LITERATURE CITED

BENT, A. C. 1968. Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237. Washington, D.C.

CASE, R. M., & R. J. ROBEL. 1974. Bioenergetics of the bobwhite. J. Wildl. Manage. 38: 638–652.

KENDEIGH, S. C. 1949. Effect of temperature and season on the energy resources of the English Sparrow. Auk 66: 113–127.

———, & G. C. WEST. 1965. Caloric values of plant seeds eaten by birds. Ecology 46: 553–555.

MARTIN, A. C., H. S. ZIM, & A. L. NELSON. 1951. American wildlife and plants. New York, McGraw Hill.

SHUMAN, T. W. 1984. Energetic responses of avian granivores to winter in northeast Kansas. M.S. thesis, Manhattan, Kansas State Univ.

———, R. J. ROBEL, A. D. DAYTON, & J. L. ZIMMERMAN. 1988. Apparent metabolizable energy content of foods used by Mourning Doves. J. Wildl. Manage. 52: 481–483.

SNEDECOR, G. W., & W. G. COCHRAN. 1980. Statistical methods. Ames, Iowa State Univ. Press.

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Evolutionary Genetics of Phalaropes

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The three species of phalaropes—Wilson's (*Phalaropus tricolor*), Red-necked (*P. lobatus*), and Red (*P. fulicaria*)—have long been considered a natural group (Cramp 1983), often equated with monophyly; and they have been classified at the familial, subfamilial, or tribal rank. An early diagnosis (Ridgway 1919) of the group read "Toes with a conspicuous lateral membrane, sometimes developed into broad scalloped lobes; tarsus excessively compressed; plumage of under parts very dense, gull-like." Several other characteristics, such as the distinctive whirling foraging behavior (Hayman et al. 1986), pronounced reversed sexual dimorphism in plumage coloration, and the lobed toes (and basal webbing) are characteristics often cited as support for naturalness (monophyly) of the group (Cramp 1983). It is unclear which of these traits qualify as synapomorphies (i.e. uniquely derived for phalaropes). For example, although each species possesses webbing on the toes, each has a distinctive pattern (illustrated in Coues [1927]). The distinctive whirling foraging behavior also differs in detail among species (Cramp 1983). Strauch (1978) analyzed 70 skeletal characters and found only one synapomorphy, namely a particular condition of the bill, which is apparently identical in each species of phalarope. Thus, the monophyly of the phalaropes, although widely assumed, is not based on many traits that are shared by all species. The question of phalarope monophyly aside, based on plumage pattern, behavioral and vocal similarities, distribution, and habitat, most authors consider the Red and Red-necked phalaropes to be sister taxa and the Wilson's most primitive (Cramp 1983, Jehl 1968). For example, although each phalarope species was once placed in a monotypic genus (e.g. Ridgway 1919, Hellmayr and Conover 1948), the Wilson's Phalarope was retained in a monotypic genus long after the other two were made congeneric.

We used horizontal starch-gel protein electrophoresis to investigate the pattern of genetic relationships among the three species of phalaropes. We sought to test the monophyly and hypothesized relationships of the group. In addition, relatively few nonpasserine taxa have been studied electrophoretically, and it has been suggested that they should be genetically differentiated to a greater degree than passerines, owing to the presumed greater age of nonpasserine taxa (Zink in press). Our data document the level of genetic distinctiveness of phalaropes (nonpasserines) relative to other avian taxa.

Sample sizes and collecting sites of phalaropes are listed in Table 1. The following taxa, represented by one individual each (collected in Louisiana), were used as outgroups: Long-billed Dowitcher (*Limnodromus scolopaceus*), Greater Yellowlegs (*Tringa melanoleuca*), Red Knot (*Calidris canutus*), Sanderling (*C. alba*), Stilt Sandpiper (*C. himantopus*), and California Gull (*Larus californicus*; collected in California); exact locality data for specimens are available from the authors. Nomenclature follows the A.O.U. Check-list (American Ornithologists' Union 1983). Voucher specimens are housed in the Museum of Natural Science (LSUMNS), Louisiana State University, Baton Rouge, Louisiana 70803. From each individual, samples of pectoral and heart muscle and liver were pooled, minced with a razor blade, combined with 2 ml of deionized water and centrifuged at 35,000 × *g* for 20 min at 4°C. These aqueous tissue extracts were frozen at −70°C until used for electrophoresis. Meth-

TABLE 1. Sample sizes, collecting localities, and genetic variation.

