterns of phenetic similarity (Fig. 3), recovered most recognized groups of *Toxostoma* (i.e. *lecontei, cinereum,* and *rufum*), and placed *M. polyglottos* and *O. montanus* together as distant but similar taxa. In the KITSCH tree, the two members of the *curvirostre* group were divided, with *T. curvirostre* grouping with the *bendirei* group and *T. occelatum* grouping with the *lecontei* group. In the FITCH analysis (Fig. 3), *T. redivivum* was removed from the *lecontei* group, and the *rufum* group was a grade. Distances apportioned by the Fitch analysis suggest heterogeneity, such as between the sister species *T. lecontei* and *T. crissale*.

GENETIC VARIATION AND DISTANCES

Allozymes.—Heterozygosity values ranged from 1.9% (*T. curvirostre*) to 7.0% (*T. crissale*), and the unweighted average across species was 3.6% (Table 2). Genetic distances (Nei 1972) ranged from 0.0187 (*T. bendirei* vs. *T. cinereum*) to >0.5 (*O. montanus* and *M. polyglottos* vs. members of ingroup; Table 4). The relatively low genetic distance between *O. montanus* and *M. polyglottos* (0.13) confirmed their close relationship compared with that between *O. montanus* with the true thrashers. Hence, *M. polyglottos* was dropped from subsequent analyses as an outgroup.

The allozyme-based MST (not shown) indicated that *T. redivivum* was genetically closer to other "sickle-billed" thrashers than to *T. occelatum*, unlike the morphometric MST (Fig. 2). No other serious distortions occurred when superimposing the allozyme-based MST on the morphometric PCA plot (not shown).

Restriction fragments/sites.—The 395 restriction fragments resolved 22 haplotypes (Table 3). Within species, haplotypes generally differed by less than 1% (Table 5). Among species excluding *O. montanus*, estimates of sequence divergence among haplotypes ranged from 1.4% (*T. bendirei* vs. *T. cinereum*) to 10.9% (*T. lecontei* vs. *T. rufum*). The neighbor-joining tree based on the matrix of *p*-values depicts all conspecific haplotypes as monophyletic. Consequently, only single representatives of each species were used in subsequent interspecific phylogenetic analyses (Appendix 3), with the exception of *T. lecontei*, which Zink et al. (1997) suggested represented two species.

Sequencing.—A total of 1,911 bp was resolved: cyt *b* (435 bp), ND2 (325 bp), ND6 (186

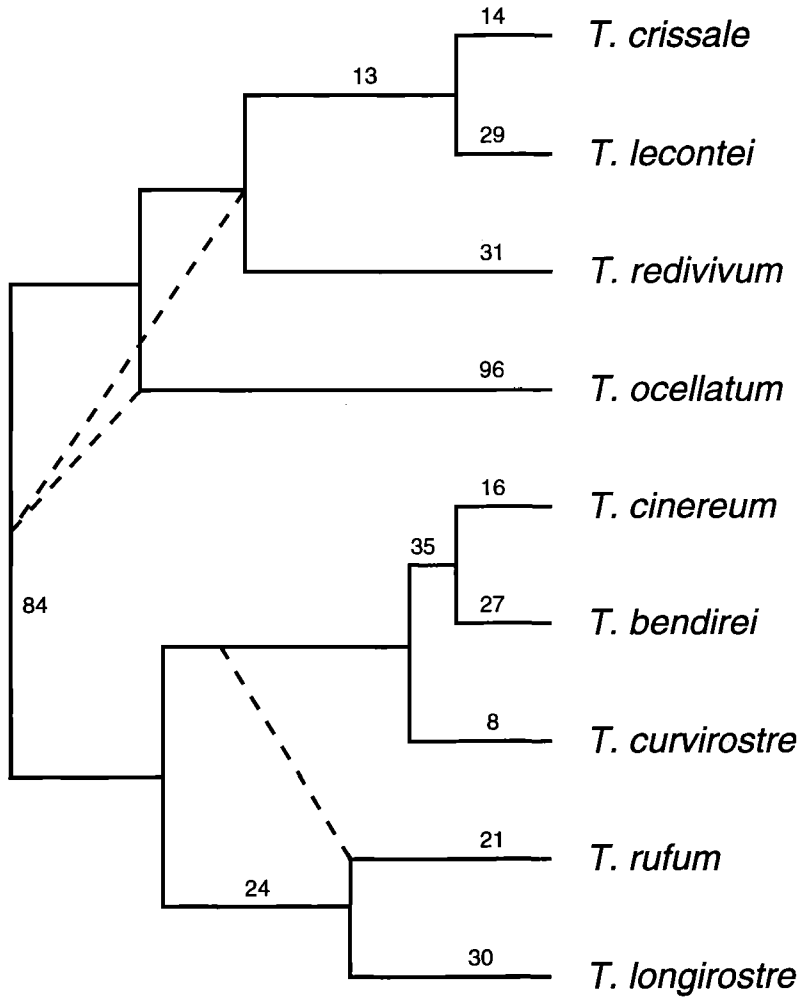

FIG. 3. Phenogram based on Fitch-Margoliash (1967) method using taxonomic distances and assuming rate constancy (routine KITSCH in PHYLIP). Dashed line indicates topology from FITCH routine that does not assume rate constancy. Numbers are taxonomic distances apportioned by the Fitch routine (the same topology was obtained using the NJ method).

