# INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

**The quality of this reproduction is dependent upon the quality of the copy submitted.** Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

U·M·I

University Microfilms International
A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor, MI 48106-1346 USA
313/761-4700 800/521-0600

Order Number 9207068

# Phylogenetic relationships of *Geothlypis* (Aves:Parulinae)

Escalante-Pliego, Bertha Patricia, Ph.D.

City University of New York, 1991

U·M·I
300 N. Zeeb Rd.
Ann Arbor, MI 48106

A

# PHYLOGENETIC RELATIONSHIPS OF GEOTHLYPIS (AVES: PARULINAE)

by

Bertha Patricia Escalante-Pliego

A Dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

1991

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

30 September 1991
date

Chairman of Examining Committee
Dr. Francois Vuilleumier
American Museum of Natural History

1 October 1991
date

Executive Officer
Dr. Peter C. Chabora

Dr. Robert Rockwell, City College

Dr. Leslie Marcus, Queens College

Dr. George F. Barrowclough, American Museum of Natural History

Dr. Robert S. Voss, American Museum of Natural History

Supervisory Committee

The City University of New York

## Abstract

PHYLOGENETIC RELATIONSHIPS OF *GEOTHLYPIS* (AVES: PARULINAE)

by

Bertha Patricia Escalante-Pliego

Adviser: Dr. François Vuilleumier

The genealogical history of 12 nominal taxa of Yellowthroats (Parulinae: *Geothlypis*; warblers) was reconstructed using allozyme variation at the population and species levels. Estimates of genetic population structure ($F_{st}$, tests of heterogeneity, genetic distances) were compared across species and used to evaluate species limits. Populations of the northern species (*G. trichas*) were little differentiated; populations of species in Mexico (*G. beldingi*) and Middle America (*G. poliocephala*) were more differentiated; and populations of the widespread South American species (*G. aequinoctialis*) were more differentiated still. The amount and degree of genetic distinctness in the South American forms suggests the existence of four species in what has been considered a single species until now.

Because sound evidence for paruline relationships (or for the sister taxon of *Geothlypis*) is lacking, several outgroups were included to reconstruct phylogenetic relationships. Comparisons of allele frequencies across taxa showed a large amount of genetic variability shared across species and genera of parulines and thraupines sampled in this study. This pattern of variability suggests that ancestral polymorphism in allozymes is pervasive and represents an important difficulty in phylogenetic reconstruction. Several methods of analyses

were employed. Distance methods (UPGMA, Fitch-Margoliash, and distance Wagner) gave different solutions compared to the other parsimony methods, perhaps due to the inclusion of several taxa with isolated ranges (marsh specialists) that could have evolved at different rates. Frequency and Wagner parsimony (alleles as characters) also gave different arrangements. Maximum likelihood and polymorphism parsimony gave very similar arrangements. These two methods use assumptions that seem to correspond better with the evolution of allozymes in lineages. The product phylogeny obtained with these two methods agrees well with variation in plumage characters, and represents the best estimate provided by the available data. According to this phylogeny Geothlypis and Oporornis together form a monophyletic taxon, but neither genus as currently recognized does by itself. The biogeographic scenario implied by this phylogeny suggests the occurrence of a population bottleneck when the common ancestor of Masked Yellowthroats dispersed from South America across the Panama Isthmus to Central and North America, followed by rapid speciation afterwards.

# A C K N O W L E D G M E N T S

My sincere appreciation goes to the members of my doctoral committee for their advice, guidance and support throughout this project. I thank François Vuilleumier for accepting me as his student and for making my stay in New York possible. His advice, encouragement and moral support were at all times very important to me. I am grateful to George F. Barrowclough who spent much time discussing concepts and correct manuscripts, and to Robert F. Rockwell, better known as Rocky, for his guidance to help me clarify my research objectives. Leslie F. Marcus was very generous and patient in guiding me in the jungle of the computer world. I benefited greatly from his expertise in data analysis. I thank Robert S. Voss for his invaluable help in discussing principles of phylogenetic analysis and biogeography, and for contributing his scientific rigor and constructive criticisms.

I extend my deep appreciation to CONACyT (Consejo Nacional de Ciencia y Tecnología) of México for financial assistance. The Frank M. Chapman Memorial Fund of the American Museum of Natural History provided additional financial support that made my studies possible through the doctoral training program of the American Museum of Natural History.

Further financial assistance for this project was received from the Frank M. Chapman Memorial Fund Committee of the Department of Ornithology of the American Museum of Natural History, the Graduate Studies Committee of the Ecology and Evolutionary Biology Program of the City University of New York, the Alexander Wetmore Fund of the American Ornithologists' Union, the Society of Sigma Xi Society, and the Association of Field Ornithologists (Alexander Bergstrom grant).

Emergency financial assistance was very generously given by the late Sadie Coats.

I thank Robert W. Dickerman for having suggested to me that I study Yellowthroats in Mexico, and for having participated in a field trip to localities where he had found Yellowthroats in the marshes of the Central Plateau of Mexico. For excellent companionship in the field, I am grateful to Miriam Torres, Roberto Chavira, Alejandro Said, Ambrosio Ramírez, Fernando Villaseñor, Carlos Escalante, Ernesto Díaz, Javier Salgado, Gabriela Ibañez, Laura Rivera, David Padilla, and Judith Vega, all of whom helped me collect and prepare birds in Mexico, and bore with me the difficulties of working in the marsh environment. Miguel Lentino found time to undertake with me the search for "Mascaritas" in Venezuela, and Carlos Bosque gave excellent advice about localities. Jose Luis Jimenez made our collecting more effective. Hesiquio Benítez accompanied me to Costa Rica to help collect yellowthroats, and we looked for Acorn Woodpeckers too, for his thesis. Ana Isabel Pereyra, Gilbert Barrantes, and Ingrid Ayub lead us to localities where we could collect "tapaojitos". Ingrid Ayub's hospitality made the search much more enjoyable and affordable. Blanca Hernández Baños assisted me in Florida and the Bahamas. I consider our trip to Abaco a complete adventure. Our journey in the mail boat from Nassau to Abaco was a very exciting and shaking experience. Two families, the Sweetings of Marsh Harbour, and the Ketchams later on, generously gave us directions, advice, shelter and food. John Mulligan Ketcham's hospitality was especially enjoyable. Scott Baker (with his truck) was a great friend to have in Orlando. He, Blanca, and I spent two days collecting yellowthroats in the sunny fields of central Florida.

To the authorities and officials who helped me to obtain collecting permits I extend my sincere acknowledgements. Graciela de la Garza, Jose María Reyes and Luis Gerardo López Lemus of the Secretaría de Desarrollo Urbano y Ecología (SEDUE) in Mexico City attentively responded to my requests. The Ministerio de Recursos Naturales, Energía y Minas, and the Museo de Historia Natural, Costa Rica; the Museo de la Universidad Central de Venezuela; the State of Florida Game and Fresh Water Fish Commission; the US Fish and Wildlife Service; and the Department of Agriculture of the Bahamas, all granted me permission to collect birds. This help is greatly appreciated.

Jay Pitocchelli, Robert M. Zink, and Scott Lanyon provided me with important tissue samples, particularly for outgroup comparisons. I am grateful to the many curators who allowed me to examine and measure specimens in the collections under their care: Richard L. Zusi (National Museum of Natural History), Frank B. Gill (Academy of Natural Sciences, Philadelphia), Raymond A. Paynter, Jr, (Museum of Comparative Zoology), Scott Lanyon and David Willard (Field Museum of Natural History), Robert W. Storer and Robert B. Payne (Museum of Zoology of the University of Michigan), John Haffner (Occidental College), Kimball L. Garrett (Los Angeles County Museum of Natural History), Lloyd F. Kiff (Western Foundation of Vertebrate Zoology), and James R. Northern (University of California at Los Angeles). I thank the authorities of the following museums, who made loans of specimens: Los Angeles County Museum of Natural History; Museum of Natural History, University of Kansas; Museum of Zoology, Louisiana State University; Museum of Zoology, University of Michigan; San Diego Natural History Museum; Peabody Museum of Natural History; Michigan State University; Museum of Vertebrate Zoology, University of California at Berkeley; Carnegie Museum of Natural

History; Royal Ontario Museum; Delaware Museum of Natural History; University of Oklahoma; University of Arizona; Florida State University; Cornell University; Field Museum of Natural History; and National Museum of Natural History.

I cannot miss the opportunity to thank many friends, students, and colleagues for numerous discussions, among them Bonnie Bain, Parker Cane, Angelo Capparella, Linda S. Ford, Rosemarie Gnam, Carole Griffiths, Nedra Klein, Gavin Naylor, Roderick Page, Town Peterson, Jay Pitocchelli, Rick Prum, and Jeff Woodbury. Special thanks go to Charles W. Myers for his moral support, and to the Department of Herpetology of the American Museum of Natural History for use of computer facilities and software programs.

Friends and colleagues from the Museo de Zoología de la Facultad de Ciencias de la Universidad Nacional Autónoma de México always gave me long distance moral support. That was a good thing to remember, especially during the long hours spent in the lab or at the computer. In particular I would like to thank Jorge Llorente and Adolfo Navarro for their persistence and dedication to carry out research in systematics in México.

It would not be fair to omit my family in this section. In all possible ways their love and assistance were crucial for the completion of this dissertation. They are my mother, Berthita, my father, Carlos, my sisters Rosita and Mary, my brother Carlos, and their children, Tania, Jimena, Mariana and Manolo, who were proud of having an aunt in New York working for her PhD.

# TABLE OF CONTENTS

# List of tables

List of figures

# GENERAL INTRODUCTION

Parulines (wood-warblers and their allies) belong to the very speciose group of New World nine-primaried oscines or Emberizidae (about 200 genera and 823 species, according to Sibley and Ahlquist 1990), whose phylogenetic relationships are still poorly understood. Traditionally, major groups within Emberizidae have been defined using characters of bill shape or of feeding niche. Anatomical characters have been insufficient to define major assemblages (Bock 1962, George 1962, Raikow 1978). Although morphological (Raikow 1978) and molecular (Sibley and Ahlquist 1990, Bledsoe and Raikow 1990) phylogenies have very low congruence among major groups, both kinds of phylogeny agree that Parulinae are a closely-related assemblage of taxa (monophyletic group) within the Emberizidae, with few problematic taxa. Allozyme data (Avise et al. 1980) also support this view. Phylogenetic relationships within parulines, however, are poorly understood.

Paruline Yellowthroats are grouped in the genus Geothlypis by the presence of a black mask. To reconstruct phylogenetic relationships in this group I undertook the following studies, results of which are herein included.

1. I examined species limits in the Baja California Yellowthroats (G. beldingi). Because the taxonomic status of populations in this taxon has been uncertain, a detailed analysis of genetic (allozymic), and morphological variation was undertaken. Results of this work are given in Chapter 1. This paper will be submitted to a professional journal for publication.
2. I studied intraspecific genetic variability in all Geothlypis taxa using allozyme electrophoresis. This comparison involved taxa with

different habitat preferences and distributional patterns. The results of this study were presented at the XXth International Ornithological Congress, in December 1990, in Christchurch, New Zealand. Due to space restrictions, locality descriptions and large tables are not included in this chapter, but are given in Chapter 3, together with related historical analyses. Chapter 2 will appear in the Proceedings of the XXth International Ornithological Congress.

3. I analyzed allozyme information with several methodologies. To contend with the unresolved phylogenetic hypothesis of parulines, I included numerous outgroups, both paruline and putative thraupine relatives, and reexamined the monophyly of the genus. The results of this analysis will soon be submitted to a professional journal for publication.

The three chapters have been written as independent papers, because I plan to publish them separately; in consequence, literature citations are included within each chapter, rather than at the end of the thesis.

## L I T E R A T U R E  C I T E D

Avise, J. C., J. C. Patton, and C. F. Aquadro.
1980. Evolutionary genetics of birds. Comparative molecular evolution in New World Warblers and rodents. J. Heredity 71:303-310.

Bledsoe, A. H. and R. J. Raikow.
1990. A quantitative assessment of congruence between molecular and non-molecular estimates of phylogeny. J. Mol. Evol. 30:247-259.

Bock, W.
1962. The pneumatic fossa of the humerus in the Passeres. Auk 79:425-443.

George, W. G.
1962. The classification of the Olive Warbler, Peucedramus taeniatus. Amer. Mus. Novit. 2103:1-41.

Raikow, R.
1978. Appendicular myology and relationships of the New World Nine-primaried Oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. no. 7.

Sibley, C. G. and J. E. Ahlquist.
1990. Phylogeny and Classification of Birds. A Study in Molecular Evolution. Yale University Press, New Haven & London.

# Chapter 1

## GEOGRAPHIC AND SEXUAL DIFFERENTIATION IN BELDING'S YELLOWTHROAT (GEOTHLYPIS BELDINGI) OF BAJA CALIFORNIA

Bertha Patricia Escalante-Pliego
Department of Ornithology, American Museum of Natural History,
and Graduate School of the City University of New York

## A B S T R A C T

Variation in allozyme and morphological characters was used to analyze population differentiation in Belding's Yellowthroats (Geothlypis beldingi) of Baja California, Mexico. Tissue samples from the San Ignacio and San José populations were assayed. Four loci were variable, two of which, GDA and ADA, showed significant differentiation suggesting low levels of gene flow. A total of 379 skins and 38 skeletons were examined from separate parts of the species range. The degree of morphological geographic differentiation was similar to geographic variation in allozymes between the two allopatric forms. Northern birds were larger than southern birds for the majority of skin and skeletal characters, a pattern that conforms with Bergmann's rule. Both populations showed a similar pattern of sexual dimorphism in which sexes differ significantly in all characters related with the flight apparatus, the males being larger in these characters. Taxonomic implications are that the two allopatric forms can be recognized as subspecies. The status of Belding's Yellowthroats in the Cape Region (G.

b. beldingi) is alarming because the suitable habitat left is very reduced. Populations of central Baja (G. b. goldmani) are less threatened at present, but will be if current trends in tourism continue. Thus, conservation measures ought to be taken soon for both subspecies.

## I N T R O D U C T I O N

The genus Geothlypis is more speciose in Mexico than in any other country where it occurs. One of the endemic Mexican species is Geothlypis beldingi (Belding's Yellowthroat), which is resident in southern Baja California (henceforth simply Baja), north to about 28º N latitude (AOU 1983). Belding's Yellowthroats are locally abundant in fresh-water marshes that are widely scattered in the deserts of the Baja peninsula. A close relative, G. trichas (Common Yellowthroat), occurs in this area during winter in several kinds of wet habitats, but breeds north and east of the peninsula in mainland Mexico and the United States and Canada. The Belding's Yellowthroat differs from the Common Yellowthroat by its larger size and more yellow pigmentation, especially behind the black facial mask.

Grinnell (1928) summarized the distribution and taxonomy of Belding's Yellowthroat. He recognized one species with two allopatric subspecies: goldmani in the central part of the peninsula between latitudes 26º and 28º N; and beldingi restricted to the Cape Region in the south (Figure 1). Although this classification has been accepted by some authors, others have disagreed. For example, Behle (1950) did not recognize the two subspecies, Miller et al. (1957) lumped G. beldingi with the Altamira Yellowthroat (G. flavovelata) of northeastern Mexico,

and Mayr and Short (1970) lumped G. beldingi and G. trichas. More recently, the AOU (1983) has recognized beldingi, flavovelata, and trichas as separate species. Hence, the taxonomic status of these populations is in doubt. Aside from the evolutionary significance of these populations, their genetic structure is of interest to conservation biologists and wildlife managers because the habitat suitable for these birds is very limited in extent and is often modified or even destroyed by human activities.

Study of variation of enzyme loci using starch-gel electrophoresis has been a useful tool for analysis of the systematics of closely related groups (Avise 1974), of geographic variation (Zink and Remsen 1986), and of population biology (Evans 1988). Recently, I collected samples of several populations of Belding's Yellowthroat to evaluate their taxonomic status, degree of intraspecific differentiation, and relationship to other populations of Geothlypis. In this paper, I report on the results of an examination of genetic variation using allozyme electrophoresis, and of an analysis of differentiation in external and skeletal characters.

## METHODS

### SAMPLES AND LOCALITIES

I visited the Baja Peninsula from 25 April to 25 May 1988, traveling from south to north searching for populations of resident yellowthroats in historical collection localitites. I found many sites to be no longer suitable, however. In the Cape Region of southern Baja I visited Miraflores, San José, Santiago, and Todos Santos (Fig. 1), but found suitable habitat only at San José (#8 in Fig. 1), where I obtained

36 birds in five days. The small fresh-water springs in the region are exploited by human communities. Local residents stated that two very dry seasons had been experienced in recent years. These two factors (exploitation and drought) probably account for the currently reduced distribution of marsh habitats in the Cape Region.