Taxon	Specimen locality (*n*)	Heterozygosity (±SE)	Polymorphic loci (%)	No. alleles/locus (±SE)
P. lobatus	California: Salton Sea (8) Louisiana: Cameron (1)	0.015 ± 0.008	11.1	1.1 ± 0.1
P. fulicaria	North Carolina: off Oregon Inlet (7)	0.066 ± 0.025	22.2	1.3 ± 0.1
P. tricolor	Louisiana: Cameron (3) Louisiana: Johnsons Bayou (1)	0.007 ± 0.007	2.8	1.0 ± 0.0

TABLE 2. Distribution (and frequencies) of alleles in phalaropes and allies. A single letter implies that the allele was fixed at 1.0 in our sample.

Locus[b] (EC no.)	Taxon[a]								
	P. l.	*P. f.*	*P. t.*	*L. s.*	*T. m.*	*C. c.*	*C. h.*	*C. a.*	*L. c.*
ICD-1 (1.1.1.42)	A (0.778) B (0.222)	A	A	A	A	C	A	A	D
MDH-2 (1.1.1.37)	A	A	B	B	C	B	A	A	D
LDH-1 (1.1.1.27)	A	A	B	C	A	D	A	A	E
PGM-1 (2.7.5.1)	A	A	B	F	G	C (0.500) E (0.500)	C	D (0.500) I (0.500)	H
PGM-2 (2.7.5.1)	A	A	A (0.875) B (0.125)	A	C	B	B	B (0.500) D (0.500)	A
ACON (4.2.1.3)	A	A	A	A	A	A	A	A	B
ME-1 (1.1.1.40)	A	G (0.786) J (0.214)	B	E	F	H	C	I	D
LA (3.4.11)	A (0.944) B (0.056)	A (0.858) B (0.071) J (0.071)	G	I	C (0.500) D (0.500)	H	C	C	E
LGG (3.4.11)	A	A	A	E	F	B	C	B	D
PPRO (3.4.13.9)	A	B	C	E	F	D	I	H	G
NP (2.4.2.1)	A	B	C	D	E	F	G	H	I
SDH (1.1.1.14)	A	A	B	D	A	A	A	A	C
ADA (3.5.4.4)	A	A (0.286) B (0.643) C (0.071)	A	D	A	C	A	A	F
GPT (2.6.1.2)	A	A	A	A	A	A	A	A	B
GPI (5.3.1.9)	A	A (0.929) B (0.071)	A	C (0.500) D (0.500)	D	D	D	D	E
αGPD (1.1.1.8)	A	A	B	A	A	A	A	A	C
CK (2.7.3.2)	A	A	A	B	A	A	A	A	C
AK-1 (2.7.4.3)	A	A	A	A	A	A	A	C	B
AK-2 (2.7.4.3)	A	A	B	A	A	B	A	A	C
6-PGD (1.1.1.44)	A (0.944) B (0.056)	A (0.857) B (0.143)	C	A	A	D	A	A	E
MPI (5.3.1.8)	A	A (0.833) B (0.167)	A	C	A	A	A	A	D
GDA (3.5.4.3)	A	A	B	A	A	A	A	A	A
GOT-1 (2.6.1.1)	A	A	A	A	A	A	A	A	B
ADH-2 (1.1.1.1)	A	A (0.786) B (0.214)	A	A	A	A	A	C	C
GSR (1.6.4.2)	A (0.944) B (0.056)	A	A	A	A	A	C	A	A
FUM (4.2.1.2)	A	A (0.833) B (0.167)	A	A	A	A	A	A	C

[a] Taxa were represented by the following abbreviations: *Phalaropus lobatus* (*P. l.*); *P. fulicaria* (*P. f.*); *P. tricolor* (*P. t.*); *Limnodromus scolopaceus* (*L. s.*); *Tringa melanoleuca* (*T. m.*); *Calidris canutus* (*C. c.*); *C. himantopus* (*C. h.*); *C. alba* (*C. a.*); and *Larus californicus* (*L. c.*).