TABLE 4. Nei (1972) genetic distances among thrashers and outgroups[a].

	1	2	3	4	5	6	7	8	9	10	11
1	0.0000										
2	0.1289	0.0000									
3	0.4735	0.4960	0.0000								
4	0.4593	0.4769	0.0187	0.0000							
5	0.4220	0.3973	0.1935	0.1748	0.0000						
6	0.6680	0.6448	0.2907	0.2728	0.1967	0.0000					
7	0.5738	0.5020	0.3141	0.3127	0.1766	0.2798	0.0000				
8	0.4992	0.4322	0.3080	0.3115	0.1678	0.3111	0.1751	0.0000			
9	0.5065	0.4598	0.1676	0.1703	0.1096	0.2382	0.1443	0.1066	0.0000		
10	0.4049	0.3897	0.2057	0.1879	0.0674	0.2420	0.1780	0.1698	0.1285	0.0000	
11	0.4014	0.3763	0.1823	0.1636	0.0787	0.2514	0.1930	0.1326	0.1305	0.0527	0.0000

[a] 1 = *Orescoptes montanus*, 2 = *Mimus polyglottos*, 3 = *Toxostoma bendirei*, 4 = *T. cinereum*, 5 = *T. curvirostre* (Arizona), 6 = *T. occelatum*, 7 = *T. redivivum*, 8 = *T. lecontei* (California), 9 = *T. crissale*, 10 = *T. longirostre*, 11 = *T. rufum*.

TABLE 5. *P*-distances among haplotypes of thrashers and outgroups based on 74 restriction sites.

	1	2	3	4	5	6	7	8	9	10	11	12
1	0.00000											
2	0.07364	0.00000										
3	0.07833	0.08159	0.00000									
4	0.07008	0.08092	0.00699	0.00000								
5	0.09327	0.07710	0.07304	0.07279	0.00000							
6	0.10317	0.07438	0.08901	0.08789	0.01390	0.00000						
7	0.08409	0.09994	0.07333	0.06491	0.08844	0.07483	0.00000					
8	0.09027	0.09485	0.07033	0.06245	0.08409	0.07101	0.02906	0.00000				
9	0.07064	0.06446	0.07033	0.06245	0.07399	0.07101	0.05475	0.05228	0.00000			
10	0.09796	0.08092	0.09466	0.08426	0.08092	0.06758	0.04237	0.04904	0.04904	0.00000		
11	0.07333	0.06758	0.08092	0.08031	0.06758	0.08409	0.10946	0.10403	0.06463	0.10102	0.00000	
12	0.07020	0.04266	0.08514	0.07697	0.07304	0.07949	0.10197	0.09742	0.07033	0.08514	0.05053	0.00000

* 1 = *Oreoscoptes montanus*, 2 = *Toxostoma occelatum* 3 = *T. curvirostre* (Texas), 4 = *T. curvirostre* (Arizona), 5 = *T. bendirei*, 6 = *T. cinereum*, 7 = *T. lecontei* (Baja California), 8 = *T. lecontei* (California), 9 = *T. redivivum*, 10 = *T. crissale*, 11 = *T. rufum*, 12 = *T. longirostre*.

bp), and $tRNA^{Glu}$ (compensatory changes omitted) plus CR (965 bp total). Sequences were deposited in GenBank (130235 to 130246 and 154427 to 154498). The partition-homogeneity test indicated that the combined coding genes exhibited a significantly different phylogenetic signal ($P = 0.05$) than the combined noncoding regions. Removing gaps from the CR eliminated this effect ($P = 0.14$). Hence, gaps were not analyzed phylogenetically, and together with removal of "missing-ambiguous" sites, 23 bp of ND6, and two difficult-to-align parts of the control region, 1,739 bp were used (823 were from noncoding mtDNA and 916 from coding regions). Of these 1,739 bp, 395 were variable and 249 were parsimony informative. Variation in coding genes consisted mostly of third-position transitions (Table 6), and most substitutions for the CR were transitions. Most CR variability occurred in the right domain (Baker and Marshall 1997). Base composition was typical of that for birds: adenine (26.3%), thymine (28.6%), cytosine (28.6%), and guanine (16.5%). Most changes involved transitions from C to T (32%) or T to C (16.7%). The TS:TV ratio, estimated by ML, was 3.5 for noncoding regions and 6.4 for coding genes (combined); the empirical value for all sequence over a minimum-length tree was 2.7. Sequence divergence within species was less than 1%, except for two divergent haplotype lineages within *T. lecontei* (Zink et al. 1997) and *T. curvirostre* (Zink and Blackwell unpubl. data); intraspecific divergence did not confound phylogenetic analysis, and we show trees with single representatives. Kimura 2-parameter values (Table 7) ranged from 0.016% (*T. bendirei* vs. *T. cinereum*) to 11.6% (*O. montanus* vs. *T. lecontei*). Kimura 2-parameter distances averaged 8.5% for coding genes (combined) and 7.6% for noncoding regions. The g1 statistic, -0.89 ($P < 0.05$), suggested signal in the data set, and the PTP test (Hillis and Huelsenbeck 1992) indicated that the observed tree was significantly shorter than random trees ($P < 0.01$). Because the trees inferred from restriction endonuclease analysis and direct sequencing were broadly overlapping, we believe that no sequences were nuclear copies of mitochondrial genes (Zhang and Hewitt 1996). Furthermore, the pattern of variation at coding genes was that expected from functional copies.

