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PHYLOGENY AND BIOGEOGRAPHY OF DABBLING DUCKS (GENUS: *ANAS*): A COMPARISON OF MOLECULAR AND MORPHOLOGICAL EVIDENCE

KEVIN P. JOHNSON[1,3] AND MICHAEL D. SORENSON[2,4]

[1]*Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108, USA; and*

[2]*Museum of Zoology, University of Michigan, Ann Arbor, Michigan 48109, USA*

ABSTRACT.—We constructed a phylogeny for the dabbling ducks (tribe Anatini) based on cytochrome-*b* and ND2 mitochondrial gene DNA sequences. This phylogeny differed in several important respects from a morphological phylogeny developed by Livezey (1991), including the distinctiveness of the blue-winged ducks from other dabbling ducks, the inclusion of the genus *Tachyeres* and exclusion of *Callonetta* from the subtribe Anateae, and the lack of support for *Mareca* as a genus separate from *Anas*. Characters from three other data sets showed greater consistency with the molecular topology than with the morphological topology. The molecular phylogeny divides the dabbling ducks into four distinct groups: (1) four South American genera, including *Amazonetta, Lophonetta, Speculanas,* and *Tachyeres;* (2) the Baikal Teal (*Anas formosa*); (3) the blue-winged ducks and allies; and (4) a large clade including wigeons, pintails, mallards, and several teal lineages. An examination of the distributions of species in light of the phylogeny indicates relatively little biogeographic structure. Geographic origin for most internal branches is ambiguous using several reconstruction methods. We suggest that the high dispersal ability of birds (especially dabbling ducks) has important implications for recovery of branches using molecular systematics. *Received 26 January 1998, accepted 27 January 1999.*

THE DISTRIBUTION OF DABBLING DUCKS (genus *Anas*) on all continents except Antarctica is unusual for a genus of birds. In addition, many taxa of dabbling ducks are isolated on oceanic islands (Lack 1970, Weller 1980). This pattern of geographic distribution suggests that members of this genus are capable of long-distance dispersal. Chesser and Zink (1994) suggest that the generally high dispersal ability of birds results in different biogeographic patterns than those commonly observed in other organisms. This high dispersal ability may result in speciation being driven by dispersal and allopatric speciation rather than classical vicariance (Wiley 1988, Chesser and Zink 1994, Ronquist 1997). The widespread distribution of dabbling ducks suggests that dispersal-driven speciation has been common in this group of birds. To fully interpret this biogeographic pattern, it is important to place species distributions in a phylogenetic context.

Phylogenetic relationships of the dabbling ducks remain controversial despite intensive study (see Livezey 1991). Livezey (1991) recognized the tribe Anatini in which he included all of the dabbling ducks and many of the "perching ducks." He classified the genus *Anas* and a few other closely related genera (*Amazonetta, Callonetta, Lophonetta, Speculanas,* and *Mareca*) within the subtribe Anateae. Livezey's (1991) detailed cladistic analysis of morphological characters contained several unresolved nodes and differed from previous taxonomic work on this group. We sought to further investigate the systematic relationships among species of *Anas* and within Livezey's subtribe Anateae using other genera within Anatini as well as additional members of the subfamily Anatinae as outgroup taxa.

Molecular characters, in the form of DNA sequences, have incredible potential to provide new characters for phylogenetic analysis (Avise 1994, Hillis et al. 1996). To reevaluate phylogenetic relationships in the dabbling ducks, we first determined DNA sequences for two mitochondrial protein-coding genes: 1,047 base pairs (bp) of the cytochrome-*b* (cyt *b*) gene and the complete (1,041 bp) NADH dehydrogenase

[3] Present address: Department of Biology, University of Utah, Salt Lake City, Utah 84112, USA. E-mail: johnson@biology.utah.edu

[4] Present address: Department of Biology, Boston University, Boston, Massachusetts 02215, USA.

subunit 2 (ND2) gene for 61 dabbling duck and outgroup taxa. Sequences of cytochrome *b* are well characterized for several avian taxa (Krajewski and Fetzner 1994, Lanyon 1994, Ellsworth et al. 1996, Nunn et al. 1996, Zink and Blackwell 1996), but ND2 has rarely been used in systematic studies. We also included sections of the flanking tRNA regions in the analysis to increase the number of characters used. Next, we compared our results with those of Livezey (1991) in both separate and combined analyses. To determine whether trees derived from morphology or mtDNA sequences are more consistent with previous studies, we compared morphological and molecular trees using the phylogenetic information in behavior (Lorenz 1941, McKinney 1978), mtDNA restriction fragments (Kessler and Avise 1984), and nuclear restriction fragments (Tuohy et al. 1992). Finally, we used the phylogeny to interpret patterns of biogeography (Brooks 1990, Ronquist 1997) and speciation in dabbling ducks.

Methods

We obtained samples of 45 species of dabbling ducks from a variety of sources, including collections of captive waterfowl, hunter-killed birds, and museum tissue collections (Table 1). In general, DNA sequence variation within species was very low (see Results), so we sequenced only one individual for 36 species. We sequenced two or three individuals representing different subspecies or geographic areas for the remaining species. We included all of the taxa of *Anas* in Livezey's (1991) analysis except *A. wyvilliana, A. oustaleti, A. albogularis, A. andium,* and *A. eatoni.* We also included a representative of *Tachyeres,* which in an analysis based on mtDNA small-subunit (12S) rDNA sequences was placed in Anatini (M. Sorenson and K. Johnson unpubl. data). Finally, we included 11 outgroup taxa to root the phylogeny, including most of Livezey's (1991) outgroup taxa plus several additional genera.

DNA sequencing.—DNA from tissue, feather, or blood samples (only one taxon was sampled from blood) was extracted, amplified via PCR, and sequenced for cyt *b* and ND2 as described by Johnson and Sorenson (1998; Genbank accession numbers AF059053 to AF059174). When multiple individuals of the same species were available, we sequenced all of both gene regions, or half of either cyt *b* or ND2, to assess within-species variation (see Table 1). We did not use samples with incomplete sequences in phylogenetic analyses.