[b] The following loci were monomorphic and fixed for the same allele in all taxa: ICD-2 (EC 1.1.1.42), MDH-1 (1.1.1.37), LAP (3.4.13.1), EST-D (3.1.1.1), GDH (1.4.1.3), GOT-2 (2.6.1.1), ADH-1 (1.1.1.1), EAP (no EC = methylumbelliferyl phosphatase), DIA (1.6.*.*), and GAPDH (1.2.1.12).

TABLE 3. Nei (1978) unbiased genetic distances (below diagonal), Rogers' (1972) genetic distances (above diagonal).

Taxon	1	2	3	4	5	6	7	8	9
1. *P. lobatus*	—	0.129	0.343	0.366	0.255	0.383	0.256	0.279	0.636
2. *P. fulicaria*	0.101	—	0.367	0.361	0.279	0.389	0.283	0.295	0.622
3. *P. tricolor*	0.409	0.427	—	0.444	0.411	0.409	0.441	0.462	0.670
4. *L. scolopaceus*	0.439	0.419	0.576	—	0.371	0.427	0.403	0.423	0.635
5. *T. melanoleuca*	0.276	0.289	0.521	0.442	—	0.354	0.236	0.256	0.663
6. *C. canutus*	0.471	0.463	0.515	0.535	0.420	—	0.347	0.367	0.663
7. *M. himantopus*	0.288	0.303	0.578	0.501	0.255	0.412	—	0.232	0.694
8. *C. alba*	0.300	0.306	0.604	0.520	0.264	0.427	0.241	—	0.631
9. *L. californicus*	1.013	0.981	1.106	1.004	1.085	1.085	1.186	0.990	—

ods for horizontal starch-gel protein electrophoresis followed standard protocols (Selander et al. 1971, Johnson et al. 1984, Zink 1986). We refer to electromorphs (bands on stained gels) as alleles; we assume electromorphs are under genetic control. Alleles were coded by their mobility from the origin, the most anodal allele was coded as "A." Isozymes were coded in the same fashion, with a "1" indicating the most anodally migrating form (e.g. Mdh-1). We used the computer program BIOSYS-1 (Swofford and Selander 1981) to compute heterozygosity, percentage of loci polymorphic, number of alleles per locus, Nei's (1978) and Rogers' (1972) genetic distances, a UPGMA phenogram, and a distance Wagner tree (rooted at the California Gull) produced using the multiple-addition criterion of Swofford (1981). The computer program PHYLIP (Felsenstein 1986) was used to construct two trees from Rogers' (1972) genetic distances, one that assumes a constant rate of evolution ("KITSCH") and one that does not ("FITCH"). The computer program GENESYS written by K. W. Corbin was used to produce 100 bootstrapped samples of loci (see Felsenstein 1985) and from each sample to compute Rogers' genetic distances and a distance Wagner network. A consensus distance Wagner network was derived from the 100 individual networks (the gull was excluded from this analysis). Several cladistic analyses have been proposed for electromorphs (see Buth 1984); the major problem is that one lacks information on ordering alleles in a transformation series. One could code each allele as a distinct state and score each taxon for the presence/absence of that allele. Alternatively, the locus can be considered the character and the electromorphs as unordered character states. Each method has drawbacks (Buth 1984, Swofford and Berlocher 1987). For example, information on allelic frequencies is ignored. We used a method of binary coding that is intermediate between these approaches. Our method takes advantage of the series of five taxa we presume to be outgroups to the phalaropes (the ingroup). Because the California Gull is so distant from the other taxa, we did not use it as an outgroup for rooting trees in the cladistic analysis of electromorphs. If an allele was present in a majority of the five outgroups, it was considered ancestral (an assumption, not fact). For instance, if a locus had alleles A, B, and C, and we deemed A ancestral, then the coding of the alleles was A (00), B (10), and C (01). Note that this places B and C each one step from A, and B and C two steps from each other—this is an assumption about the ordering of character states (e.g. C ← A → B) that could well be incorrect. Alternatively, if the ancestral state is unknown, the same three alleles would be coded as A (100), B (010), and C (001). This is the same as coding by alleles, and each state is equidistant from the others. Polymorphisms are coded to reflect the occurrence of alleles. Thus, our coding is intermediate between coding by locus and alleles. The difference is that for some loci we postulated an ancestral condition (owing in part to our use of five outgroups). We encourage considerable caution in employing such a coding scheme because of the large number of assumptions; also, a large and diverse array of outgroups seems necessary. The resulting binary character × taxon matrix was used as input into PHYLIP, and the following programs were used: bootstrapping across characters, taking into account the number of binary characters derived for each locus (BOOTM), and branch and bound program to find all most parsimonious trees (PENNY). Ancestral states were indicated for each character as either 0 (primitive) or ? (ancestor unknown).