TABLE 6. Patterns of mtDNA sequence variability by coding gene region; TS = transition, TV = transversion. For the control region, the TS:TV ratio is 2.1:1.

Gene region	First position		Second position		Third position	
	TS	TV	TS	TV	TS	TV
Cyt *b*	12	1	3	0	57	15
ND6	11	2	4	0	28	6
ND2	15	3	7	0	61	6

PHYLOGENETIC ANALYSES

The data sets analyzed by various distance, maximum-likelihood, and maximum-parsimony methods yielded many trees. To evaluate these trees, we selected 10 (Figs. 4 and 5) that illustrate the range of variation in placement of taxa from different data sets (topologies 1, 3, 5, 6, 9, 10) and traditional arrangements (2, 4, 7, 8), and compared each topology with the Kishino-Hasegawa (1989) test for each data set (Table 8). The allozyme data were unable to reject any of the topologies. The restriction-site data favored topology 4 and rejected trees 1, 2, 5, and 7. The combined sequence data from coding genes were analyzed independently (to insure that signal from coding and noncoding regions was consistent). Parsimony analyses using the two weighting schemes favored different topologies (topology 1, equal weighting; topology 10, weighted), but neither topology was significantly worse according to the nonparametric Templeton (Wilcoxon signed-ranks) test implemented in Paup*. Maximum-likelihood analyses of the two data sets (coding and total sequence) rejected topologies 4 and 6, and the combined data additionally rejected topologies 2, 3, and 5. The favored restriction-site tree was rejected by the sequence data, whereas the favored sequence topology was not significantly worse according to the restriction-site data. The "best" allozyme tree was significantly worse according to both sequence data sets and restriction sites. Bootstrapping combined sequence data produced a parsimony tree (Fig. 5) that was very similar to topology 10; the bootstrapped NJ tree (not shown) had the same topology. These results were unchanged when the "missing-ambiguous" characters were included (because some phylogenetic information is lost by their exclusion).

Topology 10 was chosen as a working hypothesis because it was the maximum-likelihood and maximum-parsimony (weighted) sequence topology and was not rejected by either allozymes or restriction sites. In this and most other topologies, several relationships consistently received high bootstrap support (Fig. 5). The *cinereum, lecontei,* and *rufum* groups were monophyletic. *Toxostoma guttatum* (Cozumel Thrasher) most likely is the basal member of the *rufum* group and is about 5% divergent from either *T. rufum* or *T. longirostre.* The relationships of *T. curvirostre* and *T. occelatum,* as well as the arrangement of the major groups, were unclear. However, bootstrap proportions

TABLE 7. Kimura 2-parameter distance matrix between thrasher species.[a]

	1	2	3	4	5	6	7	8	9	10	11	12
1	0.000											
2	0.050	0.000										
3	0.050	0.054	0.000									
4	0.081	0.081	0.078	0.000								
5	0.073	0.067	0.080	0.078	0.000							
6	0.081	0.079	0.081	0.086	0.081	0.000						
7	0.094	0.088	0.087	0.089	0.094	0.090	0.000					
8	0.087	0.082	0.085	0.086	0.080	0.015	0.094	0.000				
9	0.099	0.093	0.100	0.103	0.095	0.088	0.104	0.093	0.000			
10	0.087	0.080	0.084	0.086	0.082	0.070	0.087	0.073	0.072	0.000		
11	0.100	0.086	0.101	0.101	0.102	0.088	0.111	0.092	0.072	0.074	0.000	
12	0.110	0.094	0.108	0.108	0.113	0.092	0.115	0.096	0.072	0.081	0.026	0.000

[a] 1 = *Toxostoma longirostre,* 2 = *T. guttatum,* 3 = *T. rufum,* 4 = *T. occelatum,* 5 = *T. curvirostre,* 6 = *T. cinereum,* 7 = *Oreoscoptes montanus,* 8 = *T. bendirei,* 9 = *T. crissale,* 10 = *T. redivivum,* 11 = *T. lecontei* (California), 12 = *T. lecontei* (Baja California).