Phylogenetic analysis.—We performed analysis using the coding regions of the cyt-*b* and ND2 genes as well as portions of the flanking tRNA genes, resulting in a total of 2,147 bp in the molecular analysis. We searched for most-parsimonious tree(s) using 20 replicate heuristic searches with random taxon addition in PAUP* (Swofford 1997). To determine the sensitivity of tree topology to weighting, we performed several analyses in which we varied the weighting of transversions relative to transitions. To determine the relative support for the resulting topologies, we performed bootstrapping (Felsenstein 1985) of the molecular data using 1,000 fast bootstrap replicates in PAUP*.

We analyzed Livezey's (1991) morphological data set both separately and in combination with the DNA sequence data with all characters unordered and unweighted. We conducted a partition homogeneity test (Farris et al. 1995) to determine if significant conflict exists between the morphological and molecular data sets. We also used constrained parsimony searches to determine the number of additional steps required in the unweighted molecular data to obtain monophyly of selected clades from Livezey's (1991) tree.

To further compare molecular and morphological data sets, we determined the number of steps and consistency indices of the molecular and morphological data over the unweighted molecular tree, the morphological tree, and the combined tree. We also evaluated the number of morphological characters that showed an increase, no change, or a decrease in number of steps on the unweighted molecular tree to determine if some morphological characters are more consistent with the molecular data than with the rest of the morphological data. In addition, we evaluated alternative topologies with respect to how well each reconstructed molecular evolution. The transition-to-transversion ratio for cyt *b* and ND2 is 15:1 for this data set (Johnson and Sorenson 1998). We estimated this value independently of a phylogeny, and it provides a standard against which ratios reconstructed over the phylogeny can be compared. Reconstructed ratios that are closer to this value indicate topologies that are more consistent with this independent measure of molecular evolution. We reconstructed the average number of changes using MacClade (Maddison and Maddison 1992) and calculated the ratio of transitions to transversions of the molecular data over the three topologies.

To determine whether the morphological or molecular data were more consistent with previous analyses, we examined the consistency indices of other data sets over the morphological tree, the unweighted cyt-*b*/ND2 tree, and the combined tree. These data included behavior (Lorenz 1941, McKinney 1978), mtDNA restriction sites (Kessler and Avise 1984), and restriction fragments of nuclear repeated DNA (Tuohy et al. 1992).

Biogeographic analysis.—We used Ronquist's (1997) method to reconstruct ancestral areas of dabbling

TABLE 1. Samples used for DNA sequencing.

Taxon	English name[a]	Type[b]	Source[c]
Anas acuta	Northern Pintail	T	LSU B-20714, Louisiana, USA
Anas acuta	Northern Pintail*	T	UWBM 43948, Russia
Anas georgica spinicauda	Chilean Pintail	F	SHW (c)
Anas g. georgica	Brown Pintail*	F	SHW (c)
Anas b. bahamensis	Bahama Pintail	F	SHW (CRC-210958) (c)
Anas b. rubrirostris	White-cheeked Pintail	T	BM (42278), Argentina
Anas erythrorhyncha	Red-billed Pintail	F	SHW (c)
Anas capensis	Cape Teal	T	LSU B-10357 (c)
Anas c. crecca	Eurasian Green-winged Teal	F	SHW (c)
Anas c. nimia	Aleutian Green-winged Teal*	T	BM (JK96047), Aleutians
Anas c. nimia	Aleutian Green-winged Teal*	T	BM (JK96046), Aleutians
Anas carolinensis	American Green-winged Teal	F	FWS, California, USA
Anas gibberifrons gracilis	Australian Gray Teal	F	SHW (c)
Anas castanea	Chestnut Teal	F	SHW (c)
Anas bernieri	Madagascar Teal	F	JWPT (B3260) (c)
Anas a. aucklandica	Auckland Island Teal	F	MW (S-48561), Ewing I., New Zealand
Anas a. nesiotis	Campbell Island Teal	F	MW (S-71044), Dent I., New Zealand
Anas chlorotis	Brown Teal	F	MW (61024), Northland, New Zealand
Anas f. flavirostris	Speckled Teal	T	BM (42275), Argentina
Anas f. flavirostris	Speckled Teal*	F	SHW (c)
Anas f. oxyptera	Sharp-winged Teal	F	SHW (c)
Anas laysanensis	Laysan Duck	T	LSU B-10358 (c)
Anas luzonica	Philippine Duck	T	LSU B-19204 (c)
Anas platyrhynchos 1	Mallard	T	Maryland, USA
Anas platyrhynchos 2	Mallard	T	Maryland, USA
Anas platyrhynchos 3	Mallard*	T	UWBM 47608, Russia
Anas poecilorhyncha	Indian Spot-billed Duck	F	SHW (c)
Anas zonorhyncha	Chinese Spot-billed Duck	F	SHW (c)
Anas diazi	Mexican Duck	F	FWS, Arizona, USA
Anas rubripes	American Black Duck	F	FWS, Maryland, USA
Anas fulvigula	Mottled Duck	F	FWS, Louisiana, USA
Anas superciliosa rogersi	Australian Black Duck	T	MV (762), Victoria, Australia
Anas melleri	Meller's Duck	T	JWPT (B3523) (c)
Anas undulata	Yellow-billed Duck	T	JWPT (B3555) (c)
Anas sparsa	African Black Duck	T	LSU B-18923 (c)
Anas americana	American Wigeon	F	FWS, Texas, USA
Anas sibilatrix	Chiloe Wigeon	T	LSU B-20764 (c)
Anas penelope	Eurasian Wigeon	T	LSU B-20719, California, USA
Anas strepera	Gadwall	F	FWS, Texas, USA

TABLE 1. Continued.

