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ABSTRACT

This study examines the genetic variation in 45 taxa of all tribes and most species of North American waterfowl (Anatidae) with a starch-gel electrophoretic survey of protein variation at 25 loci. Relationships were estimated using the resulting data from the patterns of allozyme variation and summarized in both phenetic and cladistic branching diagrams. The branching diagrams (phylogenetic trees) are employed to help compare and contrast phylogenetic relationships relative to other hypothesis. Although results of this study generally concur with classic phylogenetic trees and the taxonomic designations of the current American Ornithologists' Union (AOU) *Check-list*, exceptions are noted. Genetic data strongly contradict inclusion of *Chen canagica* (emperor goose) within the genus *Chen*. *Clangula hyemalis* (oldsquaw) and *Melanitta nigra* (black scoter) do not cluster on the branching diagrams as would be predicted from classical analysis. It is possible that they form a divergent group within the Tribe MERGINI.

† † †

The classification of waterfowl (Anatidae), while having been recently revised (American Ornithologists' Union [AOU] 1983, 1991), has remained controversial for the past several decades (Bellrose, 1980). Recognizing that avian taxa appeared to be oversplit relative to other taxa, Delacour and Mayr (1945) made a strong case for more inclusive genera and pooled many monotypic groups in the Anatidae. This taxonomic reasoning was followed in a number of subsequent studies (e.g. Brush, 1976; Delacour, 1954–1964; Johnsgard, 1961).

Early taxonomic studies of avian species typically involved analysis of morphology, plumage, and behavior. Delacour and Mayr (1945) employed behavior patterns, anatomy, and plumage in the study of Anatidae, while Johnsgard (1961) relied primarily on behavior and Livezey (1986) on morphology. Molecular analyses were recognized as being of value to avian taxonomy, beginning with Sibley's (1960) electrophoretic evaluation of avian egg-white proteins.

While Sibley's avian studies (e.g. Sibley, 1968, 1970; Sibley and Ahlquist, 1972; Sibley et al., 1969) were focused at the generic and familial levels, later studies largely involved the attempt to identify avian species and their relationships. These studies involved the electrophoretic analysis of egg white, blood, and feather proteins (Brown et al., 1970; Brush, 1976; Ford et al., 1974; Morgan et al., 1976; Shaughnessy, 1970). They succeeded to varying degrees, but were limited primarily by the uncertain homologies and genetic basis of the few protein phenotypes detected (Brush, 1979).

Current electrophoretic avian studies use more refined histochemical staining techniques. Identification of up to ten alleles each from 20–30 biochemically detectable loci (Aquadro and Avise, 1982; Avise et al., 1980a; Johnston, 1983; Mindell and Sites, 1987; Seeb et al., 1986; Yang and Patton, 1981) is typical, making electrophoresis a valuable tool for measuring genetic distances and estimating phylogenetic relationships (Ankney et al., 1986; Baker, 1990; Barrett and Vyse, 1982; Barrowclough, 1983; Barrowclough et al., 1981; Browne et al., 1993; Gutierrez et al., 1983; N. Johnson et al., 1988; Morgan et al., 1976; Patton and Avise, 1986; Sherman, 1981; Smith and Zimmerman, 1976; Zink, 1982). Protein-electrophoretic analyses have been developed for the enforcement of wildlife laws and are employed when identification of a species is otherwise impossible (e.g. Harvey, 1990; Oates et al., 1983; Seeb et al., 1990; Utter, 1991).

Electrophoretic analysis of protein variation was employed in this study to examine phylogenetic relationships among individuals representing all of the tribes and most of the species of waterfowl found in

Table 1. Scientific classification of the species of the family Anatidae (swans, geese and ducks) analyzed in this study [after AOU (1983) and Bellrose (1980)]. Common names follow Bellrose (1980).

Subfamily	Tribe	Scientific name	Common name
Anserinae	DENDROCYGNINI	1. *Dendrocygna bicolor helva*	Fulvous whistling-duck
	CYGNINI	2. *Cygnus columbianus*	Tundra swan
	ANSERINI	3. *Anser albifrons frontalis*	Greater white-fronted goose
		4. *Anser albifrons gambelii*	Tule goose
		5. *Chen caerulescens caerulescens*	Snow goose
		6. *Chen caerulescens caerulescens*	Blue goose
		7. *Chen caerulescens atlantica*	Greater snow goose
		8. *Chen rossii*	Ross' goose
		9. *Chen canagica*	Emperor goose A
		10. *Chen canagica*	Emperor goose B
		11. *Branta bernicla nigricans*	Black brant
		12. *Branta bernicla hrota*	American brant
		13. *Branta canadensis canadensis*	Canada goose
		14. *Branta canadensis minima*	Cackling Canada goose
Anatinae	CAIRININI	15. *Aix sponsa*	Wood duck
	ANATINI	16. *Anas crecca*	Green-winged teal
		17. *Anas rubripes*	American black duck
		18. *Anas fulvigula*	Mottled duck
		19. *Anas platyrhynchos*	Mallard
		20. *Anas acuta*	Northern pintail
		21. *Anas discors*	Blue-winged teal
		22. *Anas cyanoptera*	Cinnamon teal
		23. *Anas clypeata*	Northern shoveler
		24. *Anas strepera*	Gadwall
		25. *Anas americana*	American widgeon
	AYTHYINI	26. *Aythya valisneria*	Canvasback
		27. *Aythya americana*	Redhead
		28. *Aythya collaris*	Ring-necked duck
		29. *Aythya marila*	Greater scaup
		30. *Aythya affinis*	Lesser scaup
	MERGINI	31. *Somateria mollissima*	Common eider
		32. *Somateria spectabilis*	King eider
		33. *Polysticta stelleri*	Steller's eider
		34. *Histrionicus histrionicus*	Harlequin duck
		35. *Clangula hyemalis*	Oldsquaw
		36. *Melanitta nigra*	Black scoter
		37. *Melanitta perspicillata*	Surf scoter
		38. *Melanitta fusca*	White-winged scoter
		39. *Bucephala clangula*	Common goldeneye
		40. *Bucephala islandica*	Barrow's goldeneye
		41. *Bucephala albeola*	Bufflehead
		42. *Lophodytes cucullatus*	Hooded merganser
		43. *Mergus merganser*	Common merganser
		44. *Mergus serrator*	Red-breasted merganser
	OXYURINI	45. *Oxyura jamaicensis*	Ruddy duck

North America. The phylogenetic relationships were examined using both phenetic and cladistic approaches, with branching diagrams constructed for each to summarize the electrophoretic data.

MATERIALS AND METHODS

A total of 429 individuals, representing 40 species and 5 subspecies, was collected (Table 1) from the U.S. Fish and Wildlife Service in the states of Alaska, California, Colorado, Nebraska, and Washington. As soon as possible after collection, samples were frozen, shipped on dry ice to the laboratory, and subsequently stored at -20° C. In most cases a complete wing was obtained for the study, while in other cases a sample consisted of a one-gram piece of muscle. In preparation for electrophoresis, small pieces of muscle were extracted and placed in 12 × 72 mm culture tubes to which equal volumes of water were added.

Electrophoresis followed procedures outlined in May et al. (1979) and Utter et al. (1974). Three buffer systems were employed: 1) MF–tris-boric acid EDTA gel with tray buffer (pH 8.5) (Boyer et al. 1963); 2) RW–tris-citric acid gel buffer (pH 8.5) with lithium hydroxide-boric acid tray buffer (pH 8.5) (Ridgway et al. 1970); and 3) AC+–modification of the amine-citrate buffer of Clayton and Tretiak (1972). In the AC+ buffer system, the tray remained unchanged (pH 6.1), while the gel buffer was raised to pH 6.4 with N-(3-aminopropyl) morpholine. Staining for enzyme activity followed methods outlined in Allendorf et al. (1977), Harris and

Table 2. Proteins: their locus abbreviations, buffer systems and Enzyme Commission numbers. Buffer systems are abbreviated as described in the text. Loci found to be monomorphic throughout a family are marked with an asterisk.