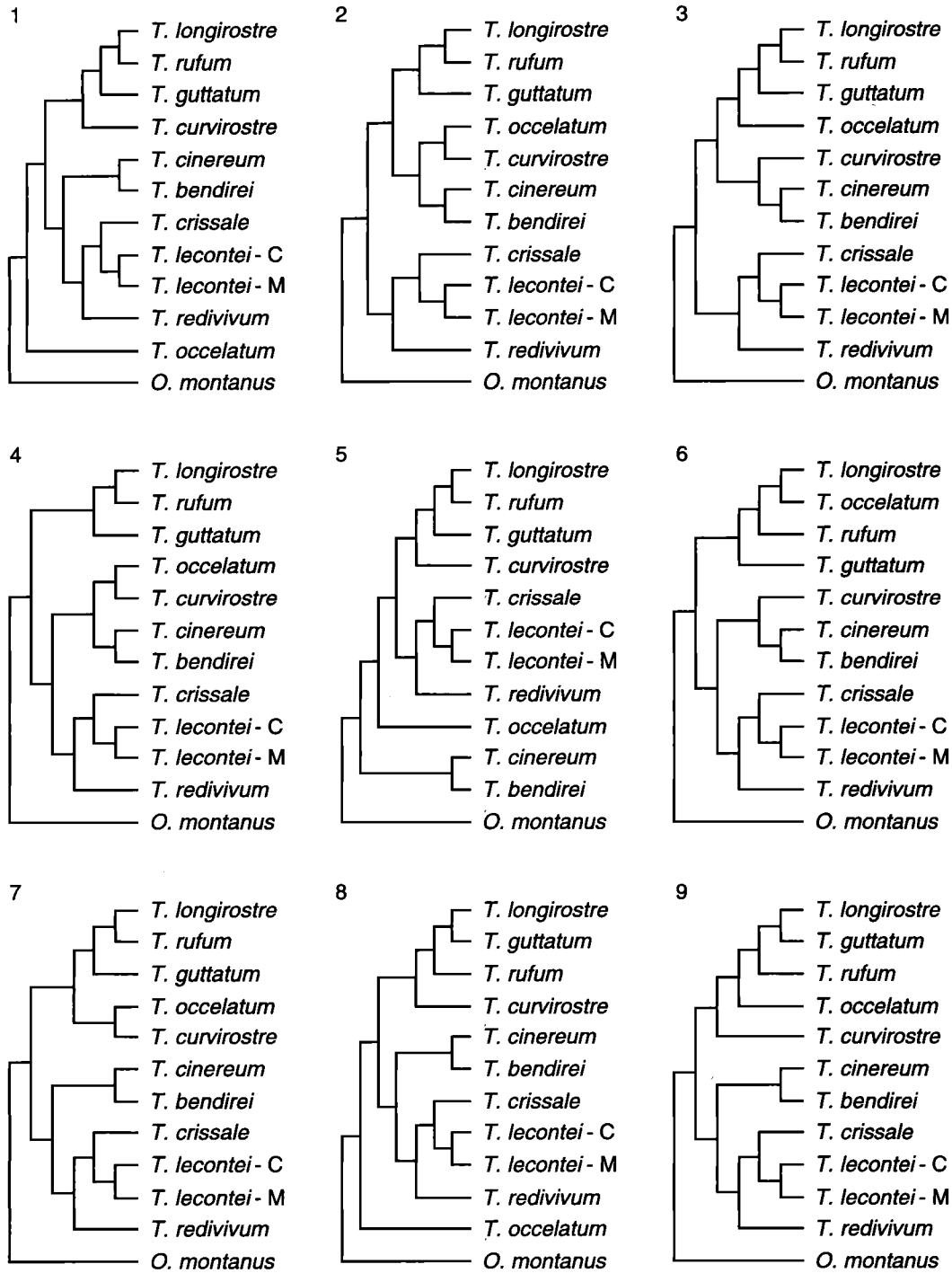

FIG. 4. Nine topologies resulting from phylogenetic analyses of allozymes, restriction sites, and mtDNA sequences. For *T. lecontei*, "C" refers to California and "M" to Baja California, Mexico.