In the northern part of the range, I found resident yellowthroats at San Ignacio (#1 in Fig. 1) and Mulegé (#2). I collected only at San Ignacio where suitable habitat was more extensive. San Ignacio lies at the mouth of fresh-water springs that create permanent marshes and palm oases in the middle of the peninsula; from there streams run south to Laguna San Ignacio. Yellowthroats live in the extensive marsh along the spring. A sample of 18 birds was obtained. Two other historical localities, Purísima and Comondú (# 3 and 4 in Fig. 1), are too remote and could not be visited. For comparison, samples of populations of the Common Yellowthroat (G. trichas) were obtained from the northern part of Baja (14 km E San Telmo), and from mainland Mexico (4 km W Jamay, E Lago de Chapala, Jalisco, and other localities on the Mexican Plateau). A total of 69 birds were collected from Baja, and 85 from the mainland. Samples of Altamira Yellowthroats (G. flavovelata, N=7) were also compared, as part of a larger study (Escalante-Pliego, in prep.).

Birds were collected in mist nets. Samples of liver, heart, and breast muscle were stored in liquid nitrogen soon after death, and were deposited within two months in an ultracold freezer (-76$^0$ C). Specimens were prepared as partial round skins and complete skeletons.

## ALLOZYME ELECTROPHORESIS

Starch-gel allozyme electrophoresis was used to assay all individuals. I used standard electrophoretic procedures (Richardson et

al. 1986). Several buffer systems were experimented with in an attempt to find hidden variation (Aquadro and Avise 1982). Variation was assayed at 32 enzymatic loci: ACON-1 and ACON-2 (E. C. number 4.2.1.3), ACP (3.1.3.2), ADA (3.5.4.4), ADH (using Hexenol as substrate, 1.1.1.1), DIA (1.6.2.2), EST-1 and EST-D (3.1.1.1), FUM (4.2.1.2), GDA (3.5.4.3), GDH (1.4.1.3), GOT-1 and GOT-2 (2.6.1.1), αGPDH (1.1.1.8), G3PD (1.2.1.12), G6PD (1.1.1.49), IDH-1 and IDH-2 (1.1.1.42), LAP (3.4.11), LDH-1 and LDH-2 (1.1.1.27), MDH-1 and MDH-2 (1.1.1.37), ME (1.1.1.40), NP (2.4.2.1), PEP-A (anodal leu-ala substrate), PEP-B (leu-gly-gly substrate), and PEP-C (cathodal,leu-ala substrate) (3.4.11), PGM1-3 (2.7.5.1), and SDH (1.1.1.14). Eight additional loci were not considered in the analyses due to poor resolution in the gels. Samples of Common Yellowthroat from several other populations were run simultaneously with the samples of Belding's Yellowthroats to permit determination of homologies. Alleles were scored and identified with letters according to mobility, from anodal to cathodal, across all species assayed in the larger-scale study. Analyses were performed using the computer program BIOSYS-1 (Swofford and Selander 1989) and FSTAT (see acknowledgments). Genotype frequencies were used to obtain estimates of genetic variability (heterozygosity, number of alleles, and percentage of polymorphic loci) and of genetic differentiation ($F_{st}$, contingency table analysis of heterogeneity, and genetic distances).

## EXTERNAL MORPHOLOGY

Six measurements were taken from 379 study skins, including specimens obtained during this study as well as specimens from several museum collections: (1) length of exposed CULMEN; (2) width of bill (at distal end of nostril, BILL WIDTH); (3) heigth of bill (at distal end of

nostril, BILL DEPTH); (4) length of closed WING (chord); (5) length of TAIL; and (6) length of TARSUS (from Baldwin et al. 1931). A total of 379 specimens from 10 localities were measured (233 adult males, 144 adult females, and two immatures of undetermined sex). Localities with 5 specimens or fewer were not included for computations. Sexes were separated for geographic analyses. Within sex and localities, no gross departures from normality were observed (Kolmogorov D, $P<0.05$). Analyses were performed using the computer packages SAS (SAS Institute Inc, 1987) and SS-STP (see Acknowledgments).

## SKELETAL MORPHOLOGY

The only skeletal specimens available for analysis were those collected for this study. A total of 38 adults and two fully grown immatures from San José and San Ignacio were measured. Sixteen measurements were taken with a digital caliper under a magnifier: (1) PREL, premaxilla length; (2) SKW, skull width at postorbital processes; (3) SKL, skull length (tip of premaxilla to occipital condyle); (4) MAL, mandible length (symphysis to auricular condyle); (5) SYM, minimum mandible length (symphysis width); (6) STL, sternum length (xiphial area to ventral labial prominance); (7) COR, coracoid length (form sternocoracoidal process to coracohumeral surface); (8) HUM, greatest humerus length; (9) ULN, ulna length (olecranon process to external condyle); (10) CMC, carpometacarpus length (carpal trochlea to facet for digit III); (11) PHA, phalanx length (digital to metacarpal facets); (12) SYNW, synsacrum width (across posterior iliac crests); (13) SYNL, synsacrum length (prezygapophysis to processus dorsolateralis); (14) FEM, greatest femur length; (15) TBT, greatest tibiotarsus length; and (16) TMT, greatest tarsometarsus length. Although only 18 out of 640

values were missing, this caused 11 individuals to be excluded from multivariate analyses. Sexes were separated for geographic analyses.

I used principal components analysis as an exploratory technique to ordinate individuals and to look for differences among classes, either between localities or between sexes, and also to investigate patterns of covariation. After excluding individuals with missing values, the number of males was reduced to 16 and that of females to 13, for geographic comparisons; San José was reduced to 18 and San Ignacio to 11 for sexual comparisons. In multivariate analyses, sets with fewer observations than variables (here, females and San Ignacio) have problems of overdetermination; another problem associated with sample size is that no axis can be interpreted after the first due to large errors (Gibson et al. 1984, Marcus 1990). To explore some of these restraints I bootstrapped the principal components to obtain variance estimates for each eigenvector (Marcus 1990). I also performed another principal components analysis using only eight variables taken to represent all complexes of body morphology: skull (SKW, SKL), pectoral girdle plus forelimbs (COR, HUM, and ULN), and pelvic girdle plus hindlimbs (SYNW, FEM, and TBT). The pattern obtained with the second analysis was the same as that obtained when using all variables, hence only results of analyses with all variables are presented here.

## R E S U L T S

### ALLOZYMES

Four of the 32 loci scored were variable: ADA, GDA, PGM-1, and PGM-3 (Table 1). Genotype frequencies at each variable locus were tested for departure from Hardy-Weinberg equilibrium within populations; none

differ significantly. Mean heterozygosity over loci are: 0.041 ± 0.023 SE for San Ignacio and 0.064 ± 0.032 SE for San José. Percentage of polymorphic loci was 9.4 for San Ignacio and 12.5 for San José. The average number of alleles per polymorphic locus was 1.75 for San Ignacio, and 3.0 for San José.

For the four variable loci, among-population component of genetic variation ($F_{st}$) is zero for two loci (PGM-1 and PGM-3) with very similar allelic frequencies in both populations, but is higher for the other two variable loci (0.050 for ADA and 0.359 for GDA). The mean Wright's $F_{ST}$ over loci is 0.084 (corrected for sampling bias $F_{st}$ is 0.095; bootstrapped 95 % confidence interval: 0.000 - 0.271). Tests of heterogeneity of allelic frequencies between populations are non-significant for PGM-1 and PGM-3, but significant for the other two loci: ADA $X^2$ = 11.862 (DF 5, $P \geq 0.05$), GDA $X^2$ = 29.314 (DF 1, $P \geq 0.0001$). Using Slatkin's (1985) formula for estimating levels of gene flow with private alleles, I estimate the rate of immigration to be only 0.288 individuals per generation between the two populations. Genetic distances obtained between the two populations were 0.010 (Nei's [1978] unbiased distance, and 0.104 (modified Rogers' distance [Wright 1978]).

## EXTERNAL MORPHOLOGY

Sexual dimorphism. Only localities with large sample sizes (from 25 to 169: Santiago 59, San Ignacio 66, San José 165, and Todos Santos 35) were analyzed for sexual dimorphism. *T*-tests showed the following: males and females differ significantly in WING and TAIL in all populations ($P \leq 0.05$, Figure 2); the Santiago and San Ignacio populations differed significantly in CULMEN and TARSUS, but not San José ($P<0.08$ and $P<0.16$, respectively), or Todos Santos ($P<.52$ and $P<0.40$, respectively). In a

two-way analysis of variance, none of the interaction terms for locality and sex were significant ($P \geq 0.05$), suggesting a lack of geographic variation in sexual differences, except for TARSUS ($P < 0.03$).

Geographic differentiation. Table 2 shows geographic and sexual variation in mensural characters. Analysis of variance separated by sex showed significant geographic differences ($P \leq 0.05$) in all measurements except TARSUS in females ($P \leq 0.08$). Northern birds were larger than southern birds in all characters except BILL DEPTH in both sexes. CULMEN, WING, and TARSUS showed overlap in subsets of locality means. TAIL, however, showed sharper differentiation: in males, northern and southern birds formed two distinct subsets (Figure 3). Principal component analysis of males for log-transformed data from the variance-covariance matrix, using four variables CULMEN, WING, TAIL, and TARSUS, had TAIL weighted most heavily on the first component, and TARSUS most heavily in the second, grouping the northern populations on one side of the cloud, but not separating them from southern populations, suggesting the same pattern found in single variables.

## SKELETAL MORPHOMETRICS

Sexual differentiation. Both localities showed a similar pattern of sexual dimorphism in skeletal characters, where males and females were significantly different in all features of the flight apparatus (STL, COR, ULN, HUM, CMC, and PHA) (Table 5). The highest difference was in STL and ULN: in San José, males were 1.27 and 1.21 standard deviations larger than females, respectively, or 6.9 and 6.0 percent larger. In San Ignacio, males were 0.97 and 1.39 standard deviations larger than females for STL and ULN, respectively, or 5.4 or 6.6 percent larger.

Other characters showed significant differences in San José, but the degree of difference is smaller (Table 5). In the principal components analyses, the two geographic samples showed the same pattern: the first component had larger coefficients for STL, COR, HUM, ULN, CMC, and PHA (and SYNL in San Ignacio), with some contribution from other variables in the hindlimbs and skull. The top two plots of Figure 4 show the complete separation of females and males along the first principal component. In a two-way analysis of variance, none of the interaction terms for locality and sex were significant ($P \leq 0.05$), suggesting a lack of geographic variation in sexual differences, except for PHA ($P \geq 0.05$).

Geographic differentiation. Variation in 16 characters separated by sex and population are given in Table 3. *T*-tests for geographic differentiation in males showed significant differences for 4 out of 16 characters (HUM, SYNW, TBT, and TMT). In females, significant differences were detected in 8 of 16 characters (again HUM and SYNW; plus PREL, SKL, MAL, STL, PHA, and FEM). In all characters, birds from San Ignacio were larger than those of San José. However, sample sizes for females were more unequal.

Multivariate analysis gave similar results. Character weightings of the first principal component were rather equitably distributed among characters and were all positive (Table 4). Coefficients were high for TBT and TMT in both sexes. The projection of these individuals on the first principal component does not separate the populations of San Ignacio and San José completely, but groups most individuals of each sample in separate parts of the axis (bottom two plots of Figure 4).

# D I S C U S S I O N

## GENETIC VARIABILITY AND DIFFERENTIATION

The ADA locus showed a high level of polymorphism. Of six alleles found at this locus, three (*f,k,o*) were unique to Belding's Yellowthroats, whereas three other alleles (*e,h,m*) occur also in other Geothlypis taxa (Escalante-Pliego in prep.). Similarly, the two alleles at each of the PGM-1 and PGM-3 loci also occur in other Geothlypis taxa, but differ in frequency from those of Belding's populations (Escalante-Pliego, in prep.). Similar differences were found by Zink and Klicka (1990).

Heterozygosities documented here for G. beldingi are similar to those reported for warblers (Barrowclough and Corbin 1978) and other birds (Barrowclough 1983, Barrowclough et al. 1985, Capparella 1988). On the basis of the three parameters used to estimate intrapopulation variability, San Ignacio seems less variable than San José. Localities in the northern part of the range appear to be more distant from each other, or more isolated, than populations in the Cape region. If so they could have smaller effective population sizes which may reduce their genetic diversity. At the GDA locus, the loss of the *e* allele (i.e. fixation of *k*), common in most other species of yellowthroats (Escalante-Pliego in prep.), supports this view. Other insular bird populations commonly present a pattern of loss (i.e., Johnson and Marten 1988).

Estimates of $F_{st}$ differ greatly among the polymorphic loci. With so few variable loci, the overall standard error of $F_{st}$'s estimates is large, as indicated by the wide confidence intervals. However, this $F_{st}$, together with tests of heterogeneity and rate of immigrants per generation, suggest that gene flow between the San Ignacio and San José

populations is very low or non-existent.

## GEOGRAPHIC DIFFERENTIATION IN MORPHOLOGICAL CHARACTERS

The analyses performed in this study indicate that Belding's Yellowthroats conform with Bergmann's rule, the northern populations being larger in most external and skeletal characters examined. Both males and females showed similar tendencies. However, fewer and smaller sample sizes in skeletons preclude more detailed numerical comparisons at this time. Although Lewontin (1974) has stated that one may doubt the validity of a statistical comparison between patterns obtained from allozymes and morphology, it is worthy of note that the qualitative similarity and degree of differentiation between both data sets are concordant in the case studied here.

## SEXUAL DIFFERENTIATION IN MORPHOLOGICAL CHARACTERS

Sexual size dimorphism is widespread in birds and other organisms (Shine 1989). In birds, males are usually larger than females, although reversed sexual dimorphism is prevalent in some groups (Amadon, 1959, Selander 1972). Sexual dimorphism is most often detected in bill size, but tarsus or wing length may also show some differences (Johnson 1980). Explanations proposed for the evolution of size dimorphism between the sexes have mainly centered on sexual selection, or intraspecific niche divergence, although natural selection unrelated to foraging has also been used to explain size differences (Rising 1987, Shine 1989). Because sufficient skeletal material is not always available, fine-scale morphological studies of sexual dimorphism are few, but their results are promising. For instance, Johnston (1972) found complex secondary sexual size dimorphism in House Sparrows (Passer domesticus) with

pectoral and wing complex strongly dimorphic. Livezey and Humphrey (1984) found sexual size dimorphism in Steamer-ducks (Tachyeres spp.), where males were larger than females in 15 external, 30 skeletal, and 2 muscular characters. These authors found non-uniform differences, and they suggested that shape differences were sex-related morphological adaptations. In Belding's Yellowthroats, males and females are strongly dimorphic in characters of the flight apparatus, as in the House Sparrow. Small but significant differences in bill dimensions were detected in skins from localities with large sample sizes in San José and Santiago, and in skeletons from San José. Belding's Yellowthroats are sedentary, and do not separate by habitat preference; besides, perches in marshes are in a single stratum; sexual differentiation instead is perhaps related to parental role (Jönsson and Alerstam 1990). Although specific observations on the breeding behavior of Belding's Yellowthroats are not available, sexes of paruline warbler species have separate activities during reproduction, when males patrol and search for food whereas females spend more time around the nest, where incubating and brooding sometimes takes up to 80% of their time (Morse 1989). These sex-related differences in activity budgets may put more demands on flight capacities of male wings. As indicated by its occurrence in House Sparrows and Belding's Yellowthroats, representing two unrelated avian families (Ploceidae and Emberizidae, respectively), this pattern of sexual dimorphism in wing morphology may be widespread in passerine birds.

## BIOGEOGRAPHY

The genetic structure of two other Baja species has also been examined to date, the Brown Towhee (Pipilo fuscus, Zink 1988), and the

California Quail (Lophortyx californica, Zink et al. 1987). Both studies showed less differentiation among populations than I found in Belding's Yellowthroats. The habitats of the Brown Towhee and the California Quail are not as fragmented or as locally distributed in the Baja peninsula, as are the marshes where Belding's Yellowthroats live. This ecological difference, along with the sedentary habits of Belding's Yellowthroats, might explain the high level of differentiation in Belding's Yellowthroats. Phylogenetic analyses of Brown Towhees and California Quails suggested to Zink (1988) and Zink et al. (1987) that these two species have their closest relatives in California, and that they are of recent northern origin. Although a strong hypothesis regarding the geographic origin of Belding's Yellowthroats cannot be emitted at this time, the phylogenetic pattern obtained with allozymes, together with plumage pattern, suggest a southern origin from a radiation in central Mexico (Escalante-Pliego in prep.). Genetic similarity between Belding's Yellowthroat and other Geothlypis taxa indicates relatively recent divergence.

## TAXONOMY

Both populations of Belding's Yellowthroats studied genetically have two unique alleles at the ADA locus (*f* and *k*) and one at the GDA locus (*k*) not present in any other member of the genus, or in other paruline warblers (Escalante-Pliego, in prep.). The only exception is a single heterozygous individual of the Common Yellowthroat of San Telmo in northern Baja California that had the GDA-k allele. Its presence is interpreted as a trace of past hybridization. The occurrence of these unique alleles in these two isolated populations identify Belding's Yellowthroat as a monophyletic taxon. When treated as populations in

phylogenetic analyses including all other yellowthroats, the subspecies of beldingi always appear together as sister groups (Escalante-Pliego in prep.).