Protein	Locus Abbreviation	Buffer System	Enzyme Commission Number
Adenosine deaminase	*ADA*	MF	3.5.4.4
Adenylate kinase	**AK*	AC+	2.7.4.3
Albumen	*ALB*	RW	—
Aspartate aminotransferase	*AAT-1* **AAT-2*	AC+	2.6.1.1
Creatine kinase	**CK*	RW	2.7.3.2
Glucose phosphate isomerase	*GPI*	RW	5.3.1.9
Glyceraldehyde-3-phosphate dehydrogenase	**G3PDH*	AC+	1.2.1.12
Guanine deaminase	*GDA*	AC+	3.5.4.3
Hemoglobin	*HEM*	AC+	—
Iscocitrate dehydrogenase	*IDH*	AC+	1.1.1.42
Lactate dehydrogenase	**LDH-1* *LDH-2*	AC+	1.1.1.27
Malate dehydrogenase	*MDH-1* *MDH-2*	AC+	1.1.1.37
Nucleoside phosphorylase	*NP*	AC+	2.4.2.1
Peptidase	**PEP-1* *PEP-2* *PEP-3* *PEP-4*	AC+	3.4.1.1
Phosophoglucomutase	*PGM*	RW	5.4.2.2
Phosphomannose isomerase	*PMI-1* *PMI-2*	AC+	5.3.1.8
Superoxide dismutase	*SOD-1* *SOD-2*	MF	1.15.1.1

Hopkinson (1976), Selander et al. (1971), and Shaw and Prasad (1970). A list of the 25 enzymes resolved is given in Table 2.

Locus designation followed the system of nomenclature suggested by Allendorf and Utter (1976) and Shaklee (1990). For each locus, the mobility of the most common allele in mallards (*Anas platyrhynchos*) was used as a standard and designated as 100 with the mobility of all other alleles calculated relative to this allele. A mallard sample was included on every gel for reference. It was often necessary to compare each allele to several others, in addition to that of the standard mallard, when numerous alleles occurred at some loci. After electrophoresis, each sample was scored for its observed genotype. Allelic frequencies at each locus were calculated for each species.

The use of electrophoretic data to estimate phylogenetic trees has been addressed by Avise (1994), Farris (1981), Felsenstein (1981), Hartl and Clark (1989), Mickevich and Mitter (1981), and Straney (1981). Branching diagrams (phylogenetic trees) for both phenetic and cladistic approaches were constructed from a matrix of genetic distances. Distance analyses, based on the estimation of pair-wise genetic distances between taxa (Avise, 1994), avoid both the necessity of a transition series of alleles and the need for assignment of ancestral or derived states.

In this study, the phenetic approach utilizes the mutation-drift model of Nei (1972). It is assumed that time and genetic divergence are correlated, with many genes evolving at a constant rate (Forey et al., 1992; Mayr, 1991; Wilson, 1976) and genetic distances increasing with time (Avise, 1994). Unbiased distance values (D) were estimated between every pair of species from the allelic frequencies, using Nei's (1978) formula. The phenogram (Fig. 1) was produced from a matrix of D-values using the unweighted pair-group method with arithmetic averages (UPGMA) (Sneath and Sokal, 1973). Extant clusters were "right-justified" along the genetic distance axis (Avise, 1994).

A cladistic pattern among extant taxa and hypothetical ancestors, based on the most parsimonious solution instead of rates of evolution, is presented using a Wagner distance analysis (Farris, 1972). Modified Rogers' distance values (D_T) (Wright, 1978) were calculated from the allelic frequencies and subjected to the distance Wagner procedure of Swofford (1981) to generate an unrooted network. The network was rooted at the midpoint of the longest pathway between extant taxa (Avise, 1994; Farris, 1972), creating a rooted distance Wagner diagram (Fig. 2).

Both the phenogram (Fig. 1) and distance Wagner diagram (Fig. 2) are compared to a classical phylogenetic estimate (Fig. 3) derived from Bellrose (1980) and based on Johnsgard (1978). The generic and species designations are those of the AOU *Check-list of North American Birds* (1957, 1983) and AOU supplements to the check-list (1985, 1987, 1989, 1991).

BIOSYS-1 (Swofford and Selander 1981) was used to analyze the electrophoretic data and estimate heterozygosities (H).

ELECTROPHORESIS

Gene products from approximately 60 presumptive loci were initially examined, with 25 loci resolved adequately enough for routine scoring. Since no genetic variation was found at the *AK*, *AAT-2*, *CK*, *G3PDH*, *LDH-1*, and *PEP-1* loci, they were considered to be monomorphic throughout the family. The mean heterozygosity (weighted by sample size) was found to be consistent with published avian values (Aquadro and Avise, 1982; Avise, 1994; Patton and Avise, 1986).

Resulting electrophoretic patterns of most loci agreed with previously published results (e.g. Ankney et al., 1986; Avise et al., 1980a; Browne, 1993; Patton and Avise, 1986). Loci of special interest or those which had results previously unpublished are reported in this section. Allelic frequencies of all loci considered to be polymorphic can be found in Table 3.

Adenosine deaminase

One *ADA* locus was resolved in the family Anatidae. A high degree of polymorphism was exhibited both within and between a majority of the species. Heterozygotes exhibited a two-banded pattern at the *ADA* locus, consistent with a monomeric structure.

Peptidase

Peptidase zones of activity *(PEP-1, PEP-2, PEP-3)* appeared in all species of the family Anatidae. No genetic variation was found at the *PEP-1* locus (resolved with a DL-leucylglycylglycine substrate). *PEP-2,3* were resolved with DL-leucyl-DL-alanine. An additional zone of activity, *PEP-4* (also resolved with leucylalanine), appeared only in *Chen canagica* (emperor goose) and was scored on a presence or absence basis.

Mannose-6-phosphate isomerase

MPI-1, a highly polymorphic monomer, was clearly expressed in all species. *MPI-2*, another zone of activity, generally migrated at a uniform distance from *MPI-1*. *Dendrocygna b. helva* (fulvous whistling-duck) expressed *MPI-2(100)* locus mobility (identical to most of the others in the subfamily Anserinae) and was fixed for a faster *MPI-1(152)* allele. *MPI-2* was not expressed in all species examined, analogous to that of *CK-1,2* in North Ameri-