Taxon	English name[a]	Type[b]	Source[c]
Anas falcata	Falcated Duck	F	SHW (c)
Anas versicolor	Silver Teal	T	BM (42276), Argentina
Anas puna	Puna Teal	F	SHW (c)
Anas hottentota	Hottentot Teal	F	SHW (c)
Anas querquedula	Garganey	F	SHW (c)
Anas r. rhynchotis	Australian Shoveler	T	MV (2187), Victoria, Australia
Anas smithii	Cape Shoveler	B	SHW (c)
Anas clypeata	Northern Shoveler	F	FWS, Texas, USA
Anas clypeata	Northern Shoveler*	T	UWBM (1994-t078), Russia
Anas platalea	Red Shoveler	T	BM (42273), Argentina
Anas c. cyanoptera	Argentine Cinnamon Teal	T	BM (42277), Argentina
Anas c. septentrionalium	Northern Cinnamon Teal	F	FWS, California, USA
Anas discors	Blue-winged Teal	F	FWS, Florida, USA
Anas formosa	Baikal Teal	T	BM (42241) (c)
Amazonetta brasiliensis	Brazilian Teal	F	SHW (c)
Lophonetta specularioides	Crested Duck	F	SHW (c)
Speculanas specularis	Bronze-winged Duck	F	SHW (c)
Tachyeres pteneres	Magellanic Flightless Steamer Duck	F	SHW (c)
Aix sponsa	Wood Duck	F	SHW (c)
Asarcornis scutulata	White-winged Wood Duck	F	SHW (130) (c)
Aythya americana	Redhead	T	FWS, Texas, USA
Cairina moschata	Muscovy Duck	F	SHW (c)
Callonetta leucophrys	Ringed Teal	T	CC (c)
Chenonetta jubata	Maned Goose	F	SHW (c)
Cyanochen cyanopterus	Abyssinian Blue-winged Goose	F	SHW (c)
Marmaronetta angustirostris	Marbled Teal	F	SHW (c)
Pteronetta hartlaubi	Hartlaub's Duck	F	SHW (c)
Sarkidiornis melanotos	Comb Duck	F	SHW (c)
Tadorna tadorna	Common Shelduck	F	SHW (c)

[a] *indicates partial sequence only.

[b] F = feather; T = muscle tissue; B = blood.

[c] BM = Bell Museum of Natural History, University of Minnesota; CC = Cedar Creek Natural History Area, University of Minnesota; JWPT = Jersey Wildlife Preservation Trust; LSU = Louisiana State University Museum of Zoology; MV = Museum of Victoria, Australia; MW = Murray Williams, New Zealand; SHW = Sylvan Heights Waterfowl, Scotland Neck, North Carolina; UWBM = University of Washington Burke Museum; FWS = United States Fish and Wildlife Service; (c) = captive with geographic origin unknown.

ducks. In reconstructing ancestral areas from the distribution of terminal taxa, this method counts one step for dispersal, one for extinction, and zero for vicariance. We coded five biogeographic zones in the analysis: North America, South America, Africa/Madagascar, Australia/New Zealand, Eastern Asia/Pacific Islands, and Eurasia. We coded Holarctic species as polymorphic (North America and Eurasia). We used DIVA (Ronquist 1996) and MacClade (Maddison and Maddison 1992) for the dispersal-vicariance analysis. We also used MacClade to reconstruct ancestral areas with Brooks' (1990) method of unordered parsimony. We examined these reconstructions for two patterns: (1) a common area of origin for the major groups of dabbling ducks, and (2) phylogenetic conservation of biogeographic distribution (i.e. no dispersal). We also performed an alternative reconstruction of Northern Hemisphere versus Southern Hemisphere/tropics using a single binary character. We used the molecular tree resulting from 5:1 weighting of transversions over transitions in all of these analyses. Because we could not assess the sister taxon to the dabbling ducks (we made no assumptions about branching order among our 11 outgroup taxa), we only included the ingroup taxa in these reconstructions.

RESULTS

Phylogeny.—Combined analysis of cyt-*b* and ND2 sequences provided good resolution of dabbling duck relationships. The observed ratio of transitions to transversions reconstructed over the unweighted tree was 9.4 for cytochrome *b* and 9.5 for ND2. Weighting of transversions over transitions created minor differences in tree topology, and the ingroup topology was identical for all analyses with transversions weighted 3:1 or higher over transitions. This topology is hereafter referred to as the "weighted topology."

The tree resulting from 5:1 weighting (Fig. 1) differs from the tree resulting from 1:1 weighting in two major respects: (1) placement of the root of dabbling ducks and (2) branching order of seven major lineages within the teal, pintail, and mallard clade. Weighting alters the topological arrangement of four major clades at the root of the tree: *A. formosa*, four South American genera, the blue-winged ducks and allies, and the wigeon/teal/pintail/mallard clade. The unweighted tree is rooted between *A. formosa* and all other dabbling ducks, whereas the tree resulting from transversion weighting places the root between the wigeon/teal/pintail/mallard clade and the other three clades. These alternative placements were not supported above the 50% level in any of the bootstrap analyses. The other major topological differences are within the "true" dabbling ducks, specifically among seven teal/pintail/mallard clades. With both weighting schemes, the Cape Teal (*A. capensis*) is sister to the pintails; however, the arrangement of the other five clades (mallards, brown teals, gray teals, *A. crecca*, and *A. flavirostris*/*A. carolinensis*) differs considerably.

The strict consensus tree (not shown) resulting from a reanalysis of Livezey's (1991) data (restricted to taxa included in the molecular analysis) is considerably different from the molecular topologies. A partition homogeneity test (Farris et al. 1995) indicated considerable phylogenetic conflict between the morphological and molecular data sets ($P < 0.001$). Nonetheless, it is instructive to examine a tree derived from a combined analysis of the cyt *b*, ND2, and morphological data.