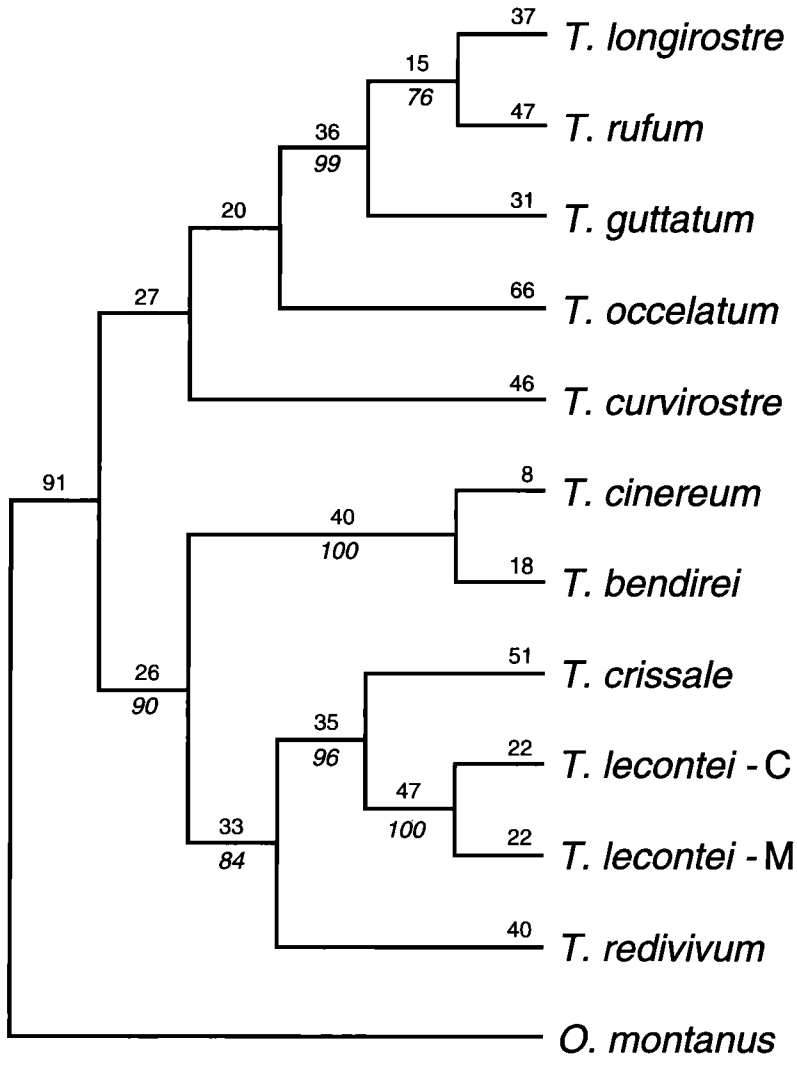

FIG. 5. Tenth topology showing typical distribution of characters supporting each node. Above branches are numbers of characters. Numbers in italics are bootstrap values. For *T. lecontei*, "C" refers to California and "M" to Baja California, Mexico.

(Fig. 5) suggested that the *cinereum* and *lecontei* clades were sister groups. The data suggest a relationship between the *rufum* group, *T. curvirostre* and *T. occelatum*. Trees 2, 4, and 7, in which *T. curvirostre* and *T. occelatum* form a clade as in Hubbard's (1973) hypothesis, tend to be significantly worse according to sequence and restriction-site data.

DISCUSSION

Morphometric evolution.—The discriminant and principal components (Fig. 2) analyses revealed that each species is well separated in skeletal morphometric space, which is consistent with the observation that the adult plumages allow unambiguous species-level discrimination. The high loadings of skull characters in the PC analysis confirms Engels' (1940) conclusion that adaptive changes in major groups involved the structures (bill curvature, mandible length, and associated musculature) associated with digging in the ground for food. Three of the four species groups described by Engels (1940) were recovered by our cluster analysis (Fig. 3), suggesting that these major groups are

TABLE 8. Maximum-parsimony (equally weighted [L1] and weighted [L2]; see text) and maximum-likelihood scores for different topologies estimated from allozyme, restriction-site, and mtDNA sequence (coding only, total sequence) data sets. Topologies are shown in Figures 4 and 5. An asterisk signifies that the data significantly reject that topology, and bold font indicates the best topology for that data set for the particular analysis. Values given for allozymes and restriction sites exclude *T. guttatum*, and no values are given for topologies 8 and 9 because they involved topological rearrangements only of this species (which was not included in any but sequence evaluations).

Topology	L1	L2	Allozymes	Restriction sites	Sequence coding	Total
1	**751**	1,124.9	481.943	−576.428*	3,233.5	5,979.5
2	758	1,146.3	481.593	−576.480*	3,247.1	6,006.1*
3	763	1,145.0	481.156	−566.053	3,241.8	6,003.2*
4	761	1,149.4	481.634	−573.816	3,249.8*	6,006.7*
5	767	1,157.3	**482.582**	−576.651*	3,247.8	6,007.5*
6	777	1,175.3	478.530	**−558.681**	3,265.5*	6,026.0*
7	754	1,127.7	481.754	−575.782*	3,232.5	5,977.9
8	758	1,136.4	—	—	3,234.1	5,985.3
9	759	1,127.3	—	—	3,229.3	5,981.0
10	758	**1,123.6**	481.342	−566.112	**3,228.9**	**5,976.3**

distinct in both traditional external characters used by Engels as well as in skeletal morphometrics. The phenetic placement of *T. ocellatum* and *T. curvirostre* conflicts with Engels' (1940) groupings, although *T. curvirostre* clusters with *T. cinereum* and *T. bendirei* as he predicted. *Toxostoma ocellatum* is not close to *T. curvirostre* in overall skeletal similarity. Inspection of species' ranges (Fig. 1) and the PC plot (Fig. 2) shows that sympatry generally is achieved only among thrashers from different major groupings. When the minimum-spanning tree (not shown) derived from mtDNA distances was superimposed on the PCA plot of skeletal means (Fig. 2), the only distortion involved *T. redivivum*, which was separated from other members of its group (*T. lecontei* and *T. crissale*) primarily along the "size" axis (PC I), and apparently was closer to *T. curvirostre*. The genetic data (Figs. 4 and 5) show this latter result to be convergence in "skeletal space" by two allopatric species (*T. redivivum* and *T. curvirostre*). Species from the same major group that are sympatric tend to be relatively genetically differentiated (e.g. *T. curvirostre* and *T. bendirei*, and *T. crissale* and *T. lecontei*). Even the sympatric species, however, tend not to be syntopic during the breeding season (Engels 1940).