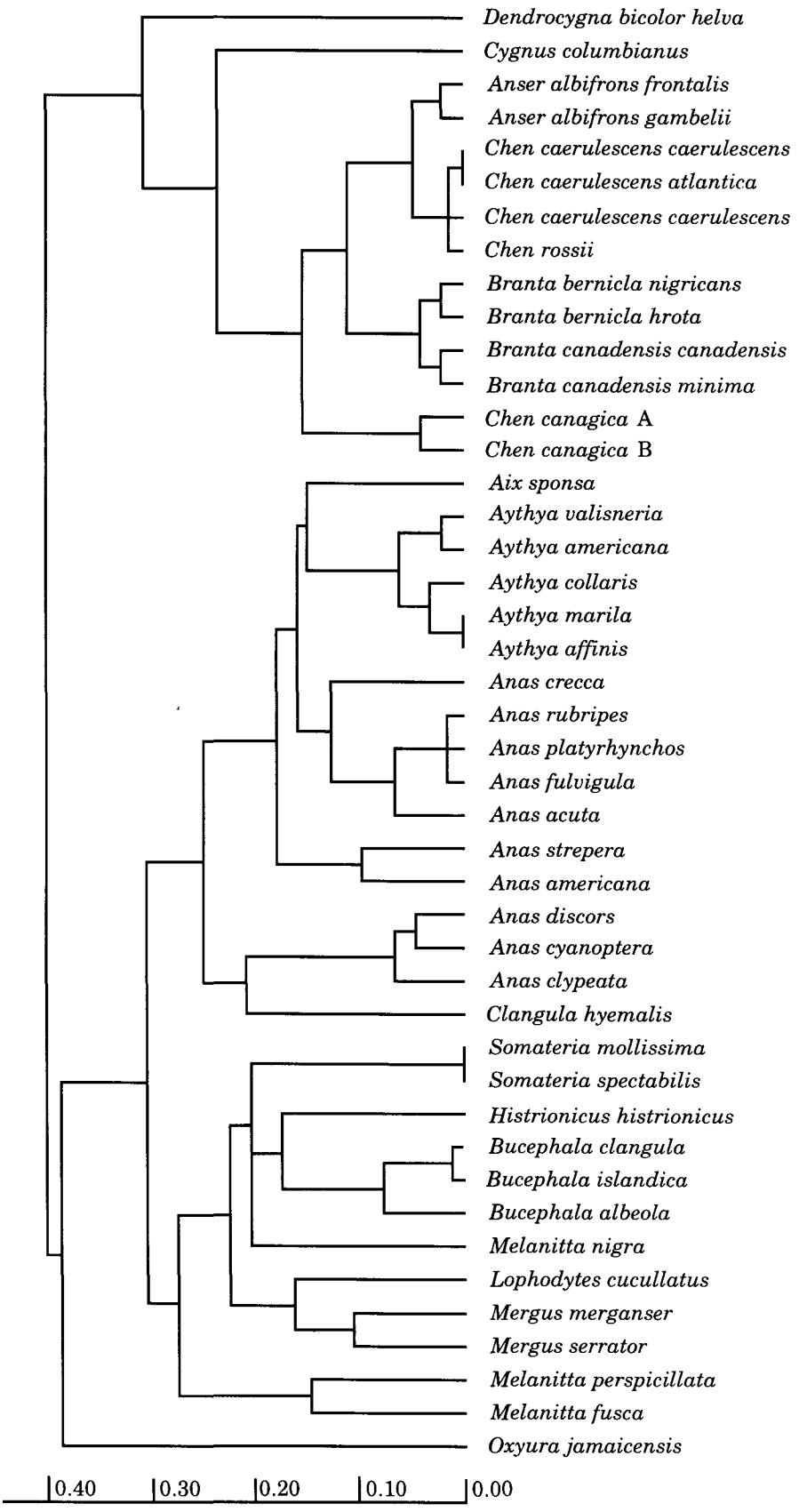

Figure 1. Phenogram constructed using the unweighted pair-group method with arithmetic averages (UPGMA) from a matrix of D-values. Phenetic relationships of the family Anatidae based upon Nel's (D) (Nel, 1978).

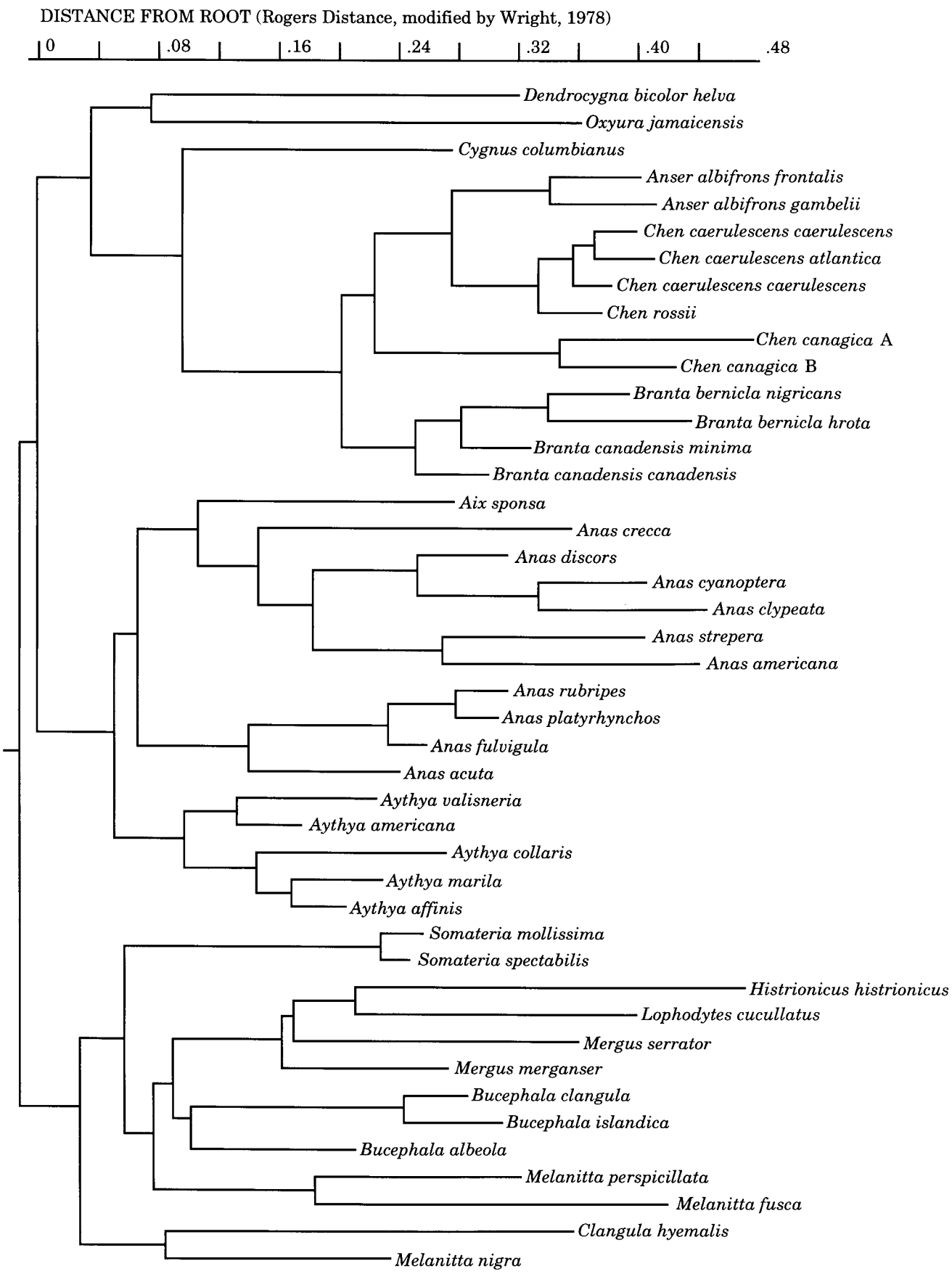

Figure 2. Distance Wagner Diagram for the family Anatidae constructed using modified Rogers' distance measure (D_r) and distance Wagner procedure of Swofford (1981).

can thrushes (Avise et al., 1980a). Although *MPI-1,2* can be interpreted as being the products of a single structural locus, consideration was also given to the identification by Finnerty and Johnson (1979) of the heritable, non-allelic variation found for xanthine dehydrogenase and aldehyde oxidase in *Drosophila melanogaster* (see also Finnerty et al., 1979, Johnson et al., 1981). It was concluded in this study, as in Avise et al. (1980a), that *MPI-1,2* were present as two sets of taxonomically useful characters. It could not be unequivocally determined, however, whether or not the two zones of activity ultimately represented the products of a single structural locus.