In general, the strict consensus of the combined data trees (not shown) was more similar to the strict consensus of the molecular trees than it was to the strict consensus of the morphological trees (symmetric difference distance [Penny and Hendy 1985] between combined consensus trees and unweighted molecular consensus tree = 23 [range 27 to 36 between individual trees] and between combined consensus tree and morphological consensus tree = 57 [range 61 to 70 between individual trees]). This is not surprising, because the molecular data set contained many more informative characters than the morphological data set. However, even though we used equal weighting in the combined analysis, the combined data consensus tree was more similar to the transversion-weighted molecular consensus tree ($d = 13$) than it was to the unweighted molecular consensus tree ($d = 25$). Specifically, the resolution of the seven teal/pintail/mallard lineages was identical to the weighted molecular consensus tree. In the combined data tree, resolution of several lineages in the blue-winged ducks and allies was also much more similar to the weighted molecular tree than to the unweighted molecular tree. This suggests that transversion weighting produces more congruence between the molecular and morphological phylogenies. Phylogenetic signal in the morphological data set, when combined with the molecular data, produced novel arrangements

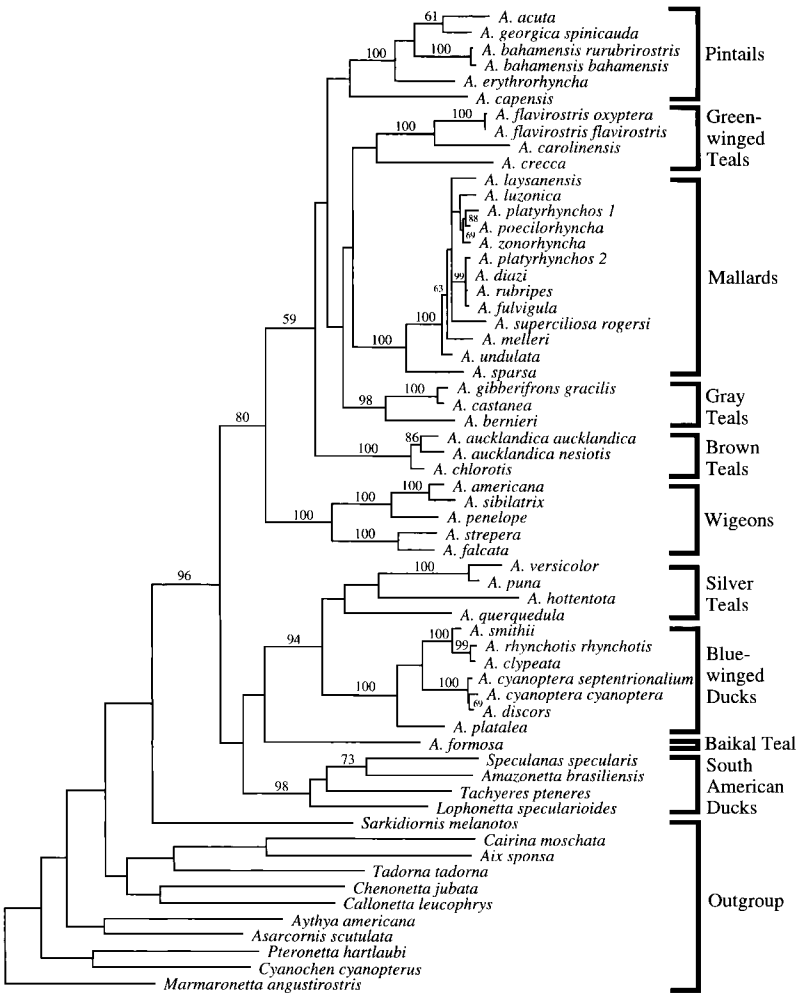

FIG. 1. Strict consensus of three trees (l = 4,231, RC = 0.291) from 5:1 weighting of transversions over transitions from cyt *b* and ND2. Branch lengths are proportional to the unweighted number of changes reconstructed over the 5:1 topology. Numbers on branches are values from bootstrap replicates of the unweighted sequences. All nodes supported in more than 50% of bootstrap replicates of the unweighted data were present in the 5:1 weighted tree. Designated outgroup taxa are *Marmaronetta, Pteronetta, Cyanochen, Aythya, Asarcornis, Chenonetta, Callonetta, Tadorna, Cairina, Aix,* and *Sarkidiornis.* In addition to the groups indicated, *A. crecca* and *A. capensis* constitute the sixth and seventh groups in the teal/pintail/mallard clade referred to in the text.

that otherwise were evident only when the molecular data were weighted.

The consistency index for the molecular data declined by 0.06 from the molecular to the morphological tree (Table 2). The consistency index for the morphological data declined by 0.25 from the morphological to molecular tree. These differences again suggest that there is heterogeneity in phylogenetic signal between the morphological and molecular data sets. A total of 87 morphological characters showed an increase in the number of steps when reconstructed over the unweighted molecular tree compared with the morphological tree, whereas 65 morphological characters showed no change. Four characters required fewer steps when reconstructed over the molecular tree, indicating that at least some morphological characters show greater consistency with the molecular data than with other morphological

TABLE 2. Number of steps and consistency indices over various topologies. Asterisk denotes that value is the midpoint of a range of values over all most-parsimonious trees.

	Data set				
	mtDNA	Livezey 1991	McKinney 1978	Kessler and Avise 1984	Tuohy et al. 1992
			Morphological tree		
No. of steps[a]	2,948*	239	28	254	71
CI[b]	0.31	0.72	0.25	0.73	0.37
			Unweighted molecular tree		
No. of steps	2,476*	365*	20	250	68
CI	0.37	0.47*	0.35	0.74	0.40
			Combined tree		
No. of steps	2,497*	333*	19	251	58
CI	0.36*	0.51*	0.37	0.74	0.64

[a] Number of steps reconstructed using unordered parsimony of data set over tree indicated.
[b] Consistency of data set over tree indicated.

characters. On the molecular tree, these four characters are perfectly consistent synapomorphies of four different groups that were not supported in Livezey's (1991) analysis. The four characters include (1) horseshoe-shaped marks on the breast feathers of *smithii, clypeata,* and *rhynchotis* (character no. 10; Livezey 1991); (2) alternating brown and white U-shaped marks on breast feathers of *strepera* and *falcata* (no. 38); (3) dark, transverse barring or spotting on the axillary feathers of *capensis* and all of the pintails (no. 91); and (4) a fine, dark breast band in the natal plumage of *gibberifrons* and *castanea* (no. 113).