Belding's Yellowthroats can be diagnosed from Common Yellowthroats by the allozyme markers mentioned above, by differences in size (Escalante-Pliego in prep.), and by plumage characters. Among populations of Belding's Yellowthroat, however, patterns of allozyme frequencies indicated lack of gene flow, and significant differentiation at some loci. Morphometric patterns of external and skeletal morphology showed geographic patterns that compare well with the patterns found in allozymes. Plumage coloration differences have been used to distinguish between two allopatric parts of the range corresponding to the two recognized subspecies (Grinnell 1928).

The genetic differentiation revealed by allozymes indicates that the two allopatric populations may represent independent evolutionary lineages. The northern and southern Belding's Yellowthroats could reasonably be ranked either as species or subspecies, but I favor the latter, because it permits the taxonomic recognition of differentiated geographic isolates, and also reflects the level of differentiation between the two forms relative to other yellowthroats.

## ECOLOGY AND CONSERVATION

Large series of skins of G. beldingi exist in several museums in North America. Most of these birds were collected during the early 1900's and in the 1930's. As I judge from the number of specimens available, some localities (e.g. San José, San Ignacio) were well collected, and probably supported large populations, in contrast to other localities (Santa Anita) with smaller, perhaps transient

populations. The growing tourist industry in the Cape Region might place a heavy demand on the scarce freshwater resources available in this region. Resident yellowthroats in Baja require permanent marshes. For the populations of the Cape Region, the only remnant of such habitat is Estero San José, which is managed by the people of San José (a town of approximately 10,000 inhabitants, with a large influx of tourists each year). Because Estero San José is a very small marsh (less than 0.1 $km^2$), yellowthroat populations here are subject to much disturbance and are clearly endangered. In Central Baja, by contrast, Belding's Yellowthroats seem to be fairly abundant. San Ignacio is a relatively unimportant stop in the tourist traffic along the peninsula, and undisturbed marsh habitat extends south from the highway for a considerable distance. A change in tourist traffic in the future could alter this balance, however, so this marsh should be protected.

## A C K N O W L E D G M E N T S

Javier Salgado, Ernesto Díaz, Laura Rivera and Gabriela Ibañez were excellent field companions and helped me to collect under difficult conditions. I am grateful to George F. Barrowclough for his help in the electrophoresis lab, for making available his computer programs FSTAT and SSSTP, and for constructive criticisms of this manuscript. Leslie F. Marcus made useful comments and made his bootstrap program available. For careful reading, comments and advice, I also thank François Vuilleumier, Robert S. Voss, Robert F. Rockwell, and A. Townsend Peterson. I thank the Department of Herpetology of the American Museum of Natural History, and the Museo de Zoología de la Facultad de Ciencias

de la Universidad Nacional Autónoma de México for their help in many ways.

For access to specimens, I am thankful to the staff in charge of the Academy of Natural Sciences of Philadelphia, the Los Angeles County Museum of Natural History, the Field Museum of Natural History, the Museum of Comparative Zoology, the Museum of Vertebrate Zoology, the National Museum of Natural History, the San Diego Museum of Natural History, and the University of Michigan Museum of Zoology.

I thank the F. M. Chapman Memorial Fund of the Department of Ornithology of the American Museum of Natural History, the Graduate Studies Committee of the Ecology and Evolutionary Biology Doctoral Program at the City University of New York, and Sigma Xi for funds provided for field work and lab assays.

## L I T E R A T U R E  C I T E D

Amadon, D.
1959. The significance of sexual differences in size among birds. Proc. Amer. Phil. Soc. 103: 531-536.

AOU.
1983. Check-list of birds of North America. American Ornithologists' Union, 6th ed.

Aquadro, C. F. and J. C. Avise.
1982. Evolutionary genetics of birds. VI. A reexamination of protein divergence using varied electrophoretic conditions. Evolution 36: 1003-1019.

Avise, J.
1974. Systematic value of electrophoretic data. Syst. Zool. 23: 465-481.

Baldwin, S. P., H. C. Oberholser, and L. G. Worley.
1931. Measurements of birds. Sci. Pub. Cleveland Mus. Nat. Hist. 2. 121 pp.

Barrowclough, G. F.
1980. Genetic and phenotypic differentiation in a wood warbler

(genus Dendroica) hybrid zone. Auk 97: 655-668.

_____.
1983. Biochemical studies of microevolutionary processes. In Perspectives in ornithology. A. H. Brush and G. A. Clark, Jr. (eds.). Cambridge Univ. Press, New York, N.Y. pp.223-261.

_____, N. K. Johnson, and R. M. Zink.
1985. On the nature of genic variation in birds. Current Ornithology 2: 135-154.

_____, and N. K. Johnson
1988. Genetic structure of North American birds. Pp. 1630-1645 in H. Ouellet (ed.) Proc. XIX International Ornithological Congress, Univ. Ottawa Press, Ottawa, Ontario, Canada.

Behle, W. H.
1950. Clines in the yellow-throats of western North America. Condor 52: 193-219.

Capparella, A. C.
1988. Genetic variation in Neotropical birds: Implications for the speciation process. Pp. 1658-1664 in H. Ouellet (ed.) Proc. XIX International Ornithological Congress, Univ. Ottawa Press, Ottawa, Ontario, Canada.

Evans, P. G. H.
1988. Electrophoretic variability of gene products. Pp. 105-162 in Cooke, F., and P. A. Buckley (eds.). Avian genetics. Academic Press, London.

Gibson, A. R. A. J. Baker, and A. Moeed.
1984. Morphometric variation in introduced populations of the Common Myna (Acridotheres tristis): an application of the jackknife to principal component analysis. Syst. Zool. 33:408-421.

Grinnell, J.
1928. A distributional summation of the ornithology of Lower California. Univ. Calif. Publ. Zool. 32: 1-300.

Johnson, N. K.
1980. Character variation and evolution of sibling species in the Empidonax difficilis-flavescens Complex (Aves:Tyrannidae). Univ. Calif. Publ. 112: 1-151.

_____ and J. A. Marten.
1988. Evolutionary genetics of flycatchers II. Differentiation in the Empidonax difficilis complex. Auk 105: 177-191.

Johnston, R. F.
1972. Ecological differentiation in North American birds. In, Allen, R. T. and F. C. James (eds.). A Symposium in Systematics, Occ. Pap. Univ. Arkansas Mus. 4: 101-132.

Jönsson, P. E. and T. Alerstam.
1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. Biol. J. Linn. Soc. 41:301-314.

Lewontin, R. C.
1974. Detecting population differences in quantitative characters as opposed to gene frequencies. Amer. Nat. 123:115-124.

Livezey, B. L. and P. S. Humphrey.
1984. Sexual dimorphism in continental steamer-ducks. Condor 86:368-377.

Marcus, L. F.
1990. Traditional morphometrics. In, Rohlf, F. J. and F. L. Bookstein. Proceedings of the Michigan Morphometrics Workshop, Spec. Publ. Univ. Michigan Mus. Zool. 2: 77-118.

Mayr, E. and L. L. Short.
1970. Species taxa of North American birds. Nuttall Ornithological Club. no. Cambridge, Massachusetts.

Miller, A. H., H. Friedmann, L. Griscom, and R. T. Moore.
1957. Distributional check-list of the birds of Mexico. Part II. Pacific Coast Avifauna 33:1-436.

Morse, D. H.
1989. American warblers. An ecological and behavioral perspective. Harvard Univ. Press. Cambridge, Massachusetts.

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

_____, T. Maruyama, and R. Chakraborty.
1975. The bottleneck effect and genetic variability in populations. Evolution 29: 1-10.

Richardson, B. J., P. R. Baverstock, and M. Adams.
1986. Allozyme electrophoresis. Sydney, Australia, Academic Press.

Rising, J. D.
1987. Geographic variation of sexual dimorphism in size of Savannah Sparrows (Passerculus sandvichensis): a test of hypothesis. Evolution 41:514-524.

SAS Institute Inc.
1987. SAS/STAT for personal computers, version 6.03. SAS Institute Inc. Cary, North Carolina, USA.

Selander, R. K.
1972. Sexual selection and dimorphism in birds. In Campbell, (ed.). Sexual selection and the descent of man 1871-1971. Aldine Publ. Co. Chicago, Illinois. Pp. 180-230.

Shine, R.
1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. 64:419-461.

Slatkin, M.
1985. Rare alleles as indicators of gene flow. Evolution 39:53-65.

Swofford, D. and R. B. Selander.
1989. BIOSYS-1, v. 1.7. A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Illinois Natural History Survey. Urbana, Illinois, USA.

Wright, S.
1978. Evolution and genetics of populations, vol. 4. variability within and among natural populations. University of Chicago Press, Chicago.

Zink, R. M.
1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. Condor 90: 72-82.

_____, and J. T. Klicka.
1990. Genetic variation in the Common Yellowthroat and some allies. Wilson Bull. 102: 514-520.

_____, D. F. Lott, and D. W. Anderson.
1987. Genetic variation, population structure and evolution of California Quail. Condor 89: 395-405.

_____, and J. V. Remsen, Jr.
1986. Evolutionary processes and patterns of geographic variation in birds. Current Ornithology 4: 1-69.

Table 1. Allele frequencies at four variable loci in two geographically isolated populations of Belding's Yellowthroats (Geothlypis beldingi) in Baja California.

| Locus | San Ignacio (Central Baja) | San José (Cape Region) |
|---|---|---|
| N[1] | (18) | (36) |
| ADA | | |
| *e* | - | .014 |
| *f* | .583 | .278 |
| *h* | .361 | .514 |
| *k* | .056 | .083 |
| *m* | - | .056 |
| *o* | - | .056 |
| GDA | | |
| *e* | - | .528 |
| *k* | 1.000 | .472 |
| PGM-1 | | |
| *b* | .306 | .361 |
| *c* | .694 | .639 |
| PGM-3[2] | | |
| *a* | .300 | .264 |
| *b* | .700 | .736 |

[1] Sample size

[2] Only 15 from San Ignacio

Table 2. Variation of mensural characters of Belding's Yellowthroats (Geothlypis beldingi) of Baja California. Mean and standard deviation are given in millimeters.

| Locality | | CULMEN LENGTH | | BILL DEPTH | | BILL WIDTH | | WING LENGTH | | TAIL LENGTH | | TARSUS LENGTH | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | $\bar{X}$ | SD | $\bar{X}$ | SD | $\bar{X}$ | SD | $\bar{X}$ | SD | $\bar{X}$ | SD | $\bar{X}$ | SD |
| **MALES** | | | | | | | | | | | | | |
| CENTRAL BAJA: | | | | | | | | | | | | | |
| San Ignacio (1) | 37 | 13.20 | ± 0.53 | 3.61 | ± 0.22 | 3.60 | ± 0.38 | 63.20 | ± 1.56 | 64.63 | ± 2.23 | 23.64 | ± 0.75 |
| Comondu (4) | 11 | 12.91 | ± 0.45 | 3.85 | ± 0.20 | 3.84 | ± 0.26 | 63.64 | ± 1.11 | 65.51 | ± 2.26 | 23.48 | ± 0.34 |
| CAPE REGION: | | | | | | | | | | | | | |
| Miraflores (5) | 8 | 12.67 | ± 0.63 | 3.97 | ± 0.22 | 3.46 | ± 0.28 | 62.18 | ± 1.25 | 61.84 | ± 2.11 | 22.92 | ± 0.62 |
| Santiago (7) | 47 | 12.99 | ± 0.50 | 3.97 | ± 0.14 | 3.42 | ± 0.14 | 62.49 | ± 1.34 | 62.73 | ± 1.79 | 23.15 | ± 0.72 |
| Santa Anita (8) | 6 | 12.84 | ± 0.42 | 3.84 | ± 0.23 | 3.11 | ± 0.19 | 61.54 | ± 0.57 | 60.92 | ± 1.73 | 22.92 | ± 0.68 |
| San Jose (9) | 95 | 12.51 | ± 0.55 | 3.88 | ± 0.18 | 3.30 | ± 0.17 | 61.89 | ± 1.47 | 62.14 | ± 1.78 | 22.82 | ± 0.73 |
| Todos Santos (11) | 18 | 12.79 | ± 0.75 | 3.66 | ± 0.41 | 3.47 | ± 0.22 | 62.52 | ± 1.04 | 62.48 | ± 2.13 | 22.94 | ± 0.44 |
| **FEMALES** | | | | | | | | | | | | | |
| CENTRAL BAJA: | | | | | | | | | | | | | |
| San Ignacio (1) | 29 | 12.85 | ± 0.42 | 3.56 | ± 0.21 | 3.66 | ± 0.33 | 60.16 | ± 1.39 | 61.91 | ± 2.13 | 23.03 | ± 0.65 |
| Comondu (4) | 9 | 12.67 | ± 0.56 | 3.70 | ± 0.28 | 3.72 | ± 0.40 | 60.32 | ± 1.29 | 62.30 | ± 1.63 | 22.72 | ± 0.32 |
| CAPE REGION: | | | | | | | | | | | | | |
| Santiago (7) | 12 | 12.51 | ± 0.58 | 3.91 | ± 0.18 | 3.34 | ± 0.11 | 59.44 | ± 1.20 | 59.89 | ± 1.66 | 22.55 | ± 0.68 |
| San Jose (9) | 70 | 12.34 | ± 0.64 | 3.78 | ± 0.23 | 3.29 | ± 0.18 | 58.97 | ± 1.36 | 59.81 | ± 1.87 | 22.65 | ± 0.72 |
| Todos Santos (11) | 17 | 12.64 | ± 0.56 | 3.70 | ± 0.34 | 3.37 | ± 0.21 | 58.57 | ± 1.35 | 59.99 | ± 2.26 | 23.09 | ± 0.59 |

Table 3. Variation in skeletal characters of Belding's Yellowthroats (Geothlypis beldingi) of Baja California. Sample sizes (N), mean (X) and standard deviation (SD) for measurements of each group.

| | San Ignacio (Central Baja) | | | | San José (Cape Region) | | | |
|---|---|---|---|---|---|---|---|---|
| (N) | Males (10) | | Females (5) | | Males (10) | | Females (15) | |
| | $\bar{X}$ | SD | $\bar{X}$ | SD | $\bar{X}$ | SD | $\bar{X}$ | SD |
| Skull: | | | | | | | | |
| PREL | 15.63 | 0.23 | 15.58 | 0.16 | 15.59 | 0.43 | 15.23 | 0.36 |
| SKW | 12.71 | 0.28 | 12.46 | 0.58 | 12.66 | 0.23 | 12.49 | 0.20 |
| SKL | 29.37 | 0.32 | 28.99 | 0.36 | 29.10 | 0.44 | 28.32 | 0.56 |
| MAL | 25.32 | 0.39 | 25.07 | 0.39 | 25.00 | 0.44 | 24.35 | 0.50 |
| SYM | 8.38 | 0.28 | 8.56 | 0.19 | 8.51 | 0.24 | 8.31 | 0.36 |
| Pectoral girdle and fore limbs: | | | | | | | | |
| STL | 16.43 | 0.39 | 15.54 | 0.31 | 16.27 | 0.35 | 15.15 | 0.26 |
| COR | 15.03 | 0.30 | 14.26 | 0.38 | 14.83 | 0.33 | 13.96 | 0.36 |
| HUM | 15.79 | 0.24 | 15.08 | 0.29 | 15.38 | 0.27 | 14.67 | 0.28 |
| ULN | 17.82 | 0.21 | 16.64 | 0.11 | 17.64 | 0.22 | 16.58 | 0.30 |
| CMC | 9.76 | 0.17 | 9.17 | 0.13 | 9.70 | 0.16 | 9.04 | 0.21 |
| PHA | 4.70 | 0.12 | 4.50 | 0.08 | 4.63 | 0.12 | 4.27 | 0.09 |
| Pelvic girdle and hind limbs: | | | | | | | | |
| SYNW | 10.09 | 0.19 | 9.91 | 0.34 | 9.86 | 0.18 | 9.59 | 0.15 |
| SYNL | 14.77 | 0.52 | 14.30 | 0.26 | 14.74 | 0.22 | 14.19 | 0.35 |
| FEM | 16.56 | 0.39 | 16.29 | 0.22 | 16.36 | 0.25 | 15.94 | 0.35 |
| TBT | 31.83 | 0.71 | 31.35 | 0.35 | 30.91 | 0.52 | 30.66 | 0.85 |
| TMT | 23.50 | 0.66 | 23.12 | 0.45 | 22.81 | 0.45 | 22.63 | 0.59 |

Table 4. Coefficients and standard deviations of four 1st principal components for Belding's Yellowthroats (Geothlypis beldingi) of Baja California. Underlining indicates consistent coefficients, whose *T* value is above 2.0. (T is the mean divided by the standard error, as estimated here from resampled data sets, see Marcus 1990).

| Comparison: | GEOGRAPHIC | | | | SEXUAL | | | |
|---|---|---|---|---|---|---|---|---|
| Group: | FEMALES | | MALES | | San Ignacio (Central Baja) | | San Jose (Cape Region) | |
| | PC1 | $S_{PC1}$ | PC1 | $S_{PC1}$ | PC1 | $S_{PC1}$ | PC1 | $S_{PC1}$ |
| PREL[1] | 0.202 | 0.099 | 0.118 | 0.132 | 0.002 | 0.047 | 0.153 | 0.054 |
| SKW | 0.120 | 0.215 | 0.167 | 0.108 | 0.239 | 0.144 | 0.070 | 0.035 |
| SKL | 0.234 | 0.070 | 0.154 | 0.078 | 0.093 | 0.046 | 0.173 | 0.032 |
| MAL | 0.260 | 0.120 | 0.211 | 0.089 | 0.062 | 0.059 | 0.168 | 0.042 |
| SYM | 0.273 | 0.137 | 0.102 | 0.181 | -0.074 | 0.100 | 0.147 | 0.072 |
| STL | 0.189 | 0.085 | 0.170 | 0.104 | 0.335 | 0.061 | 0.356 | 0.052 |
| COR | 0.295 | 0.114 | 0.260 | 0.100 | 0.360 | 0.073 | 0.353 | 0.046 |
| HUM | 0.249 | 0.074 | 0.344 | 0.063 | 0.324 | 0.043 | 0.264 | 0.030 |
| ULN | 0.220 | 0.076 | 0.210 | 0.027 | 0.376 | 0.041 | 0.346 | 0.017 |
| CMC | 0.190 | 0.152 | 0.163 | 0.068 | 0.359 | 0.076 | 0.392 | 0.028 |
| PHA | 0.386 | 0.143 | 0.211 | 0.127 | 0.243 | 0.073 | 0.423 | 0.049 |
| SYNW | 0.202 | 0.146 | 0.219 | 0.115 | 0.209 | 0.092 | 0.132 | 0.042 |
| SYNL | 0.197 | 0.079 | 0.288 | 0.142 | 0.302 | 0.081 | 0.219 | 0.042 |
| FEM | 0.221 | 0.045 | 0.330 | 0.057 | 0.214 | 0.048 | 0.142 | 0.030 |
| TBT | 0.368 | 0.084 | 0.386 | 0.072 | 0.178 | 0.037 | 0.139 | 0.064 |
| TMT | 0.257 | 0.091 | 0.401 | 0.087 | 0.191 | 0.042 | 0.118 | 0.056 |
| Eigenvalue | 0.0046 | 0.0012 | 0.0034 | 0.0006 | 0.0089 | 0.0020 | 0.0102 | 0.0028 |
| Proportion | 0.53 | | 0.42 | | 0.64 | | 0.70 | |

[1] For explanation of skeletal characters, see text.