PATTERNS OF GENETIC DIFFERENTIATION

The subfamily Anserinae

The subfamily Anserinae includes the whistling-ducks, swans, and geese: the tribes DENDROCYGNINI, CYGNINI and ANSERINI, respectively. Those in the subfamily were not diagnostic for all species from the other Anatidae at the *GDA*, *NP*, *PEP-2*, and *MPI-1,2* loci. The *ADA*, *GDA*, *GPI*, *NP*, *PEP-2,3*, *PGM*, and *MPI-1,2* loci were useful for identification within the subfamily.

DENDROCYGNINI (Whistling-ducks): *Dendrocygna.* *Dendrocygna b. helva* (fulvous whistling-duck) was the only species available from this predominantly South American tribe. *Dendrocygna* was distinguished from the other subfamily members by its electrophoretic migration patterns of alleles at the *PEP-2* loci and by large frequency differences at the *PGM* locus. Based on the phenetic and cladistic analyses, *Dendrocygna* represents the most divergent genus of the Anserinae examined. It joins the rest of the subfamily at a D of 0.33 in the phenogram (Fig. 1). Since *Oxyura* and *Dendrocygna* are sister taxa on the distance Wagner diagram (Fig. 2), and *Oxyura* is observed as being the most divergent member of the subfamily Anatinae in both the phenogram (Fig. 1) and classical taxonomy (Fig. 3), the sister group relation of the *Dendrocygna* to the remainder of the subfamily Anserinae could not be resolved in the analyses. Sibley and Monroe (1990) classify this tribe as the family Dendrocygnidae, based on the DNA-DNA hybridization studies of Sibley and Ahlquist (1983, 1987, 1990).

CYGNINI (Swans): *Cygnus.* Only specimens from one member of this tribe, *Cygnus columbianus* (tundra swan, formerly whistling swan) were available for analysis. While *Cygnus columbianus* could be distinguished from the genus *Anser* and some members of the genus *Chen* at *GPI(100)*, it differed from all of the other genera of the subfamily Anserinae at the *ADA*, *NP*, and *PMI-1,2* loci. These findings seem to coincide with the classification of the tribe as the subfamily Cygninae by Sibley and Monroe (1990) who base their classification on the DNA-DNA hybridization studies of Sibley and Ahlquist (1983, 1987, 1990). Although a phenogram and a rooted Wagner network are not necessarily expected to form concordant branching, the diagrams do exhibit identical branching in the case of *Cygnus*. In the phenetic analysis, *Cygnus* has a D of 0.29 from the members of the genera *Anser*, *Branta*, and *Chen*.

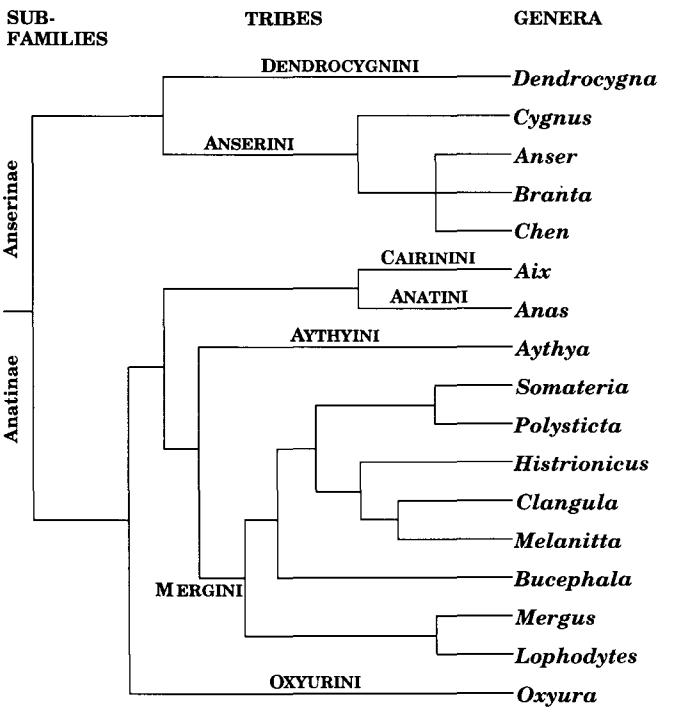

Figure 3. Phylogeny (classification) of the family Anatidae based upon structure and behavior [after Bellrose (1980) based on Johnsgard (1961, 1978)].

ANSERINI (Geese): *Anser*, *Branta*, and *Chen*. The electrophoretic data separated the ANSERINI (geese) into three heterogenous aggregations: the species *Chen canagica* (emperor goose), the genus *Branta*, and a group made up of members of *Anser* and the remaining *Chen*. Both the phenogram (Fig. 1) and the distance Wagner diagram (Fig. 2) imply that *Cygnus* may be a sister taxon to these geese.

Chen canagica (emperor goose) was the most divergent taxon examined, exhibiting an additional peptidase locus *(PEP-4)*, and differing from other members of the subfamily Anserinae by fixation for the *ADA(110)* allele. At the *MPI-1* locus, two of the five specimens, designated "Emperor A," were fixed for the *MPI*-1(110) allele, while the other three specimens, designated "Emperor B," were fixed for the *MPI-1(93)* allele. The probability is less than 0.05 that these samples represent one population which is polymorphic at the *MPI-1* locus.

Considering the *Anser/Chen* complex, *Chen c. caerulescens* (snow goose and blue goose), *Chen c.*

Table 3. Allele frequency estimates for the family Anatidae. An explanation of the numbers is given on page 130. Full names for species are given in Table 1. Sample number (N) is in parentheses following the name unless it differs at a particular locus, in which case it is given as a superscript.

TAXONOMY	*ADA*										**_ALB_					
Locus:	**100**	**107**	**95**	**110**	**113**	**98**	**103**	**79**	**120**	**105**	**100**	**98**	**102**	**101**	**97**	**104**
DENDROCYGNINI																
1. *Dendrocygna b. h.* (6)				0.25						0.75			1.00			
CYGNINI																
2. *Cygnus c.* (2)									1.00				1.00			
ANSERINI																
3. *Anser a. f.* (8)	0.38									0.62			1.00			
4. *Anser a. g.* (20)	1.00												1.00			
5. *Chen cae. c.* (20)	0.10	0.28	0.05	0.57									1.00			
6. *Chen cae. c.* (10)		0.50	0.05	0.30		0.15							1.00			
7. *Chen cae. a.* (10)	0.15	0.35	0.05	0.45									1.00			
8. *Chen r.* (10)	0.15	0.35		0.45		0.05							1.00			
9. *Chen can.* (2)				1.00									1.00			
10. *Chen can.* (3)				1.00									1.00			
11. *Branta b. n.* (11)	0.04	0.64	0.23	0.09									1.00			
12. *Branta b. h.* (2)		0.75	0.25										1.00			
13. *Branta c. c.* (10)	0.10	0.75	0.15										1.00			
14. *Branta c. m.* (17)	0.03	0.94	0.03										1.00			
CAIRININI																
15. *Aix s.* (10)			0.10				0.90							1.00		
ANATINI																
16. *Anas c.* (10)	0.50	0.22	0.07		0.14		0.07				1.00[7]					
17. *Anas r.* (10)	0.75[7]	0.15[7]	0.05[7]				0.05[7]				1.00					
18. *Anas f.* (10)	0.55	0.45									1.00					
19. *Anas p.* (31)	0.82	0.18									1.00[29]					
20. *Anas a.* (10)	0.30	0.70										1.00				
21. *Anas d.* (10)		0.11	0.28	0.11			0.28	0.22				0.05		0.95		
22. *Anas c.* (10)	0.05		0.70				0.15	0.10						1.00		
23. *Anas c.* (10)			0.56				0.22	0.22				1.00				
24. *Anas s.* (10)			0.06				0.94								1.00	
25. *Anas a.* (10)			0.15				0.80	0.05					1.00			
AYTHYINI																
26. *Aythya v.* (10)		0.95					0.05						1.00			
27. *Aythya a.* (20)		0.80					0.20						1.00			
28. *Aythya c.* (10)			0.35	0.10			0.55						1.00			
29. *Aythya m.* (5)		1.00											1.00			
30. *Aythya a.* (10)		0.95				0.05							1.00			
MERGINI																
31. *Somateria m.* (10)					1.00								1.00			
32. *Somateria s.* (3)					1.00								1.00			
33. *Polysticta s.* (7)							1.00						1.00[1]			
34. *Histrionicus h.* (2)					1.00								1.00			
35. *Clangula h.* (10)						0.44	0.56						1.00			
36. *Melanitta n.* (10)		0.06			0.94								1.00			
37. *Melanitta p.* (10)					1.00								1.00			
38. *Melanitta f.* (10)					0.25				0.75				1.00			
39. *Bucephala c.* (10)					1.00								1.00			
40. *Bucephala i.* (10)					1.00						0.05		0.95			
41. *Bucephala a.* (10)					1.00								1.00			
42. *Lophodytes c.* (10)		1.00														1.00
43. *Mergus m.* (10)					1.00											1.00
44. *Mergus s.* (10)					0.95		0.05									1.00
OXYURINI																
45. *Oxyura j.* (10)								1.00					1.00			