Levels and patterns of genetic variation at 36 loci were resolved (Tables 1, 2). The heterozygosity for our sample of Red Phalaropes, 0.066, is similar to that observed for other birds (Corbin 1987). Heterozygosity values for Red-necked (0.015) and Wilson's (0.007) phalaropes are lower than those observed for most, but not all, other birds (Corbin 1983), which is consistent with surveys of other shorebirds (Baker and Strauch in press). Values for percentage loci polymorphic and number of alleles follow the same pattern. Although not given because of small sample sizes, measures of genetic variation for the outgroup samples were consistent with values observed for other shorebirds.

The most similar pair of taxa was the Red-necked and Red phalaropes, Nei's $D = 0.101$ (Table 3). This

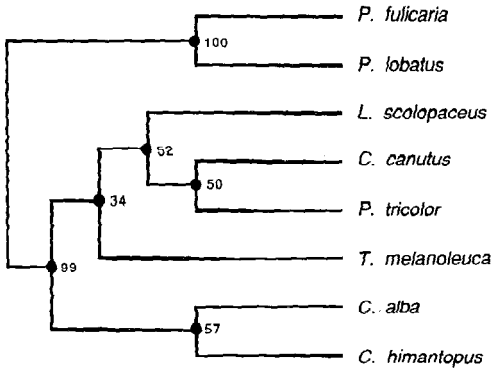

Fig. 1. Bootstrapped (100 replicates) tree across binary characters (Table 4) derived from the matrix of allelic distributions. Numbers at nodes refer to the number of times that node occurred in the 100 replicates.

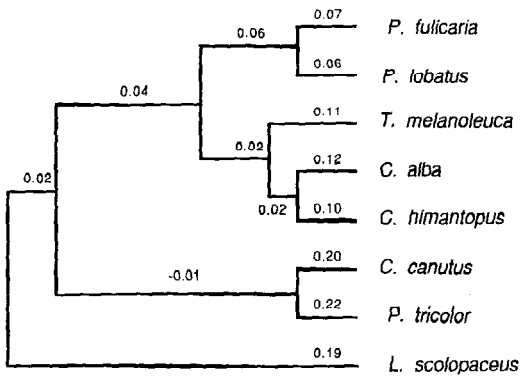

Fig. 2. Distance-Wagner tree based on Rogers' (1972) genetic distances. Although not figured, the tree was rooted at the California Gull. The %SD = 4.77.

value is consistent with that observed among many nonpasserine congeneric taxa (Gerwin and Zink in press), and only slightly higher than the comparable value for passerines (Johnson and Zink 1983). The high level of differentiation is apparent among the other taxa. Wilson's Phalarope is well-differentiated from the other phalaropes (D = 0.409 and 0.427, respectively), more so than nearly all avian congeners are from one another (Avise and Aquadro 1982, Johnson et al. 1988). Other genetic distance values in our survey are similar to those observed between members of different avian subfamilies (Gutiérrez et al. 1983, Lanyon 1987). If we apply the calibration of genetic distance suggested by Gutiérrez et al. (1983), the Wilson's Phalarope has been evolving independently for ca. 11 million years, whereas Red and Red-necked phalaropes evolved from a common ancestor ca. 3 million years ago. These dates are only rough approximations because of the large errors associated with estimating genetic distances (Nei 1978) and the calibration process itself (Gutiérrez et al. 1983).