Table 5. Sexual dimorphism in skeletal variables of Belding's Yellowthroat (Geothlypis beldingi). DI (dimorphism index) = difference of means of males and females divided by the pooled standard deviation. %D = mean of males minus females divided by mean of males.

| | San Ignacio (Central Baja) | | | San José (Cape Region) | | |
|---|---|---|---|---|---|---|
| | DI | %D | T[1] | DI | %D | T[1] |
| PREL | 0.05 | 0.3 | n.s. | 0.39 | 1.7 | * |
| SKW | 0.27 | 2.0 | n.s. | 0.19 | 0.4 | n.s. |
| SKL | 0.42 | 1.3 | n.s. | 0.81 | 1.8 | ** |
| MAL | 0.27 | 0.9 | n.s. | 0.71 | 2.6 | ** |
| SYM | -0.21 | 2.2 | n.s. | 0.23 | 2.4 | n.s. |
| STL | 0.97 | 5.4 | *** | 1.27 | 6.9 | *** |
| COR | 0.86 | 5.2 | *** | 0.96 | 5.6 | *** |
| HUM | 0.81 | 4.5 | *** | 0.80 | 4.6 | *** |
| ULN | 1.39 | 6.6 | *** | 1.21 | 6.0 | *** |
| CMC | 0.71 | 6.1 | *** | 0.79 | 6.9 | *** |
| PHA | 0.25 | 4.3 | ** | 0.45 | 7.7 | *** |
| SYNW | 0.21 | 1.8 | n.s. | 0.32 | 2.7 | *** |
| SYNL | 0.50 | 3.1 | n.s. | 0.62 | 3.8 | *** |
| FEM | 0.30 | 1.7 | n.s. | 0.47 | 2.6 | ** |
| TBT | 0.50 | 1.5 | n.s. | 0.26 | 0.8 | n.s. |
| TMT | 0.40 | 1.6 | n.s. | 0.19 | 0.8 | n.s. |

[1] Results of *t*-test; *: $P<.05$; **: $P<.01$; ***: $P<.001$.

Fig. 1. Historical localities of Belding's Yellowthroats (Geothlypis beldingi) with ranges of subspecies (modified from Grinnell 1928). Central Peninsula: 1=San Ignacio, 2=Mulegé, 3=Purísima, 4=Comondú. Cape region: 5=Miraflores, 6=Eureka, 7=Santiago, 8=Santa Anita, 9=San José, 10=Triunfo, 11=Todos Santos. Dotted line represents 1000 feet of elevation.

Fig. 2. TAIL length plotted against WING length in four populations of Belding's Yellowthroats (Geothlypis beldingi). San Ignacio from Central Baja, Todos Santos, Santiago, and San José from the Cape Region. Females are indicated by circles, and males by plus signs. Differences between sexes are significant in four populations, for both variables (*T* test, $P \leq 0.05$).

Fig. 3. Geographic variation for skins measurements in males and females of Belding's Yellowthroats (Geothlypis beldingi) of Baja California. Localities, means, subsets obtained with Gabriel's test (SS-STP), and distribution of mean classes are given.

Fig. 4. First principal component of skeletal variables in Belding's Yellowthroats. Upper two plots depict sexual dimorphism within localities; lower two plots show a geographic contrast of localitites within sexes. Coefficients of the first principal components are given in Table 4.

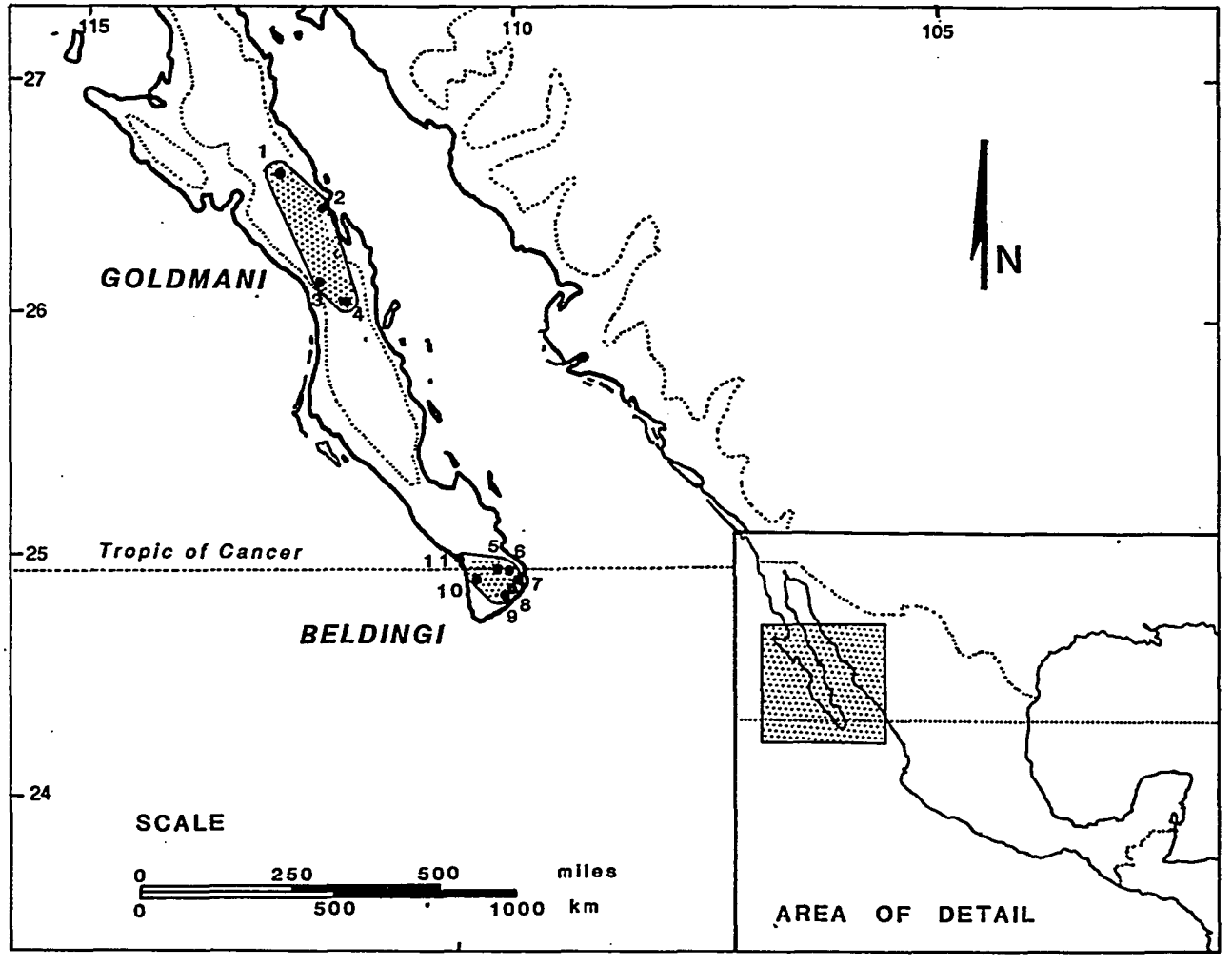

115
110
105
27
26
25
24
GOLDMANI
BELDINGI
Tropic of Cancer
1
2
3
4
5
6
7
8
9
10
11
N
SCALE
0
250
500
miles
0
500
1000
km
AREA OF DETAIL

Fig. 1

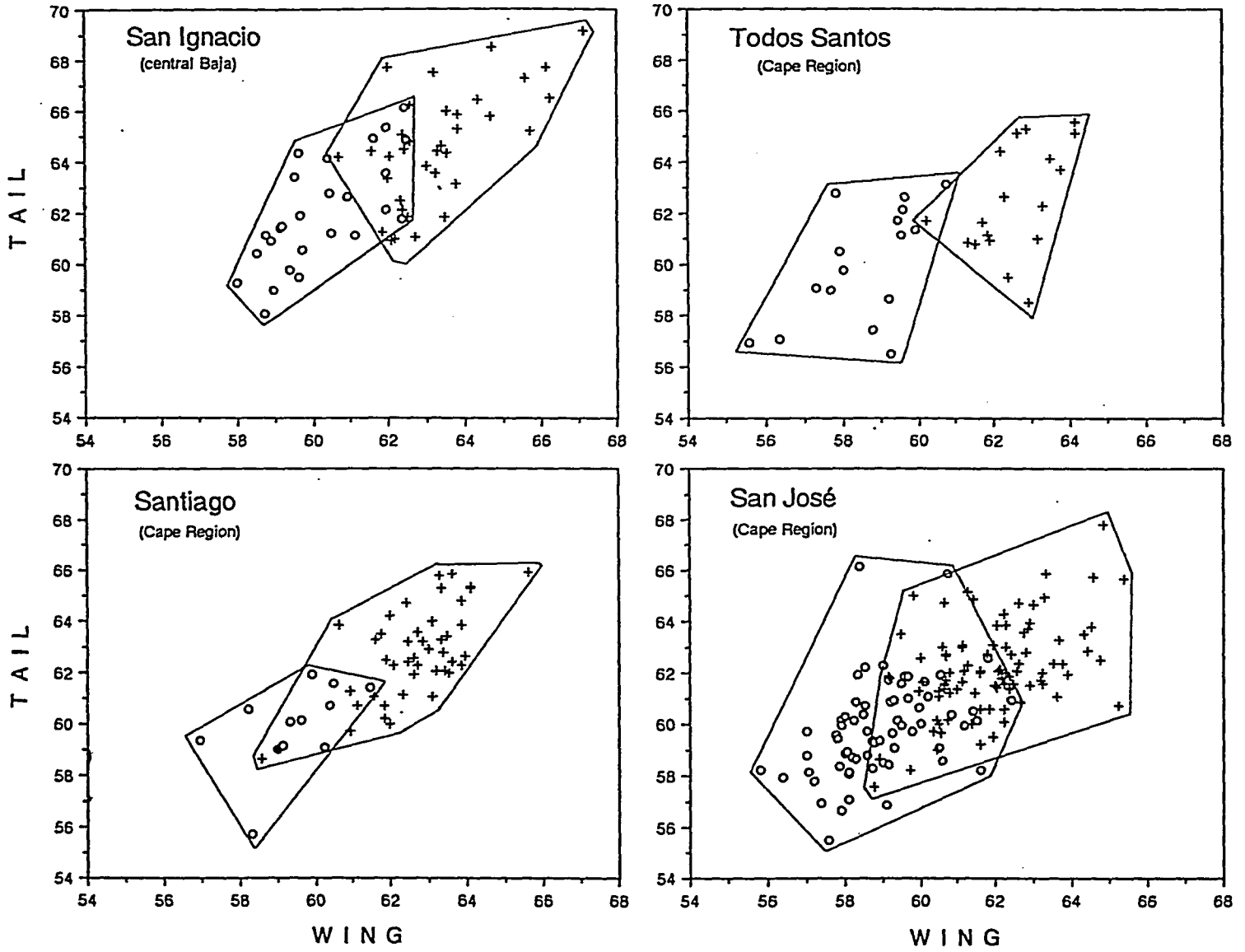
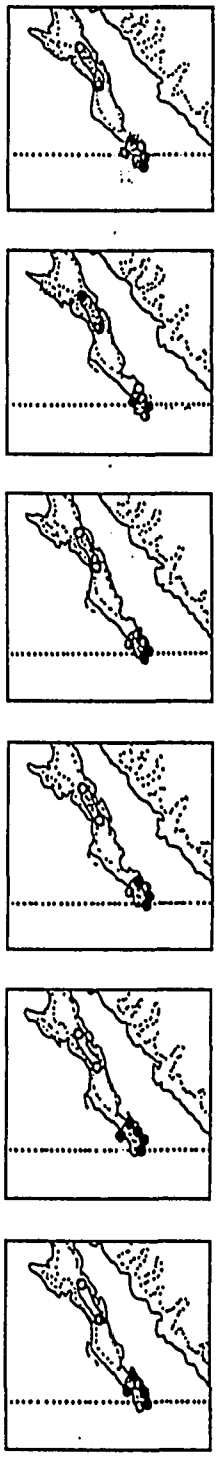

San Ignacio
(central Baja)
Todos Santos
(Cape Region)
Santiago
(Cape Region)
San José
(Cape Region)
TAIL
TAIL
WING
WING
54
56
58
60
62
64
66
68
70

Fig. 2

Fig. 3

## MALES

| Locality | Mean |
|---|---|
| **CULMEN** | |
| o San Ignacio | 13.20 |
| Santiago | 12.98 |
| Comondú | 12.91 |
| o Santa Anita | 12.84 |
| Todos Santos | 12.79 |
| Miraflores | 12.67 |
| • San José | 12.51 |
| **BILL DEPTH** | |
| Miraflores | 3.97 |
| o Santiago | 3.96 |
| San José | 3.87 |
| o Comondú | 3.85 |
| Santa Anita | 3.84 |
| Todos Santos | 3.66 |
| • San Ignacio | 3.61 |
| **BILL WIDTH** | |
| o Comondú | 3.84 |
| San Ignacio | 3.60 |
| Todos Santos | 3.47 |
| o Miraflores | 3.46 |
| Santiago | 3.42 |
| San José | 3.30 |
| • Santa Anita | 3.11 |
| **WING LENGTH** | |
| o Comondú | 63.64 |
| San Ignacio | 63.20 |
| Todos Santos | 62.52 |
| o Santiago | 62.49 |
| Miraflores | 62.18 |
| San José | 61.89 |
| • Santa Anita | 61.54 |
| **TAIL LENGTH** | |
| o Comondú | 65.51 |
| San Ignacio | 64.63 |
| Santiago | 62.73 |
| Todos Santos | 62.48 |
| San José | 62.14 |
| • Miraflores | 61.84 |
| Santa Anita | 60.92 |
| **TARSUS LENGTH** | |
| o San Ignacio | 23.64 |
| Comondú | 23.48 |
| o Santiago | 23.15 |
| Todos Santos | 22.94 |
| Santa Anita | 22.92 |
| • Miraflores | 22.92 |
| San José | 22.81 |



## FEMALES

| Locality | Mean |
|---|---|
| **CULMEN** | |
| o San Ignacio | 12.85 |
| Comondú | 12.67 |
| o Todos Santos | 12.64 |
| Santiago | 12.51 |
| • San José | 12.34 |
| **BILL DEPTH** | |
| o Santiago | 3.91 |
| San José | 3.78 |
| o Todos Santos | 3.70 |
| Comondú | 3.70 |
| • San Ignacio | 3.56 |
| **BILL WIDTH** | |
| Comondú | 3.72 |
| o San Ignacio | 3.66 |
| Todos Santos | 3.37 |
| Santiago | 3.34 |
| • San José | 3.29 |
| **WING LENGTH** | |
| o Comondú | 60.32 |
| San Ignacio | 60.16 |
| o Santiago | 59.44 |
| San José | 58.97 |
| • Todos Santos | 58.57 |
| **TAIL LENGTH** | |
| Comondú | 62.30 |
| o San Ignacio | 61.91 |
| Todos Santos | 59.99 |
| Santiago | 59.89 |
| • San José | 59.81 |
| **TARSUS LENGTH** | |
| Todos Santos | 23.09 |
| o San Ignacio | 23.03 |
| Comondú | 22.72 |
| San José | 22.65 |
| • Santiago | 22.55 |