**Loci at which electrophoretic patterns agree with previously published results.

Table 3. Continued.

	**AAT-1			**GPI							**GDA				
	100	500	-700	100	160	-66	-425	-150	385	180	100	94	108	89	81
1.	1.00			1.00							1.00				
2.	1.00			1.00								1.00			
3.	1.00					0.88				0.12				0.88	0.12
4.	1.00					1.00								1.00	
5.	1.00			0.02		0.98								1.00	
6.	1.00					0.95	0.05							1.00	
7.	1.00					0.90	0.10							1.00	
8.	1.00					1.00								1.00	
9.	1.00			1.00										1.00	
10.	1.00			1.00										1.00	
11.	0.95		0.05	1.00										1.00	
12.	1.00			1.00										0.50	0.50
13.	1.00			1.00										0.95	0.05
14.	1.00			1.00										1.00	
15.	1.00			1.00							1.00				
16.	1.00			1.00							0.50		0.50		
17.	1.00			1.00							1.00				
18.	1.00			1.00							1.00				
19.	0.98[29]	0.02[29]		0.95	0.02				0.03		1.00				
20.	1.00			1.00							1.00				
21.	1.00			1.00							0.25	0.75			
22.	1.00			1.00								1.00			
23.	1.00			1.00								1.00			
24.	1.00			1.00								1.00			
25.	1.00			1.00							1.00				
26.	1.00			1.00							1.00				
27.	1.00			1.00							1.00				
28.	1.00			1.00							1.00				
29.	1.00			0.90		0.10					1.00				
30.	1.00			1.00							0.75	0.05	0.20		
31.	1.00			1.00							1.00				
32.	1.00			1.00							1.00				
33.	1.00			1.00							No Data				
34.	1.00			1.00							1.00				
35.	1.00			1.00								1.00			
36.	1.00			1.00							1.00				
37.	1.00					0.95	0.05				1.00				
38.	1.00					1.00					1.00				
39.	1.00			1.00							1.00				
40.	1.00			1.00							1.00				
41.	1.00			1.00							1.00				
42.	1.00			1.00							1.00				
43.	1.00			1.00							1.00				
44.	1.00			1.00							1.00				
45.		1.00		0.05			0.05	0.90			1.00				

**Loci at which electrophoretic patterns agree with previously published results.

Table 3. Continued.

	**HEM				**IDH				**LDH-2				**MDH-1				**MDH-2	
	-100	-109	-118	-94	-100	-48	-95	-81	100	155	242	31	-100	-162	-31	-25	100	-136
1.	No Data				1.00				1.00				1.00				1.00	
2.	1.00				1.00				1.00				1.00				1.00	
3.	1.00				1.00				1.00				1.00				1.00	
4.	1.00				1.00				1.00				1.00				1.00	
5.	0.80			0.20	1.00				1.00				1.00				1.00	
6.	0.90			0.10	1.00				1.00				0.95		0.05		1.00	
7.	0.80			0.20	1.00				1.00				1.00				1.00	
8.	1.00				1.00				1.00				1.00				1.00	
9.	1.00				1.00				1.00				1.00				1.00	
10.	1.00				1.00				1.00				0.67			0.33	1.00	
11.	1.00				1.00				1.00				1.00				1.00	
12.	1.00				1.00				1.00				1.00				1.00	
13.	1.00[21]				0.90[21]			0.10[21]	1.00[21]				1.00				1.00	
14.	1.00				0.97			0.03	0.97			0.03	1.00				1.00	
15.	1.00				1.00				1.00				1.00				1.00	
16.	1.00				1.00				1.00				1.00				1.00	
17.	1.00				1.00				1.00				1.00				1.00	
18.	1.00				1.00				1.00				1.00				1.00	
19.	0.97	0.02	0.01		1.00				1.00				1.00				1.00	
20.	1.00				1.00				1.00				1.00				1.00	
21.	1.00				1.00				1.00				1.00				0.95	0.05
22.		0.15		0.85	1.00				1.00				1.00				1.00	
23.				1.00	1.00				1.00				1.00				1.00	
24.	1.00				0.95	0.95			1.00				1.00				1.00	
25.	1.00				1.00				1.00				1.00				1.00	
26.	1.00				1.00				0.78	0.22			1.00				1.00	
27.	1.00				1.00				1.00				1.00				1.00	
28.	1.00				1.00				1.00				1.00				1.00	
29.	1.00				1.00				1.00				1.00				1.00	
30.	1.00				1.00				1.00				1.00				1.00	
31.			1.00		1.00				1.00				1.00				1.00	
32.	0.17		0.83		1.00				1.00				1.00				1.00	
33.	1.00				1.00				1.00				1.00				1.00	
34.		1.00			1.00				1.00				1.00				1.00	
35.		1.00			1.00				1.00				1.00				1.00	
36.		1.00			1.00				0.95		0.05		1.00				1.00	
37.	1.00				1.00				1.00				1.00				1.00	
38.			1.00		1.00				1.00				1.00				1.00	
39.	1.00				1.00				1.00				1.00				1.00	
40.	1.00				1.00				1.00				0.85	0.15			1.00	
41.	1.00				1.00				1.00				1.00				1.00	
42.	1.00				1.00				1.00				1.00				1.00	
43.	1.00				1.00				1.00				1.00				1.00	
44.	1.00						1.00		1.00				1.00				1.00	
45.	1.00				1.00				1.00				1.00				1.00	

**Loci at which electrophoretic patterns agree with previously published results.

Table 3. Continued.