The reconstructed transition/transversion ratios over the morphological, unweighted molecular, and combined trees, respectively, were 8.31, 9.41, and 9.43. The transition/transversion ratio on the combined tree is actually closest to the phylogeny independent estimate of the ratio for this mitochondrial data set, whereas the morphological topology did not perform well by this measure.

We examined the consistency indices of other data sets that could be examined cladistically over the morphological tree (our reanalysis of Livezey [1991]), the unweighted molecular tree, and the combined tree. In all three cases, the consistency index over the molecular tree was higher than over the morphological tree (Table 2). This is especially notable for the behavioral (McKinney 1978) data, which required only 20 steps on the molecular trees compared with 28 steps on the morphological tree. In two of the three data sets, the combined tree resulted in fewer steps than the unweighted molecular tree (Table 2). This analysis indicates that the molecular and combined phylogenies are more consistent with previously published data sets.

Within-species sequence variation.—Samples of Holarctic species from Russia (*A. clypeata, A. platyrhynchos,* and *A. acuta*) showed very little difference from North American haplotypes of these same species (0.0, 0.18, and 0.0%, respectively, over 545 bp of cyt *b*). We sequenced two divergent haplotypes of the Mallard (*A. platyrhynchos*) from North American individuals and found them to be paraphyletic in the molecular analysis. These two haplotypes differed by 0.58%, and one of them was identical in sequence to our samples of Mexican Duck (*A. diazi*) and American Black Duck (*A. rubripes*). The other Mallard haplotype grouped with the spotbills and the Philippine Duck (*A. luzonica*) and was 0.047% divergent from *A. poecilorhyncha.* We also observed this "Asian-Pacific" haplotype in the Mallard from Russia.

Two other species pairs showed very low genetic divergence: Chestnut Teal (*A. castanea*) and Gray Teal (*A. gibberifrons*) at 0.047% (consistent with an analysis of wild-caught individuals by Sraml et al. 1996), and Cinnamon Teal (*A. cyanoptera*) and Blue-winged Teal (*A. discors*) at 0.0 to 0.19% over 2,147 bp. We sequenced two subspecies of Cinnamon Teal, and the South American subspecies (*cyanoptera*) was identical to the Blue-winged Teal, whereas the North American subspecies (*septentrionalium*) was 0.19% divergent, resulting in paraphyly of

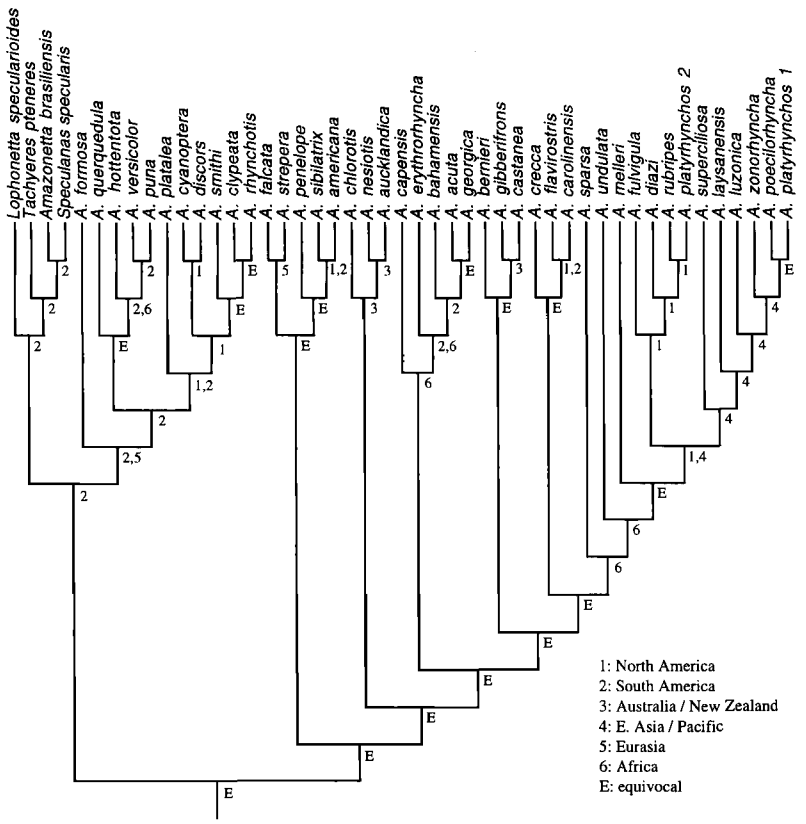

FIG. 2. Biogeographic reconstruction of ancestral areas using Ronquist's (1997) method of dispersal-vicariance analysis. Subspecies are combined and the weighted molecular (Fig. 1) topology is shown.

Cinnamon Teal haplotypes. Another interesting result was the extremely high (5.8%) divergence between *Anas crecca* and *Anas carolinensis*, Eurasian and North American species, respectively, that appear very similar in plumage. This level of divergence is similar to the genetic distance (5.7%) between Mallard and Northern Pintail (*Anas acuta*), for example, as well as between many other morphologically diverse species pairs. Two individuals of the subspecies *A. crecca nimia* from the Aleutian Islands were identical to *A. crecca crecca* over 555 bp of ND2. *Anas georgica georgica* and *A. georgica spinicauda* differed at only two positions (0.13%) over 1,592 bp from both genes.