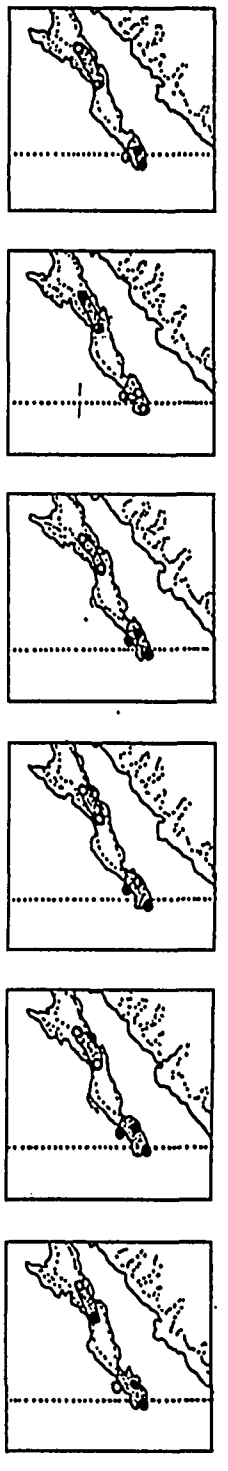
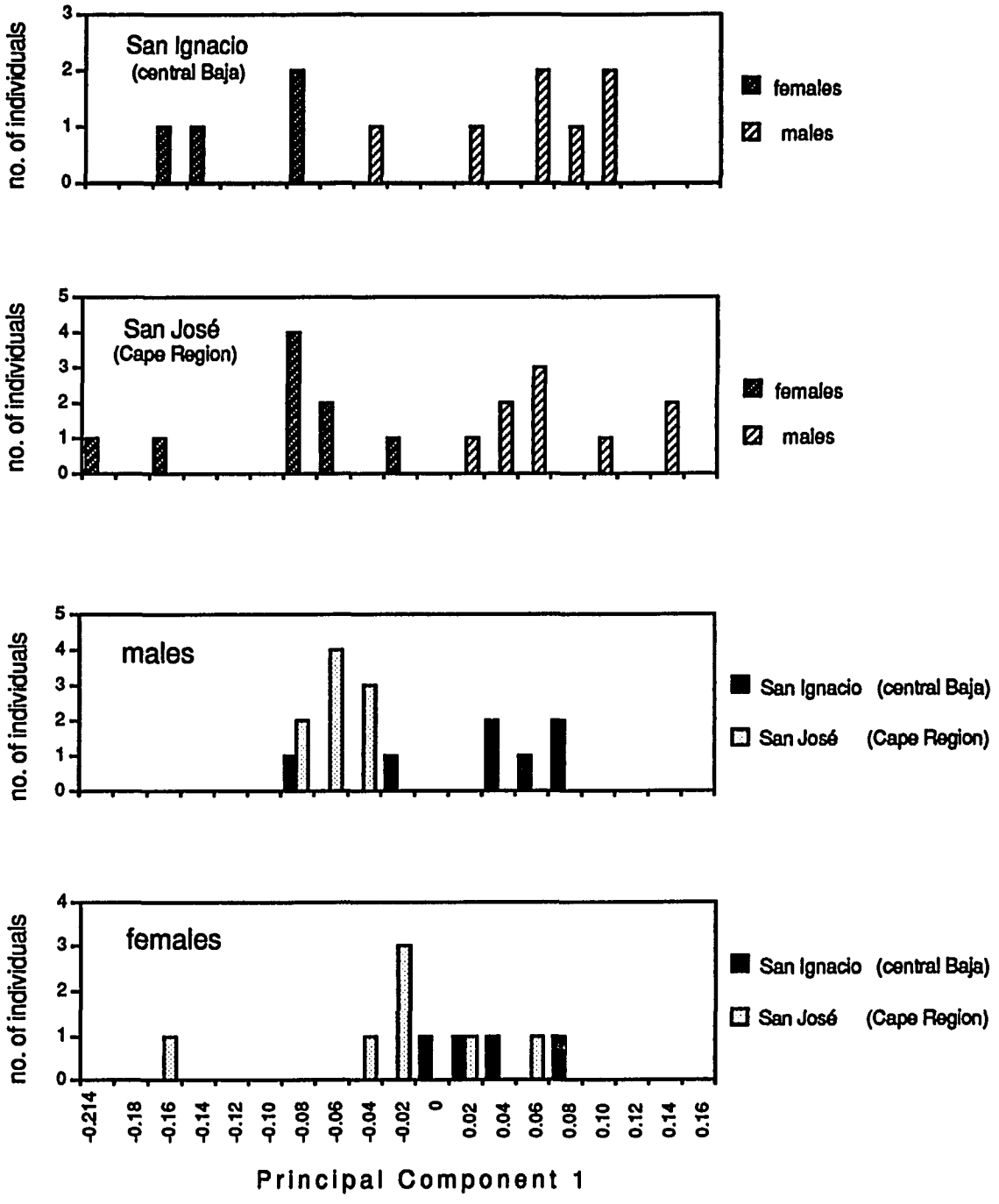


Fig. 4


San Ignacio
(central Baja)
females
males
no. of individuals
San José
(Cape Region)
females
males
no. of individuals
males
San Ignacio (central Baja)
San José (Cape Region)
no. of individuals
females
San Ignacio (central Baja)
San José (Cape Region)
no. of individuals
-0.214
-0.18
-0.16
-0.14
-0.12
-0.10
-0.08
-0.06
-0.04
-0.02
0
0.02
0.04
0.06
0.08
0.10
0.12
0.14
0.16
Principal Component 1

Chapter 2

# GENETIC DIFFERENTIATION IN YELLOWTHROATS (PARULINAE: GEOTHLYPIS)

by

Bertha Patricia Escalante-Pliego

Department of Ornithology, American Museum of Natural History, City University of New York, and Museo de Zoología de la Facultad de Ciencias de la Universidad Nacional Autónoma de México

## A B S T R A C T

Allozyme variation is analyzed within and among populations of Neotropical and Nearctic species of Yellowthroats (Parulinae: Geothlypis). Results indicate that the populations assayed have levels of variability comparable with those of other birds. As indicated by $F_{st}$ values, heterogeneity tests, and genetic distances among populations, the Northern Temperate species (G. trichas) is less differentiated genetically than Neotropical taxa. The Baja California populations of G. beldingi are only slightly differentiated; more so are the Middle American populations of G. poliocephala. Differentiation among the Neotropical populations of the G. aequinoctialis complex is substantial and coincides with populations having disjunct ranges. It is likely that there is more than one species in G. aequinoctialis as previously understood. These results, along with other findings on Amazonian forest species, indicate that Neotropical avifaunas are more genetically differentiated than are their Nearctic relatives. This suggests that they could be older evolutionarily.

# I N T R O D U C T I O N

As part of a study on the phylogeny of Yellowthroats (Parulinae: Geothlypis), I used allozyme electrophoresis to survey genetic variation in a series of populations of nine taxa. This technique provides data for phylogenetic analyses among closely related species, and for estimating parameters of population differentiation within species. Studies of the genetic structure of natural populations provides information critical to an understanding of population dynamics, modes of speciation, and phenotypic diversity (Templeton 1980, Barrowclough 1983, Zink and Remsen 1986).

The study of genetic diversity within and among the more than 2500 species of Neotropical birds is in its infancy. In the few species examined to date (only about twelve intraspecifically), workers have found that populations of avian species living in Amazonian forests are more structured spatially than are populations of temperate species, but have equivalent levels of genetic variability (Braun & Parker 1985, Capparella & Lanyon 1985, Capparella 1987, Gerwin & Zink 1989, Hackett & Rosenberg 1990, Gill & Gerwin 1989). To place these findings in a broader context, it is critical to investigate species associated with Neotropical habitats other than lowland rainforests. Because of their wide distribution in open wetlands, warblers of the genus Geothlypis offer an opportunity to compare genetic variability, population structure, and habitat restriction in both temperate and tropical America.

In this paper, I summarize data obtained from an electrophoresis analysis of members of this complex. My objective is to evaluate the nature of allozymic variation at the population and geographic levels in

Neotropical and Nearctic Yellowthroats in the light of our knowledge of such variation in other species.

## THE YELLOWTHROAT COMPLEX

As currently recognized (American Ornithologists' Union 1983), Geothlypis is composed of nine species, most of which are allopatric. Geothlypis taxa inhabit marshes, but most forms have broader habitat tolerances, and also occupy other wetlands where tall grass, brush, second growth and sugarcane grow.

In North America, G. trichas (Common Yellowthroat) is widely distributed (Figure 1) with populations ranging from completely migratory in the north, to sedentary in central Mexico. In this latter area they co-occur in marshes of the interior valleys with G. speciosa (Black-polled Yellowthroat). In the southernmost part of its range (South Central Mexico), G. trichas also overlaps with G. poliocephala (Gray-crowned Yellowthroat); they both breed in sugarcane fields that have replaced natural marshes. None of these instances of sympatry seem to involve close relatives, based on an analysis of plumage characters (Escalante-Pliego, in prep.). Besides G. speciosa, forms with restricted ranges also associated with marshes are G. beldingi (Belding's Yellowthroat) in the Peninsula of Baja California, and G. flavovelata (Altamira Yellowthroat) in northeastern Mexico. Although sharing an affinity for wet habitats, other Yellowthroats have broader habitat tolerances. G. nelsoni (Hooded Yellowthroat) is found in Mexico along the humid slopes of the eastern mountains. G. rostrata (Bahama Yellowthroat) occurs in bush and abandoned sugarcane fields in some of the Bahama Islands. In the lowlands of Mexico, Central America, and

western South America south to Ecuador, G. poliocephala and G. semiflava (Olive-crowned Yellowthroat) replace each other from north to south near streams in marshy and humid brushy areas of second growth lowland forests. In Nicaragua, Costa Rica, and western Panama, where their ranges are in contact, G. poliocephala is found in drier areas (Figure 2).

The South American representative of the group, G. aequinoctialis (Masked Yellowthroat) is widely distributed, and occurs in several kinds of wetlands, including marshes. The geographic range of the aequinoctialis complex is made up of four disjunct areas (Figure 3): the peripheral form of western Costa Rica and western Panama (chiriquensis), sometimes regarded as a separate species (AOU, 1983); the trans-Andean or Pacific slope form (auricularis group); and two cis-Andean forms, one north (nominate aequinoctialis group), and one south of the Amazon Basin (velata group).

## M E T H O D S

### STUDY AREAS AND SAMPLES

Samples were collected on breeding grounds in Mexico, Costa Rica, Venezuela, Florida (USA), and the Bahamas, between 1987 and 1989 (Figures 1, 2, and 3). Exact localities are available from the author. The habitat visited in Chapala, Cuitzeo, and Zupitlán is marshland. The marshes of the interior basins of Mexico have been much reduced in the last 500 years through alluviation, desiccation and artificial draining (Tamayo and West, 1964). Aside from marshes, G. trichas was found in sugarcane fields around Cuitzeo, and Yautepec. In the arid peninsula of Baja California, marshes are widely scattered. In northern Baja

California, G. trichas was found along the streams that originate in the western slope of the Sierra de Juárez (San Telmo). In the central desert of the peninsula G. beldingi was found in the springs of San Ignacio, and at the southern tip of the Peninsula (San Jose). The extensive marsh at Altamira (Laguna Champayan) receives a large discharge from the Panuco River. The lake and inundated area around it extends several hundred square kilometers. At San Vito (Costa Rica) and Caucagua (Venezuela), the habitats where Geothlypis was found, are flooded seasonally but are not true marshes; grassy meadows in San Vito, brush and sugarcane fields in Caucagua. The remainder of the localities have a range of open and humid lands or scrub along streams.

Following collection, liver, heart, and breast muscle were preserved in liquid nitrogen until transported to the laboratory, where they were stored at -70ºC.

Additional samples from the USA (Rhode Island), Peru, and Bolivia were obtained from other frozen tissue collections (see Acknowledgements).

## ELECTROPHORESIS

Allozyme variation was assayed for 271 Yellowthroat tissue samples for 32 enzymatic loci following standard techniques (Selander et al. 1971, Harris & Hopkinson 1976, Richardson et al. 1986). The 32 loci scored are: ACON-1, ACON-2, ADA, ADH, DIA, EAP, EST-1, ESTD, FUM, GDA, GDH, GOT-1, GOT-2, GPDH, G-3-PDH, G-6-PDH, IDH-1, IDH-2, LAP, LDH-1, LDH-2, MDH-1, MDH-2, ME, NP, PEP-A, PEP- B, PEP-C, PGM-1, PGM-2, PGM-3, and SDH.

Parameters of genetic variability and differentiation were estimated using several computer programs: BIOSYS-1 (Swofford and

Selander 1989) for allelic frequencies, heterozygosities, percent of polymorphic loci, chi square tests of heterogeneity, Hardy- Weinberg equilibrium tests, Nei's (1978) and Rogers' (1972) genetic distances; NEI2 for heterozygosities and genetic distances, and BOOTFST which provides Wright (1978) $F_{st}$ values with their confidence intervals calculated through a bootstrap approach.

# R E S U L T S

## GENETIC VARIABILITY

Of the 32 loci scored, 10 were monomorphic for all populations, 6 were private polymorphisms unique to individual populations, and the other 16 showed shared polymorphisms among populations and/or species. For samples with over five individuals, none of the variable loci showed significant ($P<.001$) departures from Hardy-Weinberg equilibrium. Detailed allelic frequencies will be reported elsewhere (Escalante-Pliego, in prep.). Table 1 shows the average heterozygosity per locus, and the percent of polymorphic loci for each population. Measures of interpopulational differentiation were calculated for species with more than one representative sample.

## POPULATION DIFFERENTIATION IN YELLOWTHROAT SPECIES

The samples of the G. trichas used in this study comprise a considerable part of the total geographic range. Tests of heterogeneity were not significant for 15 of 19 variable loci. Two loci at which electrophoresis detected substantial geographic differentiation were PGM-1 and PEP-B. At the PGM-1 locus ($P<.001$), the western samples,

including San Telmo and three localities of west-central Mexico, shared a polymorphism which was absent in the eastern samples (Rhode Island, Florida, and Zupitlán). At the PEP- B locus the heterogeneity test among populations was significant (P<.009); all the samples have the same common allele in frequencies ranging from 0.5 to 1.0; the frequencies of the less common allele showed no apparent geographic trend. At the G-6-PDH locus, allelic frequencies were significantly different (P<.045) because of the absence of an uncommon allele in two populations (Zupitlán and Rhode Island). At SDH a significant difference (P<.015) was due to the presence of an allele in the northeasternmost population assayed (Rhode Island). This allele is shared with Bahamian G. rostrata. Mean $F_{st}$ values in the trichas complex was 0.077 (95% confidence interval: 0.012-0.112). Averaged Nei's genetic distance for all G. trichas populations was 0.004. Only the GDA locus showed a significant difference (P<.005) between the two samples of G. beldingi on the Peninsula of Baja California. The $F_{st}$ value was 0.059 (95% confidence interval 0.001- 0.171); Nei's (1978) genetic distance was 0.011. The two single samples of G. poliocephala came from widely separated areas of their distribution that represent some of the well differentiated subspecies. Tests of heterogeneity were significant for two loci: PEP-C (P<.001), and PGM-2 (P<.07); the $F_{st}$ value was 0.199 (95% confidence interval 0.027-0.281), and Nei's (1978) genetic distance was 0.011.

In G. aequinoctialis of South America and Costa Rica, fixed differences were found between various populations at the GDA and ME loci. Differences were also large at other variable loci, giving significant tests of heterogeneity at 8 of 12 loci (P<.005 for five loci, P<.02 in three loci). This consistent differentiation across loci is reflected in a high $F_{st}$ value of 0.553 (95% confidence interval:

0.312-0.751). Averaged Nei (1978) genetic distances among the four populations were 0.1245, but the sample from Venezuela had a higher average value (0.1445). The use of Rogers' distances provided similar results. A clustering of Rogers' distances superimposed in the distribution of the G. aequinoctialis complex is shown in Figure 3.

## D I S C U S S I O N

Levels of intrapopulation variability (Table 1) in Geothlypis species are within the range of those previously reported for birds (Braun & Parker 1985, Capparella 1987, Nevo et al. 1984). Due to differences in sample size, and because heterozygosities have large standard errors, a statistical test cannot be performed among the populations associated with different habitats. However, it is noticeable that G. speciosa had low heterozygosity and few polymorphic loci. Some populations that are restricted to marshes, such as G. beldingi and G. trichas of Zupitlán, also have low numbers of polymorphic loci, but similar heterozygosity scores. A dissimilar pattern in other marsh inhabitants is observed in Table 1.