	**NP										PEP-2						
	100	**87**	**113**	**79**	**93**	**73**	**40**	**107**	**123**	**55**	**100**	**82**	**107**	**94**	**114**	**75**	**88**
1.		0.08		0.08		0.84											
2.			1.00									1.00					
3.								1.00				1.00					
4.								1.00				1.00					
5.								1.00				1.00					
6.								1.00				1.00					
7.								1.00				1.00					
8.								1.00				1.00					
9.								1.00				1.00					
10.								1.00				1.00					
11.								1.00			0.09	0.09		0.82			
12.								1.00						1.00			
13.								1.00[21]				0.79	0.02	0.17		0.02	
14.								1.00			0.06	0.24		0.70			
15.		0.90				0.10					0.94		0.06				
16.		0.94[9]				0.06[9]					0.21		0.07		0.72		
17.	0.75	0.20		0.05							0.95	0.05					
18.	0.70	0.25	0.05								0.60	0.25	0.10			0.05	
19.	0.77	0.19	0.02			0.02					0.92	0.02					
20.	0.55	0.35	0.05	0.05							0.67		0.22	0.06	0.05		
21.	0.88[8]	0.06[8]	0.06[8]								0.05		0.10	0.80	0.05		
22.	0.72		0.28											1.00			
23.	1.00[6]													1.00			
24.	0.05			0.95							0.07		0.93				
25.	0.10		0.05	0.75	0.05	0.05							1.00				
26.				1.00									1.00				
27.				0.89		0.11					0.15		0.85				
28.				0.93[7]		0.07[7]					1.00						
29.				0.90	0.10						1.00						
30.			0.05	0.90		0.05					1.00						
31.	1.00										0.14	0.86					
32.	1.00											1.00					
33.	0.08	0.75			0.17						No Data						
34.							1.00				1.00						
35.	0.05				0.90			0.05					0.14	0.86			
36.			0.95					0.05			0.38		0.06	0.56			
37.					1.00												
38.					1.00									1.00			
39.			0.95						0.05		0.94						0.06
40.			1.00								0.71						0.29
41.									1.00		0.86		0.07		0.07		
42.				0.50	0.50						0.43		0.57				
43.										1.00	1.00						
44.				0.64	0.36						0.92	0.08					
45.						1.00					0.83		0.17				

**Loci at which electrophoretic patterns agree with previously published results.

Table 3. Continued.

	PEP-2 (cont.)		*PEP-3*										*PEP-4*		**PGM	
	79	**66**	**100**	**86**	**95**	**108**	**89**	**80**	**104**	**75**	**92**	**91**	**No Loc.**	**100**	**100**	**140**
1.		1.00		0.75	0.25								1.00		1.00	
2.					1.00								1.00			
3.				1.00									1.00			
4.				0.75				0.25					1.00			
5.							0.94	0.06					1.00			0.03
6.							1.00						1.00			
7.							0.83	0.17					1.00		0.25	
8.							0.60				0.40		1.00			
9.							1.00							1.00		
10.							1.00							1.00	0.17	
11.					0.05		0.18				0.77		1.00			
12.							0.75				0.25		1.00			
13.			0.35		0.60		0.05						1.00		0.05	
14.				0.03	0.85		0.06				0.06		1.00		0.03	
15.			0.06	0.22	0.72								1.00			
16.									1.00				1.00		0.79[7]	0.21[7]
17.			0.95				0.05						1.00		1.00	
18.			0.75		0.15				0.10				1.00		1.00	
19.	0.06		0.95		0.02		0.02		0.01				1.00		1.00	
20.			0.85		0.05				0.10				1.00		0.95	0.05
21.			0.17	0.33	0.33			0.11	0.06				1.00		0.94[8]	0.06[8]
22.				0.29	0.57		0.14						1.00		0.90	0.10
23.				0.50	0.50								1.00		1.00	
24.			0.85	0.15									1.00		1.00	
25.			1.00										1.00		1.00	
26.			0.25		0.70							0.05	1.00			
27.			0.88		0.12								1.00		0.13	
28.			1.00										1.00		0.30	
29.			0.90		0.10								1.00		0.50	
30.			0.72	0.06	0.22								1.00		0.20	
31.			1.00										1.00			
32.			1.00										1.00			
33.			1.00										1.00		0.50	
34.					1.00								1.00		1.00	
35.			0.05		0.05	0.90							1.00			
36.							0.95	0.05					1.00		0.05	
37.	1.00						0.78		0.22				1.00			
38.			1.00										1.00			
39.						0.05			0.95				1.00		0.90	
40.									1.00				1.00		1.00[8]	
41.					0.10				0.90				1.00			
42.					1.00								1.00		1.00	
43.				0.05	0.95								1.00			
44.				0.15	0.60			0.15		0.10			1.00			
45.			0.20						0.80				1.00			1.00[8]

**Loci at which electrophoretic patterns agree with previously published results.

Table 3. Continued.

	**PGM (cont.)		MPI-1										MPI-2	**SOD-1		**SOD-2	
	55	72	100	120	133	55	67	110	75	93	152	142	No Loc. 100	-100	-33	100	250
1.											1.00		1.00	1.00			1.00
2.	1.00		1.00										1.00	1.00			1.00
3.	1.00									0.88		0.12	1.00	1.00		0.12	0.88
4.	1.00									1.00			1.00	1.00			1.00
5.	0.97									0.95	0.05		1.00	1.00		0.03	0.97
6.	1.00									0.95	0.05		1.00	1.00			1.00
7.	0.75									1.00			1.00	1.00			1.00
8.	1.00									1.00			1.00	1.00			1.00
9.	1.00							1.00					1.00	1.00			1.00
10.	0.83									1.00			1.00	1.00			1.00
11.	1.00							0.09		0.91			1.00	1.00			1.00
12.	1.00									1.00			1.00	1.00			1.00
13.	0.95							0.14[21]		0.86[21]			1.00[21]	1.00			1.00
14.	0.97									1.00			1.00	1.00			1.00
15.	0.95	0.05	1.00										1.00	1.00		1.00	
16.			0.11				0.72			0.17			1.00	1.00		1.00	
17.			0.65	0.35									1.00	0.95	0.05	1.00	
18.			0.80	0.10	0.05			0.05					1.00	1.00		1.00	
19.			0.84	0.11	0.03							0.02	1.00	1.00		1.00	
20.			0.85				0.15						1.00	1.00		1.00	
21.			0.40			0.15	0.45						1.00	1.00		1.00	
22.			0.30				0.70						1.00	1.00		1.00	
23.			0.25			0.35	0.35		0.05				1.00	1.00		1.00	
24.			0.55	0.10			0.35						1.00	1.00		1.00	
25.							0.95			0.05			1.00	1.00		1.00	
26.	1.00		0.95	0.05									1.00	1.00		1.00	
27.	0.87		0.75	0.10			0.15						1.00	1.00		1.00	
28.	0.70		0.95		0.05								1.00	1.00		1.00	
29.	0.50		0.90									0.10	1.00	1.00		1.00	
30.	0.80		1.00										1.00	1.00		1.00	
31.	1.00								1.00				1.00	1.00			1.00
32.	1.00								1.00				1.00	1.00			1.00
33.	0.50		0.90				0.10						1.00	1.00		No Data	
34.							1.00						1.00	1.00			1.00
35.	1.00			0.10		0.80	0.10						1.00	1.00		1.00	
36.	0.95								0.95	0.05			1.00	1.00		1.00	
37.	1.00										0.33	0.67	1.00	1.00			1.00
38.	1.00											1.00	1.00	1.00			1.00
39.	0.10		0.20						0.50	0.30			1.00	1.00			1.00
40.									1.00				1.00	1.00			1.00
41.	1.00		0.06					0.06	0.83	0.05			1.00	1.00			1.00
42.									1.00				1.00	1.00			1.00
43.	1.00		0.20						0.80				1.00	1.00			1.00
44.	1.00			0.05						0.95			1.00	1.00			1.00
45.										0.10	0.05	0.85	1.00	1.00			1.00

**Loci at which electrophoretic patterns agree with previously published results.

atlantica (greater snow goose), and *Chen rossi* (Ross' goose)–members of the Ross'/snow goose cluster–were found to be identical, differing from the greater white-fronted/tule goose representatives of *Anser* by the large frequency differences at the *ADA* and *PEP-3* loci. *Anser a. frontalis* (greater white-fronted goose) and *Anser a. gambelli* (tule goose) appeared to have distinguishing loci, most notably *ADA*. While the tule geese were fixed for the *ADA(100)* allele, all of the greater white-fronted geese possessed the *ADA(100)* allele at a frequency of only 0.38.