Biogeography.—We used the weighted molecular tree in the biogeographic analyses because it was better corroborated by the morphological data than was the unweighted molecular tree, and it was more fully resolved than the unweighted combined tree. Reconstruction of ancestral areas using either Ronquist's (1997) dispersal-vicariance analysis (Fig. 2) or Brooks' (1990) unordered parsimony method (Fig. 3A) suggests that there is little biogeographic structure in the phylogeny. The reconstruction of ancestral areas for most nodes is equivocal in both analyses. Although most of the nodes for ancestral areas of major clades are ambiguous, three clades have Africa/Madagascar reconstructed as an area of origin using Brooks' (1990) method: pintails, gray teals, and mallards. Ronquist's method reconstructs an African origin for the mallards and pintails, but leaves the origin of the gray teals as ambiguous. Africa is also a possible area of origin for the entire clade of pintails, teals, and mallards; however, this is not completely consistent between the two reconstruction methods. Most other clades have an ambiguous reconstruction because of the lack of phylogenetic consistency in continental distribution. One group that shows strong phylogeographic structure, however, is a clade of four South American genera:

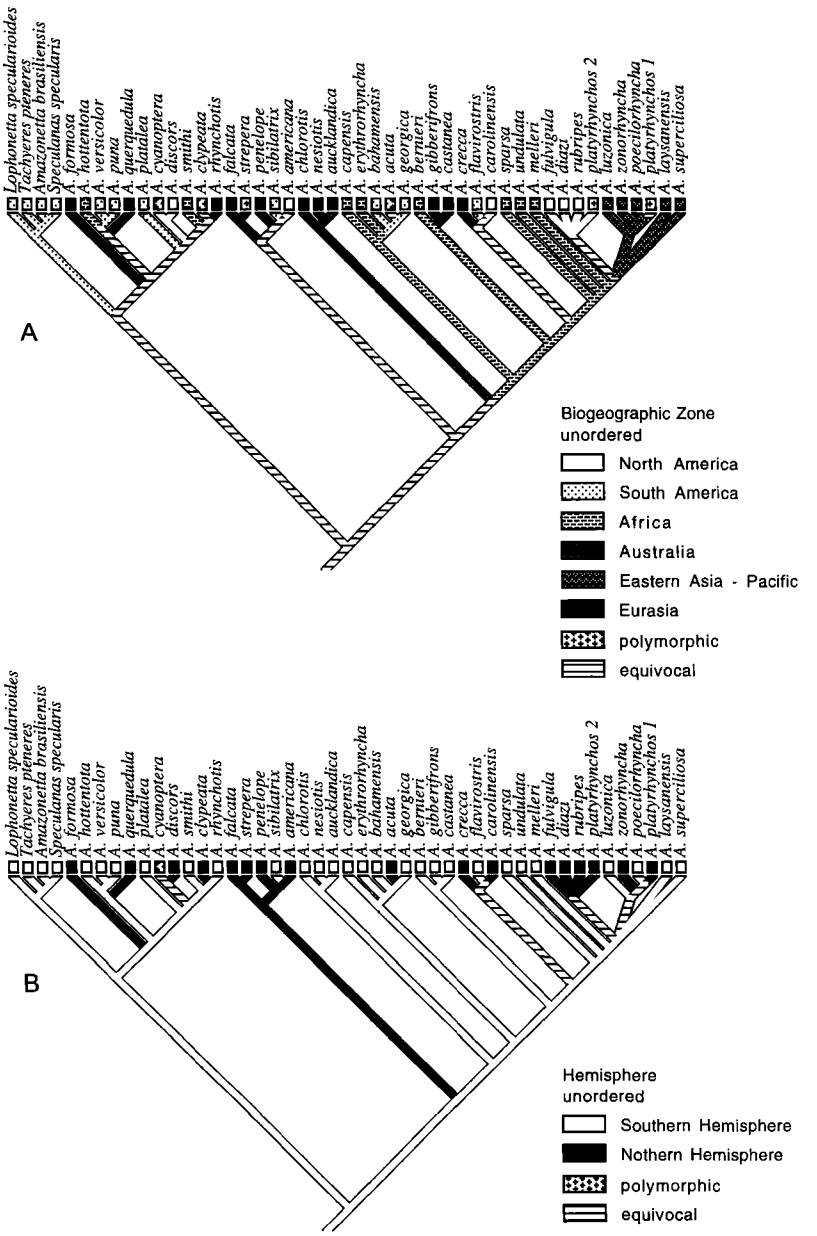

FIG. 3. (A) Biogeographic reconstruction of ancestral areas using Brooks' (1990) method of unweighted parsimony. Subspecies are combined and the weighted molecular topology (Fig. 1) is shown. (B) Reconstruction of hemisphere using coding of Northern and Southern hemisphere and unweighted parsimony. Subspecies are combined and the weighted molecular (Fig. 1) topology is shown.

Amazonetta, Tachyeres, Lophonetta, and *Speculanas.* Most other clades include representatives from several continents, making the reconstruction of area of origin ambiguous.

When Northern Hemisphere and Southern Hemisphere are coded as a binary character, it appears that the dabbling ducks had their origins in the tropics and Southern Hemisphere (Fig. 3B). Based on this reconstruction, there are at least eight independent colonization events of the Northern Hemisphere and at least one recolonization of the Southern Hemisphere

from the Northern Hemisphere (but perhaps as many as five).

Discussion

Phylogeny

In general, analysis of mtDNA sequences produced a well-resolved and well-supported phylogeny for the dabbling ducks. This molecular phylogeny and a phylogeny derived from morphological characters (Livezey 1991) differ in several important respects, but they also share many features.

Major lineages and rooting.—Further outgroup analysis is required to resolve relationships among species in the outgroup and to determine the sister taxon of the dabbling ducks. An analysis of mitochondrial 12S rDNA data (M. Sorenson and K. Johnson unpubl. data) provides strong support for the exclusion of *Callonetta* and the inclusion of *Tachyeres* in the ingroup, and the present analysis also is consistent with this finding. Using the unweighted cyt-*b*/ND2 data, 74 additional steps are required in the shortest trees in which *Callonetta* is part of the ingroup and *Tachyeres* is not.