The sample of G. trichas from Zupitlán shows some signs of isolation: Zupitlan's average genetic distance of 0.0052 is higher than that of the combined average of all the populations in the trichas complex (0.0036). These values are due to significant differences in frequencies at the PGM-1 and PEP-B loci, as mentioned earlier. Zink and Klicka (1990) examined allozyme variation in the trichas complex using samples from presumed sedentary (Texas), and migratory (Minnesota) populations, and found an $F_{st}$ value of 0.04. An equivalent comparison

using San Telmo, Rhode Island and Florida samples also yields an $F_{st}$ value of also 0.04. Considering the sedentary populations in the south only, the $F_{st}$ value increases to 0.08, but if we ignore Zupitlán, the three remaining populations yield a value of 0.034, similar to the northern part of the trichas complex. Because they colonize and breed in sugarcane fields, populations in the rest of the Mexican Plateau perhaps have maintained a larger amount of gene flow in contrast to those of the more arid part of the Plateau where Zupitlan is located.

For other forms, such as G. beldingi of Baja California, the scattered distribution of marshes seems to have affected population structure and restricted gene flow. The slight phenotypic differentiation between the two populations is concordant with the slight genetic differentiation in these two populations. The estimates of $F_{st}$ and Nei's (1978) genetic distance for the Middle American G. poliocephala were approximately twice those in the trichas complex and in beldingi. This genetic divergence is paralleled by phenotypic distinctiveness.

The results for the aequinoctialis complex were more surprising as they suggest more advanced differentiation than the current classification reflects. Very high $F_{st}$ values, significant tests of heterogeneity, and large genetic distances show a pattern of divergence between the northern Amazonian form aequinoctialis and the other three forms. This pattern contrasts with the phenotypic differentiation observed. Plumage patterns are conservative in the complex, except for a reduction of the mask patch in the Pacific slope form (auricularis).

In this first study of a non-forest group, the Neotropical species of Geothlypis showed increasing levels of population differentiation

from north to south. $F_{st}$ values of Nearctic populations of the trichas complex compare well with other values found in warblers of North America, such as 0.03 in well marked subspecies of Dendroica coronata (Barrowclough 1980). $F_{st}$ values increased in the Middle and South American Geothlypis species. The genetic distance values obtained here correlate well with values obtained for parulines (Barrowclough & Corbin 1978), with an average Nei's (1978) genetic distance of 0.100 for species level differentiation. In this context, the four allopatric forms of the aequinoctialis complex would seem to deserve species rank.

## A C K N O W L E D G E M E N T S

Financial support was provided by the Frank M. Chapman Memorial Fund (American Museum of Natural History), the Alexander Wetmore Fund (American Ornithologists' Union), the Graduate Studies Committee of the Biology Program (City University of New York), and Sigma Xi. I thank officers and colleagues who helped me to obtain collecting permits: Secretaría de Desarrollo Urbano y Ecología (México), Ministerio de Recursos Naturales, Energía y Minas (Costa Rica), Department of Agriculture (Bahamas), State of Florida Game and Fresh Water Fish Commission, and the U. S. Fish and Wildlife Service. Many people shared in the field work with me and made much of my investigation possible. I am especially grateful to Robert M. Zink and Jay Pitocchelli for providing me with partial tissues for assays. I thank George F. Barrowclough, François Vuilleumier, Town Peterson, Charles Myers, and Angelo Capparella for advice and help. I am indebted to my friends and colleagues at the Museo de Zoología de la Facultad de Ciencias de la

UNAM (México) for uninterrupted moral support.

## L I T E R A T U R E  C I T E D

American Ornithologists' Union.
1983. Check-List of birds of North America. American Ornithologists' Union. 6th Edition.

Barrowclough, G. F.
1980. Genetic and phenotypic differentiation in a Wood Warbler (genus Dendroica) hybrid zone. Auk 97:655- 668.

_____.
1983. Biochemical studies of microevolutionary processes. Pp. 223-261. In: Perspectives in Ornithology (A. H. Brush and G. A. Clark, eds.). New York, Cambridge University Press.

_____ and K. W. Corbin.
1978. Genetic variation and differentiation in the Parulidae. Auk 95:691-702.

Braun, M. J. and T. A. Parker, III.
1985. Molecular, morphological, and behavioral evidence concerning the taxonomic relationships of "Synallaxis" gularis and other synallaxines. Pp. 333-346 in Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely and F. G. Buckley, eds.). Ornithological Monographs No. 36.

Capparella, A.
1987. Effects of riverine barriers on genetic differentiation of amazonian forest undergrowth birds. PhD. thesis. Louisiana State University and Agricultural and Mechanical College.

Capparella, A. P. and S. M. Lanyon.
1985. Biochemical and morphometric analysis of the sympatric, Neotropical, sibling species Mionectes macconnelli and M. oleagineus. Pp. 347-355 in Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely and F. G. Buckley, eds.). Ornithological Monographs No. 36.

Gerwin,, J. A. and R. M. Zink.
1989. Phylogenetic patterns in the genus Heliodoxa (Aves: Trochilidae): An allozymic perspective. Wilson Bulletin 101: 525-544.

Gill, F. B. and J. A. Gerwin.
1989. Protein relationships among Hermit Hummingbirds. Proceedings of the Academy of Natural Sciences of Philadelphia 141:409-421.

Hackett, S. J. and K. V. Rosenberg.
1990. Comparison of phenotypic and genetic differentiation in south american antwrens (Formicaridae). Auk 107: 473-489.

Harris, H. and D. A. Hopkinson.
1976. Handbook of enzyme electrophoresis in human genetics. Oxford: North Holland Publications Company.

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

Nevo, E., A. Beiles, and R. Ben-Shlomo.
1984. The evolutionary significance of genetic diversity: ecological, demographic and life history correlates. Pp. 13-213 in Evolutionary dynamics of genetic diversity. (G. S. Mani, ed.). New York, NY, USA.

Richardson, B. J., P. R. Baverstock, and M. Adams.
1986. Allozyme electrophoresis. Sydney, Australia. Academic Press.

Ridgely, R. S. and G. Tudor.
1989. The Birds of South America. Vol 1. University of Texas Press, Austin, Texas, USA.

Rogers, J. S.
1972. Measures of genetic similarity and genetic distance. Studies in Genetics. Univ. Texas Publ. 7213: 145- 153.

Selander, R. K., M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry.
1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (Peromyscus polionotus). Studies in Genetics VI. University of Texas Publication 7103: 49-90.

Swofford, D. L. and R. B. Selander.
1989. BIOSYS-1. A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Champaign, Illinois, USA.

Tamayo, J. L. and R. C. West.
1964. The hydrography of Central America. In, Handbook of Middle American Indians. Vol. 1. Natural environment and early cultures. Univ. Texas Press. Austin, Texas, USA.

Templeton, A.
1980. Modes of speciation and inferences based on genetic distances. Evolution 34: 719-729.

Wright, S.
1978. Evolution and the genetics of populations. Volume 4. Variability within and among natural populations. University of Chicago Press, Chicago, Illinois, USA.

Zink, R. M. and J. T. Klicka.
1990. Genetic variation in the Common Yellowthroat and some allies. Wilson Bull. 102:514- 520.

Zink, R. M. and J. Van Remsen.
1986. Evolutionary processes and pattern of geographic variation in birds. Current Ornithology vol. 4 (R. F. Johnston, ed.). Plenum Press, NY, pp. 1-69.

TABLE 1. Genetic variation in populations of Geothlypis species calculated over 32 loci.

| | Habitat | N | Het | SE | P.L. |
|---|---|---|---|---|---|
| Geothlypis trichas | | | | | |
| Rhode Island (USA) | s | 13 | .0411 | (.0160) | 22 |
| Osceola (Florida, USA) | s | 13 | .0449 | (.0146) | 31 |
| Zupitlan (México) | m | 15 | .0298 | (.0206) | 13 |
| Yautepec (México) | c | 15 | .0322 | (.0156) | 19 |
| Cuitzeo (México) | m,c | 14 | .0585 | (.0213) | 28 |
| Chapala (México) | m | 12 | .0531 | (.0242) | 19 |
| San Telmo (México) | s | 15 | .0509 | (.0226) | 19 |
| Geothlypis beldingi | | | | | |
| San Ignacio (México) | m | 18 | .0384 | (.0194) | 9 |
| San Jose (México) | m | 36 | .0442 | (.0248) | 13 |
| Geothlypis flavovelata | | | | | |
| Altamira (México) | m | 7 | .0633 | (.0307) | 16 |
| Geothlypis nelsoni | | | | | |
| Huauchinango (México) | s | 14 | .0500 | (.0233) | 19 |
| Geothlypis rostrata | | | | | |
| Abaco (Bahamas) | s | 17 | .0481 | (.0211) | 19 |
| Geothlypis speciosa | | | | | |
| Cuitzeo (México) | m | 23 | .0106 | (.0080) | 9 |

TABLE 1

(continued)

| | Habitat | N | Het | SE | P.L. |
|---|---|---|---|---|---|
| *Geothlypis semiflava* | | | | | |
| Pto Viejo (Costa Rica) | s | 19 | .0343 | (.0155) | 28 |
| *Geothlypis aequinoctialis* | | | | | |
| San Vito (Costa Rica) | m | 9 | .0577 | (.0285) | 13 |
| Santa Cruz (Bolivia) | m? | 2 | .0469 | (.0345) | 6 |
| Lambayeque (Perú) | m? | 3 | .0521 | (.0309) | 9 |
| Caucagua (Venezuela) | s | 8 | .0656 | (.0242) | 25 |
| *Geothlypis poliocephala* | | | | | |
| Cartago (Costa Rica) | s | 5 | .0250 | (.0196) | 6 |
| Yautepec (México) | c | 13 | .0478 | (.0212) | 22 |

Habitat: s = shrubby and along streams; m = marsh; c = cane fields.

N = sample size.

Het = Average heterozygosity per locus. P.L. = per cent of polymorphic loci (99% of frequency criterion).

Fig. 1. Distributional range of four Geothlypis species and sample localities mentioned in the text. US: Rhode Island (not in map); Florida, Osceola. Bahamas, Abaco. México: Hidalgo, Zupitlan; Morelos, Yautepec; Michoacan, Lago de Cuitzeo; Jalisco, Lago de Chapala East; Baja California Norte, San Telmo; Baja California Sur, San Ignacio ; Baja California Sur, San Jose; Tamaulipas, Altamira.

Fig. 2. Distributional range of four Geothlypis species and sample localities mentioned in the text. Mexico: Michoacan, Lago de Cuitzeo; Morelos, Yautepec; Puebla, Huauchinango. Costa Rica, Cartago; El Limon, Puerto Viejo.

Fig. 3. Branching diagram from distance Wagner procedure using Rogers distances for the four samples of G. aequinoctialis superimposed on distributional ranges (adapted from Ridgely & Tudor 1989). Branch lengths are arbitrary. Localities: San Vito (Puntarenas, Costa Rica); Caucagua (Miranda, Venezuela); Lambayeque (Peru); and Santa Cruz (Bolivia).

Fig. 1

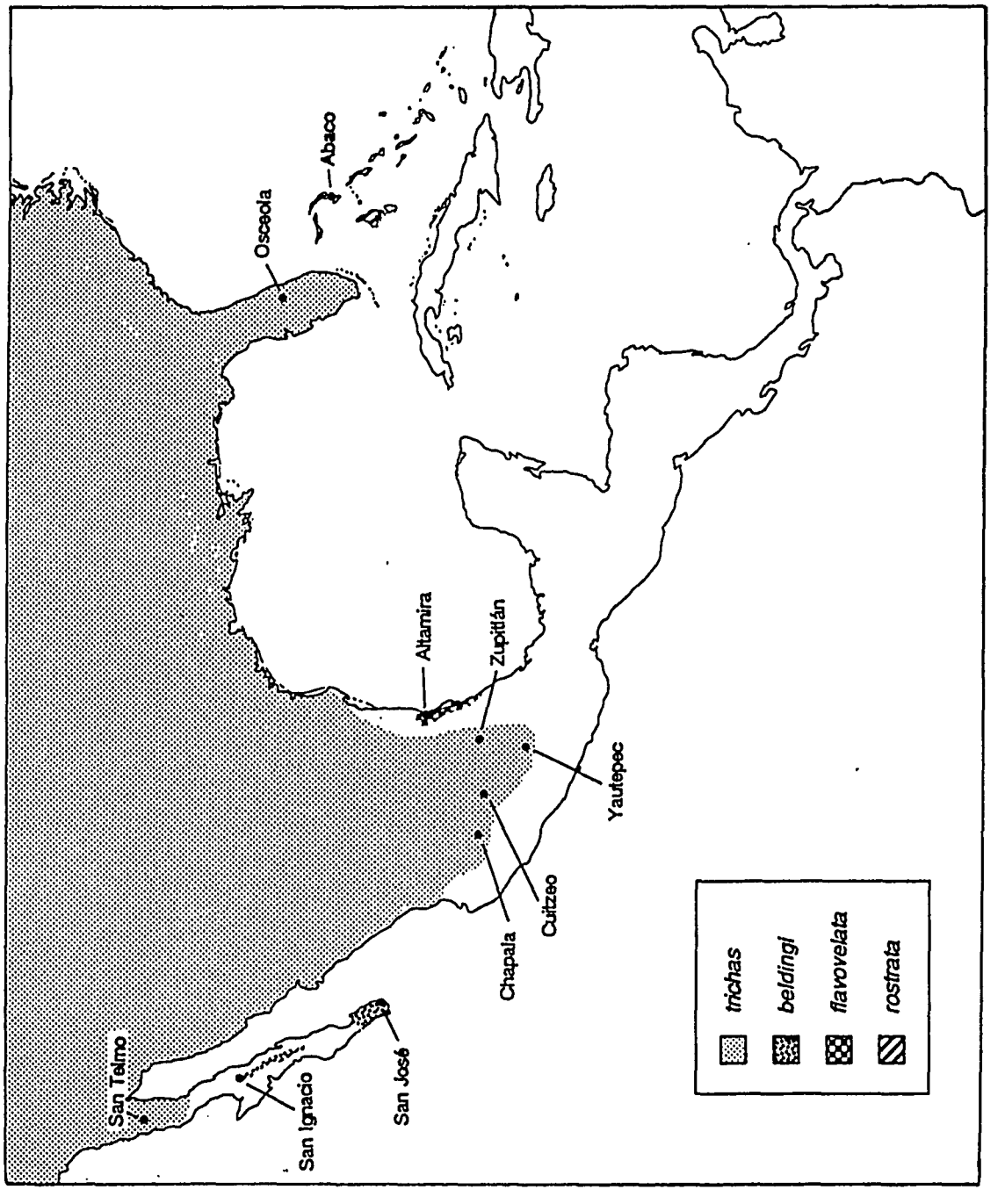

Abaco
Osceola
Altamira
Zupitlán
Yautepec
Cuitzeo
Chapala
San José
San Ignacio
San Telmo
trichas
beldingi
flavovelata
rostrata