Branta, most similar to the *Anser/Chen* complex, excluding *C. canagica*, differed from the group at the *ADA*, *PGI*, and *PEP-2* loci. Genetic differences were exhibited within *Branta* at the *PGM* and *PEP-2,3* loci. Although no fixed differences occurred, allelic frequency differences found at these loci may allow discrimination between *Branta b. nigricans* (black brant) and *Branta b. hrota* (American brant) at the *PEP-3* locus, and between *Branta c. canadensis* (Canada goose) and *Branta c. minima* (cackling Canada goose) at the *PEP-2* locus.

The subfamily Anatinae

Anatinae, the largest and most complex subfamily, contains the "typical" ducks. With some exceptions, the relationships based on the phenogram parallel the generic relationships, and the major clusterings on the Wagner diagram reflect the divisions into tribes. The three tribes (ANATINI, AYTHYINI, CAIRININI) are clustered with the Anserinae in the distance Wagner diagram (Fig. 2), in contrast with their placement on the phenogram (Fig. 1) and in classical taxonomy (Fig. 3). However, the common root is extremely short, 0.049, and its placement is subject to interpretation.

CAIRININI (Muscovy ducks and allies): *Aix*. The genus *Aix* is represented by one species in North America, *Aix sponsa* (wood duck), which is the only North American member of the tribe. It differed at the *ADA*, *ALB*, *NP*, *PEP-2,3*, and *PGM* loci from the majority of both *Aythya* and *Anas*. Concurring with existing literature, *Aix* is closest to *Anas* on the distance Wagner diagram (Fig. 2), but is closest to *Aythya* on the phenogram (Fig. 1).

ANATINI (Dabbling ducks): *Anas*. The genus *Anas*, a large polytypic aggregation, was examined. Large frequency differences were found at the *ADA*, *ALB*, *NP*, and *PEP-2,3* loci for the ten species analyzed. *Anas platyrhynchos* (mallard), *Anas fulvigula* (mottled duck), and *Anas rubripes* (American black duck) form a genetically close knit group. *Clangula hyemalis* (oldsquaw), one of the most dissimilar MERGINI, is polyphyletic with *Anas* in the phenogram (Fig. 1), but does not cluster with the genus in the distance Wagner diagram (Fig. 2) nor in classical taxonomy (Fig. 3).

AYTHYINI (Pochards and allies): *Aythya*. *Aythya affinis* (lesser scaup) and *Aythya marila* (greater scaup) were electrophoretically identical to a great degree. With small N sampled, *Aythya americana* (redhead) and *Aythya valisineria* (canvasback) differed only for allelic frequencies at the *PEP-3* locus. *Aythya collaris* (ring-necked duck) differed from the rest of AYTHYINI at the *ADA* and *PEP-3* loci. The five species of *Aythya* constitute one of the least differentiated genera studied.

MERGINI (Eiders, Scoters, Mergansers and Allies): *Somateria*, *Polysticta*, *Histrionicus*, *Clangula*, *Melanitta*, *Bucephala*, *Lophodytes*, and *Mergus*. Patton and Avise (1986) identified relationships within MERGINI and between MERGINI and AYTHYINI as potential areas of disagreement between their genetic phylogeny and classical phylogenies. Because the phylogenetic relationships suggested by our analyses of fourteen species in eight MERGINI genera are very similar to the classical phylogenies, only those of interest or which disagree are discussed.

The genetic relationships among the *Bucephala* (common goldeneye, Barrow's goldeneye, and bufflehead), *Histrionicus* (harlequin duck), *Somateria* (common eider and king eider) and two of the *Melanitta* (surf scoter and white-winged scoter) conform to accepted taxonomy. However, since *Melanitta nigra* (black scoter) and *Clangula hyemalis* (oldsquaw) are nearest relatives in the distance Wagner diagram (Fig. 2), a common ancestral divergence from the rest of the MERGINI may be indicated.

While relationships in the phenogram (Fig. 1) among *Lophodytes cucullatus* (hooded merganser), *Mergus merganser* (common merganser), and *Mergus serrator* (red-breasted merganser) are in agreement with the current generic designations, this agrees in the distance Wagner diagram (Fig. 2) if *Histrionicus histrionicus* (harlequin duck) is included.

The *Polysticta stelleri* (Steller's eider) samples, shipped from Alaska, were unfortunately permitted to warm during transit, resulting in the loss of enzyme activity from several of the more labile enzymes. As a consequence of the partial loss of enzymes, Steller's eider was not included in the cluster analyses and, in turn, not placed on the distance diagrams (Figs. 1, 2 and 4). The species was included in Table 3 because it differed from the *Somateria* (common eider and king eider) by a fixation for alternate alleles at the *ADA*, *HEM*, and *MPI-1* loci.

OXYURINI (Stiff-tailed Ducks): *Oxyura*. *Oxyura jamacensis* (ruddy duck) was determined for alleles at