Many features of the ingroup topology are at odds with Livezey's (1991) morphological analysis and classical taxonomic work (e.g. Delacour and Mayr 1945). First, the molecular data strongly support (96% of bootstrap replicates) the monophyly of a "dabbling duck" clade that includes all *Anas* species, including taxa placed in *Mareca* by Livezey (1991), as well as four additional taxa: *Tachyeres, Amazonetta, Lophonetta,* and *Speculanas.* These four South American taxa form one of four lineages at or near the base of the ingroup in the molecular tree. The three other major lineages within the dabbling ducks are the Baikal Teal (*Anas formosa*); the blue-winged ducks and allies; and a large clade that includes the wigeons, teals, pintails, and mallards. We suggest that the tribal designation Anatini is most appropriately applied to this set of four major clades, the monophyly of which is strongly supported.

Baikal Teal.—In the weighted molecular tree, the Baikal Teal is sister to the blue-winged ducks and allies; however, this relationship is not strongly supported. In Livezey's (1991) tree, the Baikal Teal falls within a green-winged teal clade. This arrangement requires an additional 64 steps with the unweighted molecular data. In an analysis of conflict between the morphological and molecular data (Johnson 1997), the character states for *A. formosa* are a significant source of conflict between the two data sets. The genetic distance of this species to others within the dabbling ducks suggests it is not closely related to any other extant species.

Blue-winged ducks and allies.—Several taxa whose relationships have previously been uncertain fall at the base of the blue-winged duck clade: *A. versicolor, A. puna, A. hottentota,* and *A. querquedula.* These four species were included in a clade with the green-winged teals by Livezey 1991. However, there is 96% bootstrap support for the placement of these taxa in a clade with the blue-winged ducks in the combined analysis. The monophyly of the more typical blue-winged ducks (subgenus *Spatula*) is strongly supported in both data sets.

The low divergence and paraphyly of the Cinnamon Teal and Blue-winged Teal are surprising, but verified by another study (Kessler and Avise 1984) that found Blue-winged Teal was paraphyletic with respect to Cinnamon Teal. In our study, only one individual Blue-winged Teal was analyzed, and in Kessler and Avise's (1984) study, only one individual Cinnamon Teal was analyzed. Based on these results, these species may be mutually paraphyletic (i.e. there may be several different haplotypes of Cinnamon Teal intermixed with multiple different Blue-winged Teal haplotypes). Either these two species diverged very recently and still share ancestral haplotypes, or hybridization and introgression have occurred recently. More population-level sampling and investigation of nuclear genes are needed to distinguish these two scenarios.

Wigeons/teals/pintails/mallards.—The final major clade of dabbling ducks strongly supported by the molecular and combined data analyses includes wigeons, mallards, pintails, and five teal clades. This large group is also characterized by several complex behavioral display characters (see McKinney 1978). The wigeons are the basal members of this group and sister to the other seven clades, the relationships among which are not well supported and are sensitive to weighting scheme. The branch lengths among these seven clades are relatively short, suggesting a rapid radiation of

these groups, but the monophyly of each clade is well supported (Fig. 1).

Wigeons.—The wigeon clade includes five of the six taxa placed in the genus *Mareca* by Livezey (1991). *Anas falcata* and *A. strepera* are sister taxa and together are sister to the three wigeons: *A. penelope*, *A. americana*, and *A. sibilatrix*. All members of this group are distributed in the Northern Hemisphere except *A. sibilatrix*, which occurs throughout southern South America and is the sister species of *A. americana*. This topology suggests that *sibilatrix* was derived from a northern ancestor that colonized South America. The molecular data refute a sister relationship between Cape Teal and the wigeons, as suggested by morphological data (Livezey 1991). If the designation of the genus *Anas* is to be maintained across most of the major dabbling duck lineages, then the elevation of the genus *Mareca* for the wigeons is not warranted. Specifically, the sister relationship of wigeons to teals/pintails/mallards, exclusive of blue-winged ducks, is strongly supported in both the molecular and combined analyses. In addition, the placement of the wigeons as sister to all other species of *Anas*, as in Livezey's (1991) tree, would require 36 additional steps in the unweighted molecular data.

Pintails.—Monophyly of the pintails is strongly supported, and there is some indication that the Cape Teal is sister to the pintail clade. Strong support exists for a sister-species relationship between Brown Pintail (*A. georgica*) and Northern Pintail, but the placement of two morphologically similar species, the Red-billed Pintail (*A. erythrorhyncha*) and the White-cheeked Pintail (*A. bahamensis*), is not well supported.

Austral teals.—None of our analyses supported the monophyly of the "austral teals," but rather separated these species into two major clades: the gray teals and the brown teals (Fig. 2). Six additional steps are required in the unweighted molecular data when the austral teals are constrained to be monophyletic. The striking male plumage similarity between the Chestnut Teal and the brown teals have caused several to suggest (Delacour and Mayr 1945, Livezey 1991) that these two are sister taxa. However, the Chestnut Teal and Gray Teal are nearly identical in sequence (see also Sraml et al. 1996) and form a strongly supported clade with the Madagascar Teal (*A. bernieri*).

Green-winged teals.—Based on the weighted molecular and the unweighted combined analysis, *A. crecca*, *A. carolinensis*, and *A. flavirostris* form a clade. Surprisingly, however, the sister taxon of *A. carolinensis* is the monomorphic *A. flavirostris* and not *A. crecca*. Although many authors (e.g. Delacour and Mayr 1945, AOU 1998) have suggested that *A. crecca* and *A. carolinensis* be considered the same species (because only minor plumage differences occur between them), these taxa are highly divergent genetically. The paraphyletic relationship between them is unexpected given their morphological similarity, but 30 additional steps are required in the unweighted molecular data to make these two species-sister taxa. In fact, bootstrap support for the inclusion of *A. crecca* in this clade is less than 50%. The strongly supported sister relationship between *A. flavirostris* and *A. carolinensis* suggests that *A. flavirostris* evolved from birds colonizing South America from the Northern Hemisphere.