Phylogeny, biogeography, and sequence evolution.—Three of the four traditional groups were confirmed by sequence data. Although the sister-species status of *T. rufum* and *T. longirostre* was most likely (bootstrap proportion of 78%; Fig. 5), they differ by 5.0% sequence divergence (Table 7), which is greater than that between the phenotypically distinctive *T. bendirei* and *T. cinereum*. *Toxostoma guttatum* was distinct from either *T. rufum* or *T. longirostre*, which is inconsistent with classifications that considered it to be a diminutive subspecies of *T. longirostre* (AOU 1983). Thus, the Cozumel Thrasher has had a relatively long independent evolutionary history. Given the small area of this island, and the frequent hurricanes of major environmental influence, it seems unlikely that *T. guttatum* has persisted for a long period solely on this small island. Rather, we hypothesize it to be a relict species. Maps of sea level at the height of the Pleistocene (e.g. Rosen 1978) show that considerably more exposed land surrounded the Yucatan Peninsula 18,000 years ago than exists today, which might have provided more habitat for this species. The level of genetic distinctness shows that conservation of *T. guttatum* is important for the preservation of diversity in the genus. Future studies need to include this taxon in nuclear gene trees as well as in morphometric studies.

The relationships of *T. curvirostre* and *T. occelatum* are problematic (Figs. 4 and 5), and the two taxa do not appear to be sister species. Although a close relationship between *T. occelatum* and *T. curvirostre* is apparent in the color plate in Hubbard (1973), we believe their similarity is overemphasized relative to skeletal morphometrics and side-by-side comparison of study skins (Fig. 3). The phylogenetic hypotheses suggest that *T. curvirostre* and *T. occelatum*

are related to the *rufum* group. Inspection of adult *T. longirostre* and *T. occelatum* reveals similarity in bill size and spots on the plumage. Hubbard (1973) suggested that speciation in *curvirostre-occelatum* was analogous to the *cinereum* group in that a southern taxon (*occelatum*) become isolated and evolved darker ventral spotting. However, whereas *T. bendirei* and *T. cinereum* differ by less than 2% sequence divergence, *T. occelatum* and *T. curvirostre* differ by 7.7% (Table 7), implying a much older common ancestor for the latter pair of taxa. Thus, sequence divergence between *T. occelatum* and *T. curvirostre,* along with the lack of support for their monophyly, cast doubt on Hubbard's hypothesis that the two species are closely related.

Differing placements of *T. occelatum* and *T. curvirostre* do not result simply from different rootings of the same ingroup tree (e.g. Zink and Blackwell 1998a, b). We hypothesize that nearly contemporaneous speciation events isolated *T. occelatum, T. curvirostre* and the ancestor of *T. rufum* and *T. longirostre.* Molecular phylogenetic analyses of aridland quail (genus *Callipepla;* Zink and Blackwell 1998b) and the "brown towhee" complex (genus *Pipilo;* Zink et al. 1998) also revealed lack of phylogenetic resolution for taxa with the same distributions as *T. occelatum* and *T. curvirostre.* Similar patterns of taxonomic uncertainty in these co-distributed lineages supported the hypothesis that more than one isolating barrier arose nearly contemporaneously, creating a "star phylogeny" (Lara et al. 1996).

Members of the *lecontei* group share a number of apparently derived features, such as lack of ventral spotting in both young and adult stages, nest construction, extreme digging habits, fleshy color of the mouth lining (other groups are yellow), and brown eye color (others are yellow/orange). Engels (1940:394) hypothesized that *T. crissale* and *T. redivivum* were most similar in "structure, proportions, habits and habitat preferences . . . ." Such a relationship, however, is not confirmed by either skeletal morphometrics or sequence analysis. Rather, *T. lecontei* and *T. crissale* are sister species.

Hubbard's (1973) biogeographic scenario for evolution in *Toxostoma* specifically implicated the last two rounds of Pleistocene glaciation. That is, speciation events were predicted to have occurred within the last 250,000 years. Assuming a molecular clock calibration of 2%/MY for the cyt-*b* data only, all speciation events predate one million years ago. Thus, speciation events in *Toxostoma* likely occurred much earlier in the Pleistocene or in the late Pliocene (Klicka and Zink 1997, 1998).

Contrary to statements in the literature (Taberlet 1996), the control region as a whole is not more rapidly evolving than coding genes. Instead, parts of the control region are much slower than coding genes, such as the conserved central region, whereas the 3′ and 5′ ends often are highly variable (Baker and Marshall 1997, Zink and Blackwell 1998a).

Maximum-likelihood analyses, particularly the gamma-HKY85 model, are increasingly used in phylogenetic analyses (Swofford et al. 1996). However, the parameters used in this model are unknown for many avian groups (Klicka and Zink 1998). For example, the value of the shape parameter (alpha) was estimated by Arbogast and Slowinski (1998) to be 0.22 for some avian data, indicating substantial rate heterogeneity among sites. For the 10 trees shown in Figures 4 and 5, alpha averaged 0.77 for coding genes and 0.56 for the noncoding region, indicating less rate heterogeneity among sites than found by Arbogast and Slowinski (1998). Because these values influence the results of ML analyses, further refinement will involve calculating such values for each gene independently with large numbers of individuals, species, and outgroups.