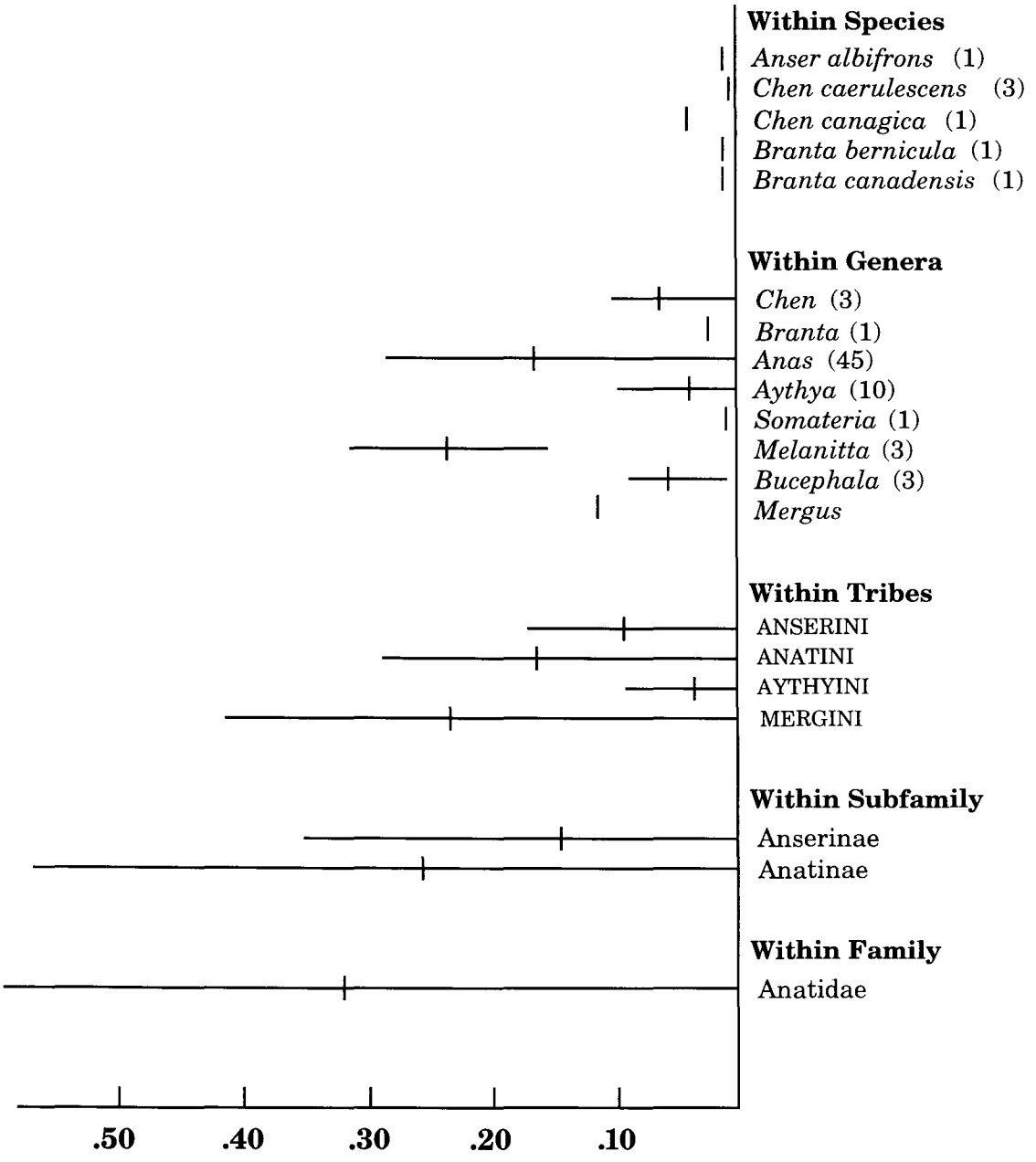

Figure 4. Means and ranges of genetic distances (Nel, 1978) at various taxonomic levels within the family Anatidae. Numbers of paired comparisons of species are given in parentheses.

the *ADA*, *AAT-1*, *NP*, *GPI* and *PGM* loci. It is observed as being the most divergent member of the Anatinae in the phenogram (Fig. 1), agreeing with classical taxonomy (Fig. 3) and the phylogenetic assignments of Johnsgard (1978) and Woolfenden (1961). Sibley and Monroe (1990) classify this tribe as the subfamily Oxyurinae, based on the DNA-DNA hybridization studies of Sibley and Ahlquist (1983, 1987, 1990). *Oxyura* joins the other members of the subfamily at a D of approximately 0.40 on the phenogram (Fig. 1). *Oxyura* shares a common root with *Dendrocygna* on the distance Wagner diagram (Fig. 2).

COMPARATIVE GENETIC DISTANCES

A summary of the means and ranges of genetic distances (D) at various taxonomic levels (Fig. 4) reveals considerable heterogeneity in interspecific genetic distances within genera (congeneric). Although genetic variation is approximately the same order of magnitude within bird species as that of other vertebrates, the degree of genetic differentiation among conspecific populations of birds is shifted to small values when compared to other vertebrates such as mammals and amphibians (Barrowclough, 1983)

DISCUSSION

Still pertinent (Bellrose, 1980) may be the early observations of Delacour and Mayr (1945) that "an over-evaluation of a few primary functional characters has led to ... confusion in the taxonomy of the Anatidae." With recent classifications attempting to reflect actual evolutionary relationships (Johnsgard, 1978; Livezey, 1986; Sibley and Ahlquist, 1982; Sibley and Monroe, 1990), the information gained in this study from the electrophoretic examination of allelic states will provide a sound basis with which to estimate phylogenetic relationships.

Comparative studies using electrophoretic data have shown that avian congeneric species are as close genetically to one another as are conspecific populations of other vertebrates (Avise et al., 1980a, 1980b, 1980c; Barrowclough and Corbin, 1978). Aquadro and Avise (1982) reported that, while the median D between species within 12 avian genera was 0.04, the same value was 0.40 for 32 non-avian genera. In this study of waterfowl, the average genetic distance between congeneric species, 0.08, supports the studies cited above (see also Patton and Avise, 1986).

Patton and Avise (1986) determined, after their analyses of the Anatidae, that close genetic similarity among members of the family was probably not due to recent divergence but rather to a deceleration in the rate of protein evolution relative to non-avian vertebrates (see also Barrowclough, 1983). Observed differences may become increasingly significant as a consequence of a decelerated rate of protein evolution.

The slowing of divergence by genetic drift, coupled with high effective population sizes, may contribute to the observation of reduced levels of avian genetic differentiation (Zink, 1986). Since geographic differentiation may be the cause of observed genetic distances which do not correlate with phenotypic similarities or differences (Barrowclough and Johnson, 1988), Avise et al. (1992) recommend that both the newer genetic and classical behavioral perspectives be considered in order to appreciate fully the geographic population structure of an avian species.

Consideration should also be given to the possibility of taxonomic over-splitting or excessive lumping (polyphyletic classification), which can often be identified by comparison of D values (Sibley and Ahlquist, 1982). Reduced values of mean D would be observed from taxonomic over-splitting, and increased values of mean D would stem from excessive lumping.

The multi-locus study of waterfowl by Patton and Avise (1986) examined electrophoretic variation at 19 loci in 26 species, with results supporting the relationships proposed by Delacour and Mayr (1945), Johnsgard (1968), and Morony et al. (1975). However, ambiguities were identified in the relationships among and between the tribes MERGINI and AYTHYINI, leading to the suggestion of further analysis. In our study, based on electrophoretic variation at 25 loci in 40 species and 5 subspecies of waterfowl, we find that the genetic relationships among North American waterfowl agree, for the most part, with classical phylogenies (Johnsgard 1978) and taxonomic relationships (AOU, 1957, 1983, 1985, 1987, 1989, 1991) previously proposed.

The particular agreement of the phenogram (Fig. 1) to the classical phylogeny (Fig. 3) may reflect the phenetic nature of previous interpretations. In previous taxonomic studies, Brush (1976), Delacour and Mayr (1945), and Johnsgard (1961) based their conclusions upon observed character state similarities, interpreting their data empirically. Close concordance observed in the diverse approaches is not completely surprising. With waterfowl being subject to several recent classical taxonomic studies, relationships within the Anatidae will become more firmly established as the information base increases.

While the phenogram is observed to agree with classical phylogeny, it exhibits the greatest similarity at the subfamily and tribal levels. The distance Wagner clustering, however, exhibits greater similarity to the classical phylogeny at the species and generic levels. Meeting both criteria is the observed divergence of *Chen canagica* (emperor goose) from other members of the genus *Chen*. *Chen canagica* has been placed in three different genera: *Philacte* (AOU, 1957), *Anser* (Delacour and Mayr, 1945; Sibley and Monroe, 1990), and *Chen* (AOU, 1983). The results of our study do not support the placement of *Chen canagica* in either *Anser* or *Chen*.

Genetic differences were found among the emperor geese examined. The specimens were collected from Izembeck Lagoon, a region on the northern side of the Alaska peninsula, which serves as a staging area for emperor geese migrating north to nest. Emperor geese nest in only two areas of the world: northwestern Alaska and eastern Siberia. Those staging on the Alaska peninsula may represent a mixture of geese bound for both nesting areas (Eisenhauer and Kirkpatrick, 1978). Since our data indicate that two discrete breeding groups exist which are more divergent than many waterfowl species, the study of additional emperor geese is warranted.

A major discrepancy common to both branching diagrams is the inconsistent placement of *Clangula hyemalis* (oldsquaw) and *Melanitta nigra* (black sco-

ter). In the phenogram (Fig. 1), *Clangula hyemalis* does not cluster with the MERGINI and *Melanitta nigra* does not cluster with the other *Melanitta* species. They jointly form a divergent MERGINI branch in the distance Wagner diagram (Fig. 2). Johnsgard (1978) suspected a close affinity of the two species, and based these suspicions on comparisons of structure and behavior.

Considerable controversy exists as to the "best" method of deriving phylogenies from electrophoretic data. Although the phenogram and distance Wagner diagram are not entirely concordant, other branching diagrams may have been developed which might provide an even better fit to the existing data.

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