Mallards.—Although paraphyly between *A. crecca* and *A. carolinensis* haplotypes was previously unreported, paraphyly of mitochondrial haplotypes in Mallards has been documented (Avise et al. 1990, Cooper et al. 1996). The sequence divergence between these paraphyletic haplotypes in the Mallard is much lower (0.58%) than in the green-winged teals, suggesting that this is a much more recent phenomenon. Within mallards, there appear to be three biogeographic groups: a basal grade in Africa, a clade in North America, and a clade of eastern Asian/Pacific Island birds. Two major mitochondrial haplotypes occur within the Holarctic dimorphic Mallard. One of the Mallard haplotypes clusters with the other North American species; in fact, there are no base substitutions over the 2,147 bp between three of these four taxa, and *A. fulvigula* differs from the others at only two positions. The other Mallard haplotype clusters with the Asian/Pacific Mallards. The biogeographic distribution of these Mallard haplotypes is not fully known although they are both widely distributed in North America (Avise et al. 1990). Avise et al. (1990) found that all American Black Duck haplotypes fell within one of the two major clades of Mallard haplotypes. The second major clade of Mallard haplotypes not shared with American Black Ducks corresponds to the Asian/Pacific haplotype that we observed. It is unclear

whether both Mallard lineages occur in Eurasia, but the single individual that we sequenced from Russia differed at only a single position from the Asian/Pacific haplotype over 545 bp of cyt *b*.

Paraphyly of Mallard haplotypes suggests at least two scenarios for speciation in the group. The first is that a dimorphic Mallard recently gave rise to both the spotbills of Asia and the monomorphic Mallard relatives of North America. Under this scenario, there has been insufficient time for lineage sorting to occur within the Mallard, leading to paraphyly of mitochondrial haplotypes. If this scenario is correct, one might predict additional Mallard haplotypes should fall in alternative positions in the tree (i.e. not just in two places). Alternatively, the dimorphic Mallard may have invaded either North America (Palmer 1976) or Eurasia and hybridized with closely related monomorphic species that were already there, resulting in partial introgression into the Mallard population of haplotypes from the monomorphic species with which the Mallards hybridized. Under this scenario, there should be only two major haplotypes, and they should be found together on only one of the two continents. Clearly, more intensive population sampling in Europe and Asia is needed to determine the full nature of this pattern.

Morphological and molecular comparisons.— Comparisons of morphological and molecular data for the dabbling ducks indicate that phylogenies derived from these data sets are largely consistent, but the placements of several taxa are in conflict (see Johnson 1997). The existence of this conflict is supported by results of a partition homogeneity test that indicated that the molecular and morphological data sets were not samples of the same underlying phylogeny. In general, the molecular phylogeny was more consistent with other published data sets and with our expectations regarding molecular evolution. When all taxa are included in the analysis, the molecular data appears to have the overwhelming phylogenetic signal. Nonetheless, several features of trees from the combined unweighted morphological and molecular data are more similar to trees from the weighted molecular data alone than they are to trees from the unweighted molecular data alone. In addition, the combined tree also showed more consistency with other studies and resulted in an estimated transition/transversion ratio that was closer to a previous phylogeny independent estimate. This suggests that transversion weighting is more highly corroborated by the majority of evidence.

Biogeography

The difficulty of reconstructing areas of origin for the dabbling ducks likely is due to their high dispersal ability. Even a phylogeographic reconstruction method that explicitly includes dispersal (Ronquist 1997) cannot overcome this problem. Perhaps in a group such as dabbling ducks, dispersal ability is so high that most methods of phylogeographic reconstruction will fail to identify single areas of origin. Nonetheless, a number of interesting biogeographic insights are provided by the molecular tree. First, it is reasonable to infer transitions between hemispheres given current distributions of related taxa. For example, some relatively clear cases of invasion of South America from the north include the derivation of *A. flavirostris* from a North American "green-winged teal" ancestor, and invasion of South America and speciation of *A. sibilatrix,* presumably from North America. In addition, it seems reasonable that *A. acuta* was derived from an ancestor in the Southern Hemisphere (presumably South America), given an African origin for the pintails (see Figs. 2 and 3) and a South American origin for *A. bahamensis* and *A. georgica.* The mallard clade appears to have originated in Africa (see Figs. 2 and 3) and radiated into an Asia/Pacific lineage and a North American lineage. It is difficult to determine the biogeographic origin of all dabbling ducks without further analysis of outgroups.

Most other groups of birds show much stronger phylogeographic signal in biogeographic distributions. In some cases, entire orders or families are restricted to single continents (e.g. Musophagiformes, Coliiformes, Batrachostomidae, Pardalotidae). Very few genera have such a global distribution as the dabbling ducks. In addition, this distribution has been generated by multiple independent colonizations of several continents and islands in different lineages of ducks. The few other genera that have a distribution similar to dabbling ducks (e.g. *Larus, Ardea, Pandion, Accipiter*) seem largely to be associated with water or are birds of prey (with

large home ranges). Phylogenetic correlations of habitat characteristics, dispersal ability, and biogeographic distribution of various species remain to be examined in a rigorous way across many taxa (see Price et al. 1997 for an analysis of these patterns in Old World wood warblers), but this trend suggests potentially interesting patterns. Perhaps species that are associated with water are able to rest on the ocean during dispersal.

Does this dispersal-driven speciation have implications for our ability to reconstruct the phylogeny of such groups? The lack of strong resolution at two different taxonomic levels within the dabbling ducks, including relationships among several major clades of dabbling ducks and among mallard species, appears to be due to short branch lengths between internodes (i.e. a "star" phylogeny; Lara et al. 1996). This suggests the occurrence of periods of rapid radiation in both the teal/pintail/mallard clade and in the mallards. The lack of strong support for the placement of several of the mallard species is surprising given that the terminal branches of these species are relatively short and homoplasy is unlikely to obscure relationships (Lanyon 1988). Perhaps climatic periods in the history of the dabbling ducks have promoted widespread dispersal. If dispersal to many continents or islands during these hypothetical periods was nearly simultaneous, then reconstruction of the phylogenetic relationships among species or lineages that radiated in this way may be essentially intractable.

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