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APPENDIX 1. Allozyme frequencies for polymorphic loci. For each locus, the frequency of the last allele is omitted and can be obtained by subtracting from 1.0. Locus (number of alleles): Est-D (2), LGG (5), LA (7), Mdh (2), Mpi (4), Ldh-1 (2), Gsr (4), Got-1 (4), Pgi (4), Sod-1 (3), 6-Pgd (3), alpha-Gpd (5), Np (8), Ada (4), Gpt (3), Acp (2), general protein (2), Ca (5), Ak (2), Hk (6), Adh (2), Gda (3), Cat (4), and Acon-1 (3). The following loci were scored as monomorphic and fixed for the same allele in all taxa: Pgm-2, Ck-1,2; Sod-2, Icd-2, Ldh-2, Got-2, Mdh-2, Sdh, and G-6-Pdh.

Mimus polyglottos

1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.9, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.1, 1.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0

Toxostoma bendirei

0.0, 1.0, 0.0, 0.0, 0.0, 0.92, 0.0, 0.04, 0.04, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.96, 0.04, 0.0, 0.85, 0.0, 0.92, 0.08, 0.0, 0.85, 0.15, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 1.0, 1.0, 1.0, 0.375, 0.0, 0.625, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.875, 0.125, 0.0, 0.79, 0.0

T. cinereum

0.0, 0.95, 0.05, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.875, 0.0, 0.0, 1.0, 0.0, 0.0, 0.91, 0.09, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 0.67, 0.33, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.75, 0.0, 0.25, 0.0, 1.0, 1.0, 1.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.875, 0.0, 0.125, 1.0, 0.0

T. curvirostre

0.75, 0.98, 0.0, 0.0, 0.02, 0.98, 0.0, 0.0, 0.0, 0.0, 0.02, 1.0, 0.94, 0.03, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.94, 0.03, 0.03, 1.0, 0.0, 1.0, 0.0, 0.95, 0.0, 0.0, 0.05, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 1.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0

T. occelatum

0.75, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 1.0, 1.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0

T. redivivum

1.0, 0.75, 0.25, 0.0, 0.0, 0.96, 0.0, 0.04, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.875, 0.0, 0.125, 0.5, 0.125, 0.375, 0.96, 0.0, 0.0, 0.0, 1.0, 0.92, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.04, 0.0, 0.96, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 1.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0

T. lecontei

1.0, 0.81, 0.0, 0.0, 0.0, .0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.875, 0.125, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.875, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0

T. crissale

0.0, 0.75, 0.0, 0.25, 0.0, 0.94, 0.0, 0.0, 0.0, 0.03, 0.03, 1.0, 0.94, 0.06, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.97, 0.03, 0.0, 1.0, 0.0, 0.92, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.47, 0.53, 0.0, 0.0, 0.0, 0.84, 0.16, 0.0, 1.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0

T. longirostre

1.0, 1.0, 0.0, 0.0, 0.0, 0.75, 0.0, 0.25, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.75, 0.0, 0.0, 0.25, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 1.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0

T. rufum

0.833, 0.90, 0.05, 0.05, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.27, 0.95, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.05, 0.0, 0.0, 0.0, 0.0, 0.95, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 1.0, 1.0, 1.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0

Oreoscoptes montanus

1.0, 0.82, 0.11, 0.0, 0.07, 0.0, 0.86, 0.0, 0.0, 0.14, 0.0, 1.0, 0.96, 0.0, 0.04, 0.0, 0.25, 0.75, 0.0, 0.95, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.05, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 1.0, 1.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 0.0, 1.0

APPENDIX 2. Means (mm) of skeletal characters. Character descriptions can be found in Robins and Schnell (1971). Characters are listed in the following order 1 = premaxilla length, 2 = premaxilla length to narial opening, 3 = premaxilla depth, 4 = nasal bone width, 5 = interorbital width, 6 = postorbital width, 7 = skull width, 8 = skull length, 9 = mandible length, 10 = minimum mandible length, 11 = mandible depth, 12 = coracoid length, 13 = scapula head width, 14 = sternum length, 15 = sternum width, 16 = sternum depth, 17 = posterior synsacrum length, 18 = length of fused vertebrae, 19 = anterior synsacrum length, 20 = synsacrum width, 21 = minimum synsacrum width, 22 = femur distal end width, 23 = femur length, 24 = tibiotarsus length, 25 = tarsus length, 26 = humerus trochanter length, 27 = humerus length, 28 = ulna length, 29 = carpal length.