Several points can be derived from the pattern of allelic (character) distributions (Table 2). The Wilson's Phalarope differs from the other phalaropes at 12 loci. This includes an apparent case of a fixed null allele at GDA (coded as a unique allele in Table 2). The Red-necked and Red phalaropes appear to be fixed for different alleles at three loci and have frequency differences at eight others. Although the phalaropes share alleles with various combinations of outgroups, these patterns should be interpreted with caution because not all possible relatives of phalaropes were included in the survey. For example, Wilson's Phalarope shares an apparently derived allele with the Red Knot at AK. Based on the pattern of allelic distribution, the monophyly of the phalaropes is supported by only two loci (LGG, GPI).

Analyses of the binary matrix of electromorphs (Table 4) do not support the monophyly of the phalaropes. For example, the bootstrapped consensus tree (Fig. 1) reveals only two nodes at a frequency of 95% or greater, which implies that confidence in the tree is unwarranted (Felsenstein 1985). The one stable node of interest that unites *P. lobatus* and *P. fulicaria* was present in 100% of the bootstrapped replicates. The remainder of the relationships are not well-supported, except one, namely the lack of phalarope monophyly. The branch and bound algorithm considered a total of 24,000 trees, and found 14 to be equally parsimonious (not shown, available from Zink). None of these indicated phalarope monophyly.

The distance Wagner tree (Fig. 2) is consistent with the trees discussed above. A consensus distance Wagner tree based on 100 bootstrapped samples of loci did not alter the conclusions derived from Fig. 2. Differences between Figs. 1 and 2 are in regions for which we have little confidence.

Although the Red and Red-necked phalaropes are sister taxa, none of the branching diagrams supports the monophyly of the phalaropes. If the phalaropes are monophyletic, which is supported by morphological evidence (Strauch 1978) and two loci (Table 2), then Wilson's Phalarope might have had an accelerated rate of genetic evolution as evidenced by the high number of allozymic autapomorphies. However, a relative rate test (Beverley and Wilson 1984) showed the genetic distance from the California Gull to each phalarope to be the same, which implies a constant rate of genetic evolution within each taxon. The techniques for clustering distance matrices that assume constancy of rates (UPGMA, KITSCH) do not portray the phalaropes as monophyletic (dendrograms available from Zink upon request). It is possible that the gull is too distant an outgroup, which might obscure rate differences. The distances from Wilson's Phalarope to other members of the "ingroup," some

TABLE 4. Binary characters derived from 20 phylogenetically informative loci (the following were not used: ACON, ME-1, PPRO, NP, GPT, GOT-1, monomorphic loci). The "A" row refers to the hypothesized ancestral states, the "F" row reveals by switching from "a" to "b" how many binary characters come from each locus.

Taxon[1]	Character
A	00????????????????0000????????????????00000000000000000000000000
F	aabbbaaaabbbbbbbbaaaabbbbbbbbaaaaabbaaaaabbbababaaabbabbaab
1	10100100010000000000000000011010000000000010000100000010100
2	00100100010000000000000000011101000000110001100001001011001
3	00010010001000000100000001000100010000000011001010001100000
4	00010001000100000000000100000000101000011000100000010100000
5	00001100000010000000111000000000100000000000000000000010000
6	01010000100001100110000100000100000000110000000100100010000
7	00100100000001000110010000000001000000000000000000000010010
8	00100100000000011111010000000100000000000000001000000000000

[1] Codes for taxa: 1 = *P. lobatus*, 2 = *P. fulicaria*, 3 = *P. tricolor*, 4 = *L. scolopaceus*, 5 = *T. melanoleuca*, 6 = *C. canutus*, 7 = *Calidris himantopus*, 8 = *Calidris alba*.

of which might be considered as valid outgroups, were similar, which also implies rate constancy.