Fig. 2

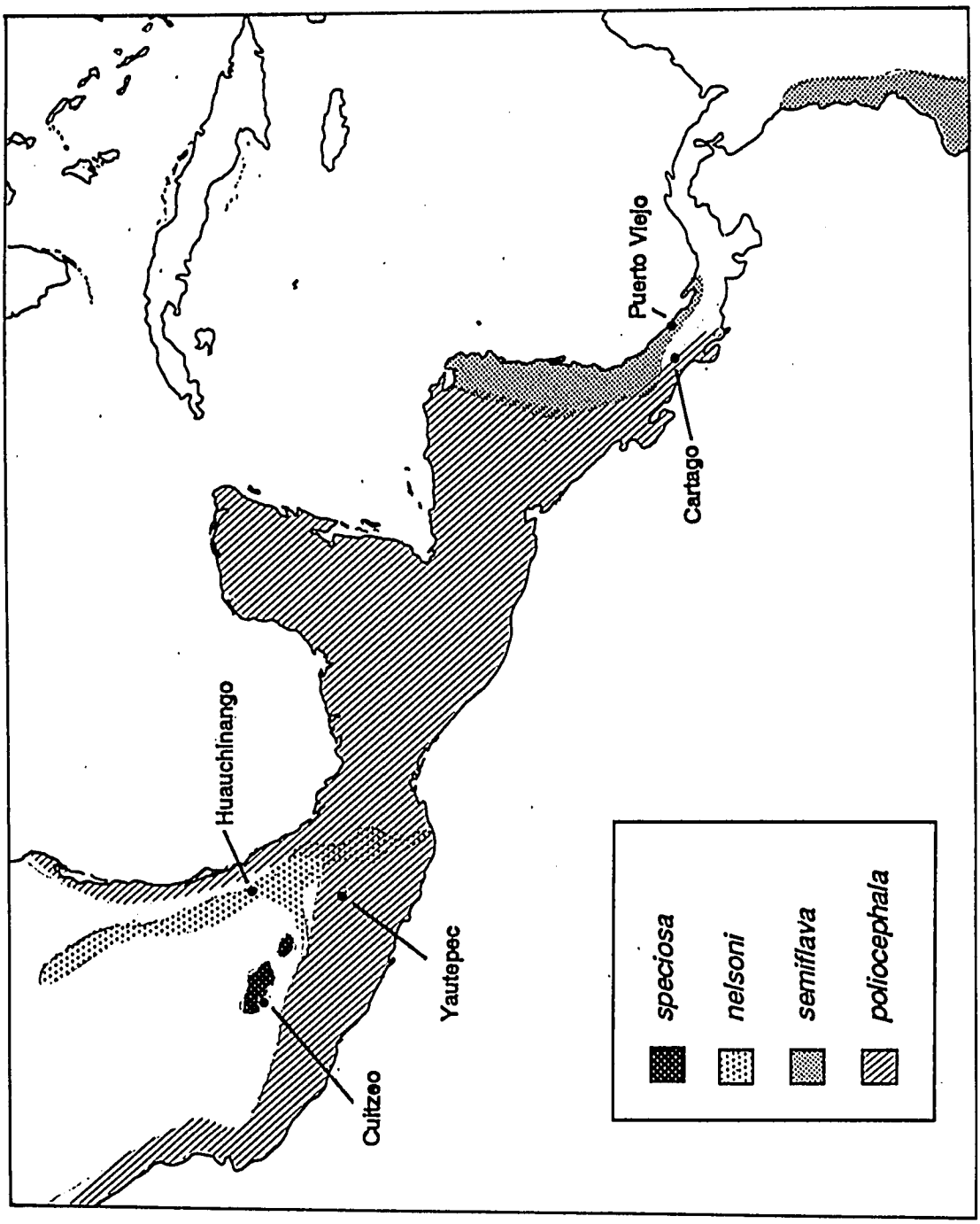
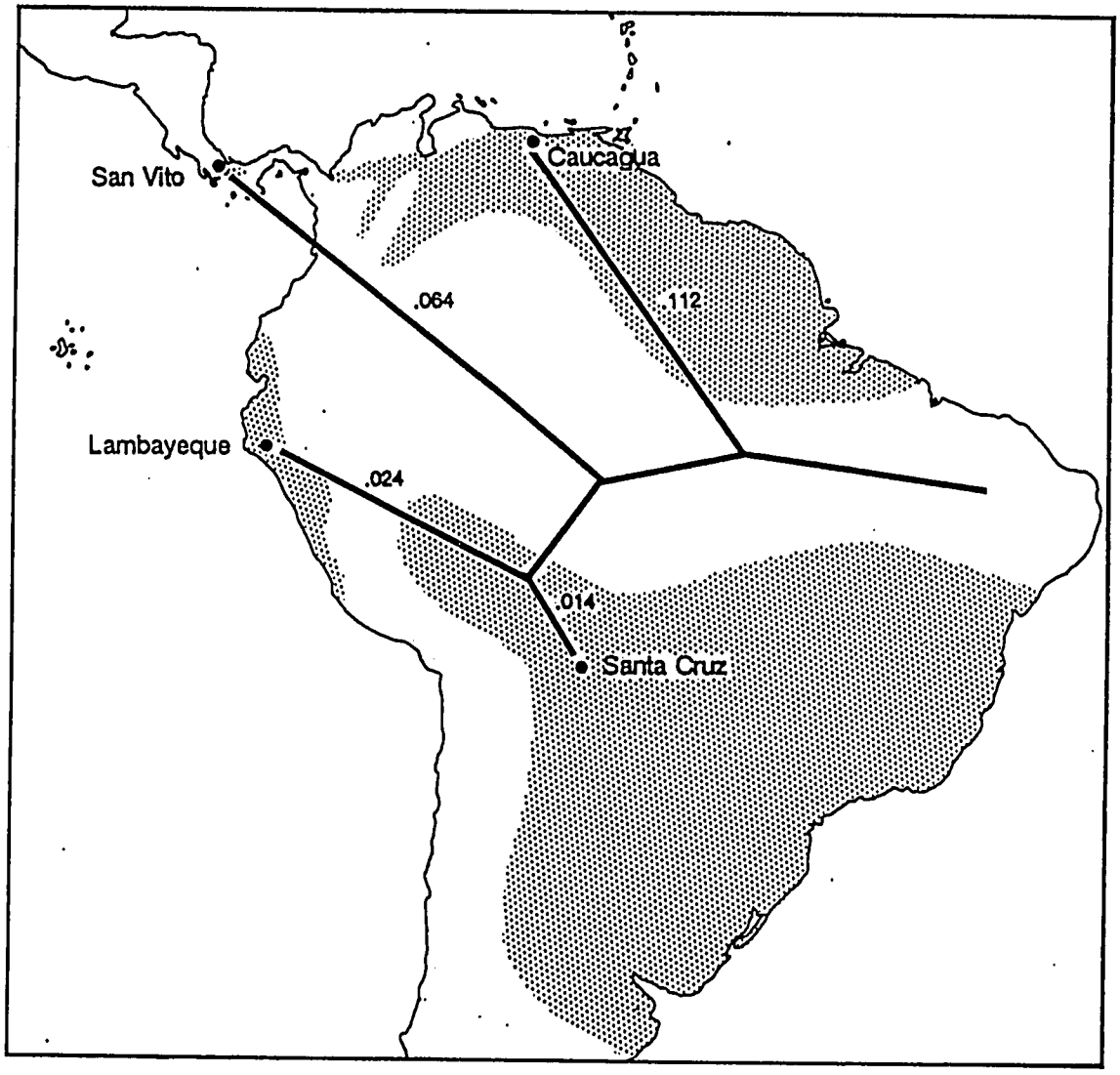

Puerto Viejo
Cartago
Huauchinango
Yautepec
Cuitzeo
speciosa
nelsoni
semiflava
poliocephala

Fig. 3



# Chapter 3

## PHYLOGENETIC RELATIONSHIPS OF YELLOWTHROATS (PARULINAE: *GEOTHLYPIS*) USING ALLOZYMES

## A B S T R A C T

In order to obtain a phylogeny of Yellowthroats (*Geothlypis*, paruline warblers), allozyme data were analyzed using a variety of methods and assumptions. Several putative outgroups were used, including *Oporornis*, *Basileuterus*, and *Protonotaria*. Data were examined either as frequency of alleles, reduction to a genetic distance, or by discrete allele coding. Methods implemented were UPGMA, Fitch-Margoliash, distance Wagner, frequency parsimony, maximum likelihood, and Wagner, Dollo, and polymorphism parsimony. The preferred solution was polymorphism parsimony, on the basis of the reasonable concordance found with plumage pattern, and with a biogeographically parsimonious scenario. This more compelling phylogenetic hypothesis indicates that neither *Geothlypis* nor *Oporornis* as currently recognized are monophyletic genera, but that together they form a monophyletic assemblage. This finding is due, in part, to the grouping of *Oporornis formosus* with *Geothlypis* as traditionally defined, rather than in *Oporornis* as has been recognized in the past. Due to the diverse solutions obtained in this study it will be desirable to test the proposed phylogeny with new data when they become available.

# I N T R O D U C T I O N

Yellowthroats are paruline warblers traditionally placed in the genus Geothlypis. They occur in marshes and other wet habitats, as well as dry and open habitats of the Americas. Taxa in this genus exhibit different patterns of distribution and behavior, such as geographically isolated versus widespread, temperate versus tropical, and sedentary versus migratory populations. Reconstructing the genealogical history of the genus is an important component for understanding biogeographic patterns, speciation, and character evolution in the group, and for comparisons with other avian groups occurring in similar habitats, or with similar life histories (Cracraft 1982, Funk and Brooks 1990, Wanntorp et al. 1990).

Paruline genera have been defined traditionally by external features such as tarsus length (i.e., Mniotilta), plumage patterns (i.e., Dendroica), wing length (i.e., Oporornis), and bill morphology and rictal bristles (i.e., Basileuterus) (Sharpe 1885, Ridgway 1902). Geothlypis is distinguished from other genera of yellowish warblers that lack white tail patches, barred wings, and rictal bristles, by a black "mask" extending widely from the forehead to the malar and auricular area behind the eye, and by the rounded shape of the wings and tail (Chapman 1907). Central and South American Yellowthroats, however, have a reduced black mask. This plumage pattern, plus overall similarity and habitat preference -but not song (Davis 1972)- indicate that Geothlypis is perhaps monophyletic, but additional characters are needed to confirm monophyly.

The phylogeny of parulines has not been investigated in detail. Morphologically, parulines as well as the rest of the nine-primaried

oscines are very similar, except for bill features (Tordoff 1954, Raikow 1978). The results of DNA hybridization (Sibley and Ahlquist 1990) and allozyme studies (Barrowclough and Corbin 1978, Avise et al. 1980) have suggested that the North American members of the subfamily Parulinae are monophyletic, but that the systematic allocation of many Central and South American genera remains uncertain (eg. Zeledonia, Conirostrum).

Because there is no satisfactory phylogenetic hypothesis for the parulines, the sister group of Geothlypis has not been clearly identified. Based on plumage similarities and the occurrence of hybrids (Bledsoe 1988), the four species of Oporornis were merged in Geothlypis in some taxonomic treatments (Lowery and Monroe 1968). Raikow (1978), however, reported that Geothlypis shares with Basileuterus a feature of the forelimb musculature that does not appear in Oporornis and other parulines. He suggested that Geothlypis and Basileuterus are sister groups. The polarity of this character is equivocal, however, with respect to other nine-primaried oscines (Emberizidae). Sibley and Ahlquist (1982) found Icteria to be closer to Geothlypis than to other parulines or emberizines based on their DNA-DNA hybridization experiments.

Because molecular studies have not included representative samples of all relevant taxa, and because morphological character states are equivocal with respect to outgroups, the monophyly of Geothlypis and the relationships of the genus to other parulines remain to be convincingly established. The purpose of this study was to investigate the phylogenetic relationships of Geothlypis using allozyme electrophoresis. Since the genus has not been revised for many years, I also studied intraspecific variability and species limits, especially in widespread forms. This detailed scrutiny allowed me to use local populations as

operational taxonomic units, and to interpret character variability by taking into account geographic variation. Results of intraspecific variability and species limits are given elsewhere (Escalante-Pliego, in prep.).

## M E T H O D S

### Collection of samples

Fresh tissue samples were collected from resident birds on their breeding grounds. A special effort was made to collect multiple samples of widespread species. Collecting localities are described elsewhere (Escalante-Pliego, in prep.); sample sizes (number of individuals collected) are given below in parentheses. All 12 nominal taxa of Geothlypis were sampled. The Common Yellowthroat, G. trichas was represented by seven samples from extremes of its geographic range (13, 13, 15, 15, 14, 12, and 15). The habitats where Common Yellowthroats were found varied somewhat throughout their range. In Baja California Norte and Florida, Yellowthroats were found along streams with cattails and reeds, whereas in the Central Plateau of Mexico resident Yellowthroats occupy marshes and cane fields. The Belding's Yellowthroat, G. beldingi, was collected at two sites in the scattered marshes of the Peninsula of Baja California (18, 36). The Altamira Yellowthroat, G. flavovelata, was sampled at Altamira, Tamaulipas, Mexico (7). The Bahama Yellowthroat, G. rostrata, was collected on Abaco, Bahamas (17), in open areas of second growth in abandoned cane fields. The Olive-crowned Yellowthroat, G. semiflava, was collected at El Limon, Costa Rica (19), in humid lowlands with secondary rain forest. One additional tissue sample from Mindo, Pichincha, Ecuador (1) was also

included. The Black-polled Yellowthroat, G. speciosa, occurs in sympatry with the Common Yellowthroat in the Central Plateau of Mexico; a sample from Cuitzeo, Michoacán, México (23) was analyzed. The Hooded Yellowthroat, G. nelsoni, was sampled 2 km NE of Huauchinango, Puebla, México (14). Two samples representing two forms of the Masked Yellowthroat were collected: G. chiriquensis at San Vito, Puntarenas, Costa Rica (9); and G. aequinoctialis from Miranda, Venezuela (8). Both forms occur in seasonally inundated habitats. Additional samples for two other forms were obtained through inter-museum loans (see acknowledgements): G. velata from Santa Cruz, Bolivia (2), and G. auricularis from Lambayeque, Peru (3). The Gray-crowned Yellowthroat, G. poliocephala, was collected from two widely separated localities: at Yautepec, Morelos, México (13), in cane fields of the humid lowlands - where it is sympatric and syntopic with the Common Yellowthroat; and at El Radio, Cartago, Costa Rica (5), in open semi-dry areas.

Samples of outgroups were either collected during spring migration in several habitats, or were obtained through loans from other tissue collections. Outgroups included were: putatively closely related species of Oporornis [O. formosus (N=13), O. agilis (8), O. philadelphia (5), and O. tolmiei (16)]; of Basileuterus [B. luteoviridis (2), B. coronatus (2), B. chrysogaster (1), B. culicivorus (2), B. rufifrons (2), B. belli (2), B. melanogenys (2), and B. tristriatus (2)]; and the single species, Icteria virens (3). Other parulines and thraupines also assayed were: Vermivora ruficapilla (1), Parula americana (1), Dendroica petechia (3), D. coronata (1), D. townsendi (1), D. virens (1), Setophaga ruticilla (2), Protonotaria citrea (3), Helmitheros vermivorus (3), Limnothlypis swainsonii (2), Seiurus auricapillus (2), S. noveboracensis (3), Wilsonia citrina (5), W. pusilla (11), W. canadensis

(5), Ergaticus ruber (2), Myioborus pictus (2), M. miniatus (2), Euthlypis lachrymosa (3) Zeledonia coronata (1), Granatellus pelzeni (2), Chrysothlypis chrysomelas (4), Hemithraupis guira (6), Thlypopsis sordida (2), T. ornata (2), T. ruficeps (6), and Piranga bidentata (1).

## Electrophoresis

Starch gel electrophoresis and specific isozyme staining recipes were used following standard protocols (Richardson et al. 1986). Initially, a sample 5 birds from each locality/species of Yellowthroat was assayed using four different buffer systems and running times, to select the conditions where the clearest separation could be obtained, and where hidden variation could be detected (Hackett 1989). Buffer systems were: Citrate-Amine pH 6.1, Citrate-Amine 7.5, Tris Citrate pH 8.0, and a discontinuous system of Lithium Borate pH 9.1 with gel buffer of Tris Citrate pH 8.6. Once the optimal conditions had been selected for each enzyme, I conducted more assays to expand the sample sizes and to include outgroups. In order to make scores comparable across gels, individual controls were repeated in subsequent gels. Finally, control gels were used to compare equally scored alleles side by side. Scoring was considered reliable when the heterozygotes showed a pattern of bands that agreed with the hypothetical quaternary structure of the enzyme being assayed (monomer: two bands, dimer: three bands, trimer: four bands, etc.), and when the homozygote of the less common allele was also present (Richardson et al. 1986). Numerous recipes investigated in bird taxa were tested to include as many loci as possible, but only 32 out of 49 gave satisfactory resolution for scoring. Loci scored and retained for analysis were: ACON-1 and ACON-2 (4.2.1.3), ACP (3.1.3.2), ADA (3.5.4.4), ADH (1.1.1.1, using hexenol as substrate), DIA (1.6.2.2), EST-

1 and EST-D (3.1.1.1), FUM (4.2.1.2), GDA (3.5.4.3), GDH (1.4.1.3), GOT-1 and GOT-2 (2.6.1.1), GPDH (1.1.1.8), G3PDH (1.2.1.12), G6PDH (1.1.1.49), IDH-1 and IDH-2 (1.1.1.42), LDH-1 and LDH-2 (1.1.1.27), MDH-1 and MDH-2 (1.1.1.37), ME (1.1.1.40), NP (2.4.2.1), PEP (3.4.11, PEP-A anodal morph using leu-ala as substrate; PEP-B (with leu-gly as substrate); PEP-C cathodal morph using leu-ala, and LAP with leucine-naphthylamide), PGM-1, PGM-2, and PGM-3 (2.7.5.1), and SDH (1.1.1.14). Discarded loci were: ALD, ALDH, AO, CK, F16PD, GAL, GOX, GPT, GSR, GUS, MPI, PEP (with phe-pro as substrate), 6PGD, PGI, SOD, XDH, and XO. G6PDH, PGM-2 and PGM-3 were not scored in outgroups other than Oporornis. Variable loci were scored according to mobility with the more anodal alleles as "a", "b", "c", etc. Including outgroups, a total of 137 gels were run for a total of 408 samples; in addition 38 control gels were run. After population structure and species limits were assessed (Escalante-Pliego in prep.), data from multi-sampled species were pooled into a single allelic frequency by species (Table 1).

## Data analysis

Because different methods of phylogenetic analyses differ in their underlying evolutionary assumptions (Felsenstein 1982), different phylogenetic results can be obtained from the same data set. However, one often finds that if the character set is highly informative, different approaches will give similar results (i.e. Page 1990). Therefore, it may be helpful to compare the results of different analytical approaches. To compare results, I examined the character support for various groupings, and introduced additional evidence provided by plumage and biogeography to obtain a phylogenetic synthesis that best accounts for all the available information.

Analyses were done using several computer programs. Individual genotypes were entered into BIOSYS (Swofford and Selander 1989), and allelic frequencies and genetic distances were calculated using this program. The widely used Nei's (1978) and corrected Rogers' genetic distances (Wright 1978) were also estimated. These data were summarized using different methods; UPGMA for Nei's and Rogers' distances; and distance-Wagner, and the Fitch-Margoliash algorithm only for Rogers' distances (computer program FITCH in the PHYLIP package, Felsenstein 1989).