Toxostoma rufum
24.22, 13.19, 3.34, 11.96, 5.58, 18.63, 18.83, 50.16, 39.28, 11.44, 3.09, 23.85, 5.08, 28.43, 12.49, 9.35, 8.68, 20.56, 13.35, 17.33, 8.88, 5.08, 27.98, 47.94, 34.32, 8.99, 27.32, 30.22, 17.12
T. longirostre
27.44, 14.87, 3.31, 11.10, 5.37, 18.93, 19.16, 53.56, 41.86, 12.23, 3.15, 22.87, 4.96, 27.39, 12.47, 8.70, 8.37, 21.32, 13.35, 16.98, 8.54, 5.21, 28.07, 48.52, 35.54, 9.08, 26.69, 29.50, 15.68
T. redivivum
31.32, 19.24, 3.58, 12.45, 5.91, 20.02, 20.57, 58.43, 45.86, 15.32, 2.88, 25.00, 5.30, 28.56, 12.94, 8.62, 10.48, 22.07, 14.37, 19.59, 8.91, 6.32, 32.13, 54.57, 39.02, 9.52, 28.47, 30.50, 16.73
T. lecontei
27.93, 17.23, 3.07, 11.38, 4.82, 18.46, 19.25, 53.01, 40.46, 13.95, 2.53, 22.30, 4.91, 25.85, 11.24, 7.54, 8.52, 18.89, 12.17, 16.88, 7.56, 5.12, 27.11, 45.68, 31.19, 8.54, 25.60, 27.70, 15.92
T. bendirei
23.27, 13.67, 3.34, 11.72, 5.77, 19.23, 20.40, 49.27, 39.06, 10.54, 3.51, 22.89, 5.01, 26.15, 11.63, 8.81, 8.20, 18.99, 12.27, 16.02, 8.10, 5.01, 26.26, 46.22, 33.73, 8.90, 27.01, 30.78, 17.60
T. occelatum
28.90, 16.05, 3.87, 11.83, 5.97, 19.83, 21.02, 56.00, 44.30, 12.28, 3.55, 24.05, 4.77, 26.58, 12.07, 8.00, 10.10, 23.22, 13.93, 18.18, 8.52, 6.03, 32.13, 52.58, 37.62, 9.07, 27.23, 27.98, 15.87
T. crissale
30.18, 19.46, 3.38, 11.05, 5.32, 18.29, 18.47, 55.45, 42.06, 14.39, 2.52, 22.38, 4.72, 25.83, 11.23, 7.81, 8.08, 19.35, 12.31, 17.05, 7.93, 5.24, 27.55, 46.46, 33.23, 8.54, 26.09, 28.18, 15.82
T. cinereum
25.95, 15.63, 3.60, 11.78, 6.23, 19.46, 20.62, 52.72, 41.20, 11.10, 3.51, 22.51, 4.91, 24.95, 12.02, 7.96, 8.56, 18.31, 12.60, 16.96, 8.16, 5.09, 26.99, 47.07, 34.39, 9.03, 27.20, 30.27, 16.97
T. curvirostre
28.66, 17.06, 3.44, 11.76, 6.10, 19.72, 20.73, 55.49, 44.02, 12.83, 3.27, 24.35, 5.26, 27.87, 12.73, 9.13, 9.06, 21.09, 13.74, 18.33, 8.92, 5.56, 28.58, 47.56, 33.48, 9.77, 28.90, 32.40, 18.20
Oreoscoptes montanus
19.22, 8.71, 2.68, 10.19, 4.22, 17.30, 18.46, 42.52, 32.49, 7.05, 2.44, 20.88, 4.76, 24.97, 11.01, 9.04, 6.85, 17.75, 11.38, 15.81, 8.08, 4.03, 23.52, 42.33, 31.09, 7.98, 23.76, 28.27, 16.36
Mimus polyglottos
20.13, 9.28, 3.16, 10.81, 5.44, 17.52, 18.12, 43.69, 34.15, 7.50, 2.78, 22.11, 4.96, 26.36, 11.38, 8.63, 7.22, 17.66, 11.73, 15.69, 7.92, 4.32, 24.42, 45.04, 33.31, 9.26, 26.99, 33.02, 18.03

APPENDIX 3. Presence or absence of 74 restriction sites for 12 species-level taxa of mimids.

Oreoscoptes montanus
11111100000001110100000001101100100111000100101000110010000101001000110000
Toxostoma occelatum
11111001101110010000011000000100000010000100001100110110000101001000110000
T. curvirostre (Texas)
11111001010011100111001000010111000010000110101001110010100100001101110001
T. curvirostre (Arizona)
11111001010011100111001000010111000011000110101001110010100101101101110001
T. bendirei
11111000000010000000001110010100001000010111111000110010000100101000110000
T. cinereum
11111000000010000000001110010100001000010101001000110010000000101000110000
T. lecontei (Baja California)
11111000000011100100001000010110000011000000001000010001000000111000110010
T. lecontei (California)
11111000010011100001001000010100000011000000001010010011000000111000111000
T. redivivum
11111010000010100000001000010100000011100000001000110011100101001010110000
T. crissale
11111001000010000000001001010100000011101000001000111001000000111000110000
T. rufum
11111001000000110000001000011100000000010010101000110110011111001010110100
T. longirostre
11111001100110000000111100111100010011000100101000110110011111001000110000