If the phalaropes are monophyletic, then the low number (two) of supporting synapomorphies suggests that the group was not in existence for long (i.e. the time required for two fixed differences to evolve) before the Wilson's Phalarope lineage diverged. This "shape" of evolutionary history, one with short-lived lineages in the distant past, is difficult or impossible to recover by analyses of any type of molecular character that shows clocklike behavior (Fiala and Sokal 1985, Lanyon 1988). That is, any character with a rate of change sufficiently rapid to evolve to a synapomorphous state on an ancient but short-lived branch will subsequently change to autapomorphic states in descendant lineages, and erase evidence of monophyly. Slowly evolving characters will not change on average during any short-lived lineage. In addition, homoplasy, which is almost certainly present in our data set, will further confound phylogenetic inference.

Our data establish clearly the genetic distinctness of Wilson's Phalarope from other phalaropes. We conclude that either Wilson's Phalarope diverged shortly after the origin of the phalarope clade or the group is not monophyletic. The hypothesis that the phalaropes are not monophyletic is intriguing. As noted above, there are few traits that qualify as synapomorphies for the phalaropes. For instance, features such as reversed sexual plumage dimorphism and polyandry are not uniquely derived within phalaropes. If the phalaropes are polyphyletic, then Wilson's Phalarope exhibits convergent evolution in a number of attributes. The many features that set the Wilson's Phalarope apart from the other two species might indicate that it is not a part of a monophyletic phalarope group. We submit that this hypothesis should be tested by analysis of independent data sets.

Because of short branch lengths linking the various outgroups included in our survey, we interpret these patterns cautiously. Our genetic distance data suggest that the calidrine (Sanderling and Stilt Sandpiper) and tringine (Greater Yellowlegs) shorebirds are more similar to each other than either is to limnodromines (Long-billed Dowitcher) or phalaropodines; the position of the Red Knot is uncertain. Jehl (1968) suggested that the phalaropes were aligned with the tringine sandpipers, whereas Lowe (1931) suggested that the phalaropes were closer to the scolopacines than any other shorebird group. Our data are consistent with Lowe's suggestion. Within the calidrines we do not have confidence of patterns of genetic relatedness. We suspect a broader allozymic survey would yield phylogenetically informative results at the level of the subfamilies (see Baker et al. 1985, Baker and Strauch in press).

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LITERATURE CITED

AMERICAN ORNITHOLOGISTS' UNION. 1983. Check-list of North American birds, 6th ed. Washington, D.C., Am. Ornithol. Union.

AVISE, J. C., & C. F. AQUADRO. 1982. A comparative summary of genetic distances in the vertebrates: patterns and correlations. Evol. Biol. 15: 151–185.

BAKER, A. J., A. LYNCH, & C. EDWARDS. 1985. Bio-

chemical genetic studies of shorebirds: methods and applications. Wader Study Group Bull. 44: 34-39.

———, & J. G. STRAUCH JR. In press. Genetic variation and differentiation in shorebirds. *In* Proc. 19th Int. Ornithol. Congr.

BEVERLEY, S. M., & A. C. WILSON. 1984. Molecular evolution in *Drosophila* and the higher Diptera: II. A time scale for fly evolution. J. Mol. Evol. 21: 1-13.

BUTH, D. G. 1984. The application of electrophoretic data in systematic studies. Annu. Rev. Ecol. Syst. 15: 501-522.

COUES, E. 1927. Key to North American birds, 6th ed. Boston, C. H. Simonds Co.

CORBIN, K. W. 1983. Genetic structure and avian systematics. Pp. 211-244 *in* Current ornithology, vol. 1 (R. F. Johnston, Ed.). New York, Plenum Press.

———. 1987. Geographic variation and speciation. Pp. 321-354 *in* Avian genetics (F. Cooke and P. A. Buckley, Eds.). London, Plenum Press.

CRAMP, S. (Chief Ed.) 1983. Handbook of the birds of Europe, the Middle East and North Africa. The birds of the Western Palearctic, vol. 3, Waders to gulls. Oxford Press, New York.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39: 783-791.

———. 1986. PHYLIP—Phylogeny inference package (version 3.0). Seattle, Univ. Washington, Dep. Genetics.

FIALA, K. L., & R. R. SOKAL. 1985. Factors determining the accuracy of cladogram estimation: evaluation using computer simulation. Evolution 39: 609-622.

GERWIN, J. A., & R. M. ZINK. In press. Phylogenetic patterns in the genus *Heliodoxa* (Aves: Trochilidae): an allozymic perspective. Wilson Bull.

GUTIÉRREZ, R. J., R. M. ZINK, & S. Y. YANG. 1983. Genic variation, systematic, and biogeographic relationships of some galliform birds. Auk 100: 33-47.

HAYMAN, P., J. MARCHANT, & T. PRATER. 1986. Shorebirds. An identification guide. Boston, Houghton Mifflin Co.

HELLMAYR, C. E., & B. CONOVER. 1948. Catalogue of birds of the Americas. Chicago, Zool. Ser. Field Mus. Nat. Hist., vol. 13, part 1, No. 3.

JEHL, J. R. 1968. Relationships in the Charadrii (Shorebirds): a taxonomic study based on color patterns of the downy young. San Diego Soc. Nat. Hist. Memoir 3.

JOHNSON, N. K., & R. M. ZINK. 1983. Speciation in sapsuckers (*Sphyrapicus*): I. Genetic differentiation. Auk 100: 871-884.

———, ———, G. F. BARROWCLOUGH, & J. A. MARTEN. 1984. Suggested techniques for avian systematics. Wilson Bull. 96: 543-560.

———, ———, & J. A. MARTEN. 1988. Genetic evidence for relationships in the avian family Vireonidae. Condor 90: 444-461.

LANYON, S. M. 1988. The stochastic mode of molecular evolution: what consequences for systematic investigations. Auk 105: 565-573.

———, & R. M. ZINK. 1987. Genetic variation in piciform birds: monophyly and genetic and familial relationships. Auk 104: 724-732.

LOWE, P. R. 1931. On the relation of the Gruimorphae to the Charadriimorphae and Rallimorphae with special reference to the taxonomic position of Rostratulidae, Jacanidae, and Burhinidae (Oedicnemidae); with a suggested new order (Telmatomorphae). Ibis 13: 491-534.

NEI, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

RIDGWAY, R. 1919. The birds of North and Middle America, vol. 8. Washington, D.C., U.S. Government Printing Office.

ROGERS, J. S. 1972. Measures of genetic similarity and genetic distance. Stud. Genet. VII. Univ. Texas Publ. 7213: 145-153.

SELANDER, R. K., M. H. SMITH, S. Y. YANG, W. E. JOHNSON, & J. B. GENTRY. 1971. Biochemical polymorphism and systematics in the genus *Peromyscus*: I. Variation in the old-field mouse (*Peromyscus polionotus*). Univ. Texas Publ. 7103: 49-90.

STRAUCH, J. G. 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatability analysis. Trans. Zool. Soc. London 34: 263-345.

SWOFFORD, D. L. 1981. On the utility of the distance Wagner procedure. Pp. 25-43 *in* Advances in cladistics. Proc. 1st Meeting Willi Hennig Soc. (V. A. Funk and D. A. Brooks, Eds.). New York, New York Bot. Gardens.

———, & S. H. BERLOCHER. 1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. Syst. Zool. 36: 293-325.

———, & R. B. SELANDER. 1981. BIOSYS-1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. 72: 281-283.

ZINK, R. M. 1986. Patterns and evolutionary significance of geographic variation in the Schistacea group of the Fox Sparrow (*Passerella iliaca*). Ornithol. Monographs No. 40. Washington, D.C., Am. Ornithol. Union.

———. In press. Summary to symposium, the genetic structure of avian populations. Proc. 19th Int. Ornithol. Cong.

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