Allelic frequencies were analyzed in two more ways. After discarding monomorphic loci and loci with only autapomorphic alleles (uninformative alleles occurring in a single taxon), the frequencies of informative loci were used as input data for the frequency parsimony method (Swofford and Berlocher 1987; FREQPARS, Swofford 1988). Because of computation constraints in the version of the program I used, all but 6 rare unique alleles, 100 in all, were analyzed using the maximum likelihood method (CONTML, in PHYLIP, Felsenstein 1989).

Finally, alleles were coded as characters for discrete data parsimony analyses (0=absent, 1=present). Although many authors recommend treating loci as characters with alleles as unordered states (Buth 1984, Mickevich and Mitter 1983, Swofford and Olsen 1990), this approach results in the loss of much information. The majority of loci in this study (92% of variable loci) exhibited only allelic frequency differences among taxa, and did not have different fixed alleles. Hence, it is appropriate to treat alleles as characters rather than character states.

Discrete data were analyzed using either the computer program PAUP (Swofford 1990) or PHYLIP (Felsenstein 1989) depending on the

assumptions allowed. In PAUP, I used unweighted Wagner parsimony (Kluge and Farris 1969), and Dollo parsimony (Farris 1977, Felsenstein 1979) to weight presences more than absences. My rationale for using Dollo parsimony does not relate to the evolutionary cost of gaining or loosing an allele, as has been argued for restriction site mtDNA characters (DeBry and Slade 1985). Instead, because several taxa were represented by small samples (i.e. Oporornis agilis), alleles that occur in small frequencies might easily remain undetected. Because Dollo parsimony weights presences more than absences, it permits one to recover a pattern using the data as originally coded without forcing convergences, except for losses or reversals.

Finally I used the alternative approach of polymorphism parsimony (Farris 1978, Felsenstein 1979) with the DOLLOP program in the PHYLIP package (Felsenstein 1989). This method allows ancestors to be polymorphic (character states are 0, 01, or 1). Unique changes are also reinforced as in Dollo parsimony and the number of polymorphic ancestors is minimized. I executed DOLLOP twelve times, each time entering taxa in a different order to increase the chance of finding the shortest trees.

Allelic information on outgroups was used to examine the monophyly of the genus, to polarize the characters and to root the trees. Three approaches were tried. (1) Global parsimony is recommended when the sister taxon of the ingroup is unknown or outgroups relationships are uncertain. Global parsimony attempts to obtain simultaneous resolution for all taxa (Maddison et al. 1984). I used this approach with algorithms that are not so memory demanding, like UPGMA and distance Wagner, and Wagner, Dollo, and polymorphism parsimony. (2) Single substitute outgroup (Donaghue 1984) was used for proposed sister taxa of Geothypis (Basileuterus, Oporornis, Icteria) or other paruline taxa with

moderate sample size and with similar plumage pattern (no wing bars and no tail patches, such as Wilsonia pusilla). (3) Composite outgroup (ComOutg) permitted me to reconstruct a putative ancestor with all alleles detected in outgroups to allow polarizing the tree without resolving the among outgroup relationships. I used this approach because sample sizes were dissimilar among outgroups and this artifact might introduced error in the data set. Information on outgroups is presented in Table 2 and Appendix 1.

### Plumage characters

Discrete characters of plumage pattern were examined and compared with allozyme characters. Only male plumage characters were included because the female plumage is almost undistinguishable among taxa of this study. Only five plumage characters were informative: throat color (unordered), white eye marks (ordered), black mask (ordered), margin behind the mask (unordered), and yellow eye brow (unordered). A sixth character (small rictal bristles) grouped Geothlypis and Oporornis outside of Basileuterus. Appendix 3 summarizes character variation in plumage characters.

## R E S U L T S

Allelic frequencies for twenty-five variable loci are given in Table 1 for 16 species of Geothlypis and Oporornis. Table 2 summarizes allelic frequencies for seventeen variable loci of parulines and thraupines used as outgroups. Presence or absence of alleles in the 25 (or 17) loci scored are summarized in Appendixes 1 and 2.

The first 8 taxa listed in Table 1 (G. trichas to G. chiriquensis) show very little differentiation across loci. Slight differences in allelic frequencies and autapomorphic alleles are the rule. The other 8 taxa show more hierarchical patterns of allelic frequency distribution in some loci. For instance, ADA, IDH-1, ME, and PEPA seem to retain more phylogenetic information. This pattern extends to the outgroup taxa, in which the majority of loci have an undifferentiated horizontal pattern (similar allele frequencies), and a few loci have hierarchical patterns (marked frequency differences, or new alleles present).

Another pattern detected in Table 1 is that taxa not only share common alleles, but also less common alleles across many taxa. For example, ADA-h, ADA-m, ESTD-a, PEPB-d, and PEPC-b occur in 5 to 13 different taxa. A comparison with outgroup taxa listed in Table 2 and Appendix 1 reveals that many of these informative alleles are also present in many of the other paruline and thraupine taxa treated as outgroups in this study, rendering the phylogenetic content of the data set difficult to assess.

## Distance analyses

Using UPGMA to cluster Nei's (1978) distances for 52 taxa did not bring all Geothlypis taxa into a single cluster. G. trichas, G. chiriquensis, O. formosus, G. nelsoni, G. semiflava, G. rostrata, G. flavovelata, G. beldingi, and G. speciosa clustered together, but the next taxon to join was P. citrea. Taxa with small or isolated distributions like G. rostrata, G. beldingi, G. flavovelata, or G. speciosa grouped lower in the cluster. A set formed by G. velata, G. auricularis, O. tolmiei, and O. philadelphia joined afterwards; and last, O. agilis. Many paruline taxa connected in between the group just

described and a cluster formed by G. aequinoctialis and G. poliocephala. After them, five other paruline taxa attached outside, and a separate cluster was formed by thraupine taxa plus I. virens, Z. coronata and G. pelzeni. UPGMA with Rogers' distances (Wright 1978) gave exactly the same topology for the taxa described above.

Nei's distances among Geothlypis taxa in the first cluster ranged between 0.005 (G. trichas and G. flavovelata), to 0.102 (G. velata and G. rostrata). By contrast, distances between G. aequinoctialis and G. poliocephala to any Geothlypis taxa ranged from 0.141 (between G. aequinoctialis and G. velata) to 0.300 (between G. poliocephala and G. semiflava).

A somewhat different topology was obtained using the distance Wagner method with Rogers' distances in all 52 taxa. Again some Oporornis taxa were intermingled with Geothlypis taxa: O. formosus falls in a group with G. trichas, G. flavovelata, G. chiriquensis, G. nelsoni, G. semiflava, G. rostrata, and G. speciosa; G. beldingi falls outside this time, in a group with G. velata, G. auricularis, G. aequinoctialis, G. poliocephala, O. tolmiei, and O. philadelphia; Protonotaria joined these two groups in a trifurcation. O. agilis falls outside in the next group. Three Geothlypis taxa with isolated ranges (beldingi, speciosa, and rostrata, but not flavovelata) joined their groups in a lower position, and G. chiriquensis was clustered in the upper branches of its group.

Sixteen taxa (Geothlypis and Oporornis), plus substitute and composite outgroups were analyzed using the Fitch-Margoliash algorithm. Appendix 4 lists, in a reduced format, the three different trees obtained using Basileuterus, Icteria, and ComOutg. Using Basileuterus or ComOutg gave exactly the same topology and rooting, dividing the 16 taxa

in two groups: one with the Geothlypis taxa that have a complete mask (trichas, flavovelata, semiflava, chiriquensis, nelsoni, formosus, rostrata, beldingi and speciosa) plus O. agilis at the base, and another formed by taxa that have a gray crown and reduced mask or no mask (except for O. agilis: G. velata, G. auricularis, G. aequinoctialis, G. poliocephala, O. tolmiei, and O. philadelphia). The operation with Icteria produced a different root, grouping G. aequinoctialis and G. poliocephala separately from all the other taxa, but kept essentially the same topology except that O. tolmiei and O. philadelphia are closer to each other. The position of the isolated taxa is similar to that obtained with distance Wagner. As can be seen in Appendix 4, branches within the trees are quite small compared to branches of taxa; while interior branches range from 0.0030 to 0.0665, taxa branches range from 0.0249 (G. trichas), to 0.163 (G. speciosa) and 0.167 (G. poliocephala). Of the interior branches, the smallest (little different from zero) are in the first group of birds with complete masks plus O. agilis.

## Analyses of allele frequencies

The two approaches that use allele frequencies directly, without transforming them into a distance value, are computer intensive; thus, it was not possible to include all taxa in a single analysis. Besides, due to small samples in outgroup taxa, frequency information for their loci have large errors.

I used the same three outgroups (Basileuterus, Icteria, and ComOutg) with the frequency parsimony algorithm (FREQPARS) as in the distance analysis. In the case of parsimony analysis, results were dissimilar among topologies given with each of the three outgroups. Between Basileuterus and Icteria the results only differed in the

position of the root. These two trees are given in a reduced format in Appendix 4. The two trees are structured at the base similarly to those obtained with distances; major differences are within the more derived group of birds with complete masks (the first eight taxa of Table 1 plus O. formosus and O. agilis). The main difference is in the allocation of O. formosus and O. agilis high in the group and in G. semiflava, G. beldingi, and G. flavovelata forming a separate group close to the base of the tree. An examination of the contribution of each locus to the tree branch lengths indicates a wide range. The lowest is SDH, which had a contribution of 0.61 or 2.41 (with Basileuterus or Icteria, respectively) in the shortest trees; the highest is ADA with 12.03 or 12.28. Variable loci with non-hierarchical patterns, like PEP-B, had large contributions of 10.15 or 10.16 in both trees; whereas loci that presented more hierarchical patterns or fixed differences, had smaller contributions: IDH1 (3.52 or 5.52), GDA (5.43 or 7.37), ME (4.88 or 5.13). This unevenness in contribution might cause differential weighting over loci, and might help one to explain some differences in tree topologies.

The other approach used with frequency data was maximum likelihood. A very similar topology (unrooted network) was obtained using either Basileuterus or Icteria, but again, a different rooting was found. The only difference between the two topologies is in the O. philadelphia and O. tolmiei order (Figure 1A and 1B). However, with ComOutg some changes occur: O. tolmiei and O. philadelphia came together, O. agilis was moved close to the base, and G. speciosa was moved up to become a more derived group (Figure 1C). All branch lengths within the trees are positive, but confidence intervals in the smaller branches included negative values; these fragile branches are indicated

by a thin line in Figure 1. Both Basileuterus and Icteria gave five strongly supported branches, and Comoutg up to seven.

## Discrete data parsimony analyses

A total of 106 alleles were detected in 16 Geothlypis and Oporornis taxa (henceforward the ingroup): 40 alleles are informative because they occur in more than one ingroup taxon, or in one ingroup taxon and in one or more outgroups. Only 7 of these informative alleles were detected exclusively in the ingroup. Sixty-six other alleles occurred in a single taxon and were not detected in outgroups (putative autapomorphies). Twenty-four other alleles were informative in outgroups (see Appendix 1).

A high proportion of the autapomorphic alleles were detected as rare alleles in G. trichas, which was the taxon represented by more populations. Another set of unique alleles occurred in higher frequencies within a particular taxon and are useful in diagnosing these taxa. These unique alleles are: ADH-c in G. speciosa; GDA-k in G. beldingi; GOT-1-e and GPDH-b in G. semiflava; GPDH-i and NP-d in G. aequinoctialis; MDH-1-b in G. rostrata; MDH-1-a and PEPA-g in G. flavovelata; PEPA-b in G. nelsoni; PEPA-h and -i in G. auricularis; and other unique alleles at the ME and PEPB loci in Oporornis taxa.

Using all 52 taxa for global Wagner parsimony, thousands of shortest trees of 228 steps were obtained. The large number of trees is due to the lack of diagnostic allelic characters for many paruline taxa. Consensus trees of 2219, 1229, and 4700 shortest trees from separate runs were the same. Strict consensus gave a monophyletic group including the taxa of Geothlypis, those of Oporornis, and Protonotaria citrea (CI=0.220. RI=0.425); most other paruline taxa, including Basileuterus,

clustered in the next lower node in a polytomy (Figure 2). These nodes were supported by several character changes, indicated in the figure legend. In the North American paruline clade (excluding Icteria) ten character changes supported the node: EAP-b had a consistency of 1.0 and represents a synapomorphy for the clade. This allele was fixed in most taxa assayed; the primitive EAP-a allele is absent in all paruline taxa except Oporornis agilis and Wilsonia citrina. Other important characters in the North American paruline node are GPDH-g and SDH-e, but there are losses in several taxa, and the consistency of these characters is consequently diminished. Four character changes support the node at the Geothlypis, Oporornis, and Protonotaria clade, but none of the changes were fully consistent in the tree. The NP locus is very informative within parulines: the NP-c allele was present in high frequencies in all Geothlypis and Oporornis taxa, but it was found also in small frequencies in a number of North American parulines and tropical American Zeledonia. A similar pattern resulted with the PEPA-d and -e alleles. The 50 % majority rule consensus shows that Geothlypis and Oporornis formed a monophyletic group in 78 percent of the trees, with Protonotaria as its sister group. Within the Geothlypis and Oporornis clade, the majority rule consensus still had a polytomy with five branches at its base. A distinctive clade within is fully resolved, this one including seven taxa with gray crowns and reduced face masks. In contrast, global Dollo parsimony did not produce a single clade that included all Geothlypis and Oporornis taxa.

Global polymorphism parsimony produced two shortest fully resolved trees that required 467 ancestral polymorphic states overall. These two trees have the same topology for the ingroup, but slightly different outgroup arrangement. In both trees Geothlypis and Oporornis taxa formed

a monophyletic group. North American parulines formed two separate groups. The group closest to Geothlypis and Oporornis includes Wilsonia canadensis, W. pusilla, Limnothlypis swainsoni, Dendroica petechia, Seiurus auricapillus, and Protonotaria. As in the other methods, Oporornis taxa did not form a single monophyletic group.

The same difficulty of using substitute outgroups in the frequency methods was encountered in discrete data analyses. Using Icteria and Basileuterus as outgroups a similar topology was produced, but with a different rooting point. Because of this disturbance, only the results with ComOutg are given here. Due to the small sample size available for Protonotaria this taxon could not be adequately used in subsequent analyses as a single outgroup, even when it tended to come very close to the taxa of concern. The resulting trees using Protonotaria as the outgroup had polytomies at their base.

One shortest tree of 91 steps for the species of Geothlypis and Oporornis was obtained with Wagner parsimony (Figure 3A). In this tree, only five characters have a consistency of 1.0, and the other thirty five resulted in homoplasies interpreted as convergences. This putative phylogeny conflicts substantially with data from plumage pattern, and implies an intricate biogeographic scenario for the differentiation sequence. In Dollo parsimony four shortest trees (120 steps long) gave a consensus tree that was almost fully resolved (Figure 3b). This tree divided 16 Geothlypis and Oporornis taxa into two groups, one basal with taxa that have gray crowns and reduced masks, and another, more derived, with nine taxa with complete mask. G. chiriquensis falls at the base of the second group, as does O. agilis also.

With polymorphism parsimony, one shortest tree of 130 polymorphic states in ancestral taxa was obtained (Figure 4). Table 3 gives the

number of polymorphic states invoked for each character/allele in this shortest trees. Variable loci with horizontal patterns had more polymorphic states within the tree (i.e., ADA, PEP-B); in contrast, loci with fixed alleles or a hierarchical pattern had less polymorphic states in ancestors (i.e., IDH), hence are less homoplastic in these trees. Four next most parsimonious trees of 131 polymorphic states were found; these trees share the same structure of the shortest tree in seven basal taxa and CompOutg, but differ in slight rearrangements of the nine taxa in the advance group. This indicates that the polymorphism tree is more robust in the lower branches.

### Phylogeny based on plumage characters

Five informative plumage characters with 14 states were insufficient to give a fully resolved phylogeny. Four shortest trees of 10 steps were obtained using Wagner parsimony (CI=0.900). A strict consensus gave the same tree where throat color, eye marks, and mask had a consistency of 1.0 but very little resolution. The other two characters, margin behind mask and yellow eyebrow, had some homoplasy and their consistency was 0.5. The strict consensus and 50% majority of shortest trees are shown in Figure 5.

## D I S C U S S I O N

Data on the allozymes of paruline warblers obtained in the present study and in earlier work by Barrowclough and Corbin (1978) and Avise et al. (1980) have shown that the various members of this subfamily are very similar genetically and could be of relatively recent evolutionary

origin. The level of differentiation among taxa, involving only shifts in allele frequencies, corresponds to intraspecific levels of population differentiation in other vertebrate taxa (e.g., rodents, Avise et al. 1980).

Polymorphic characters are potentially likely to give misleading phylogenetic information, in the form of pseudoreversals (Arnold 1981, Heads 1985, Wu 1991). Such variable characters are usually considered to be unreliable, and are not included in phylogenetic analyses. However, at low taxonomic levels, as in the group discussed here, polymorphism is rampant, at least in allozyme characters; even the invariable (within taxa) and informative loci gave conflicting patterns (GDA and ME).

Another problem in reconstructing phylogenetic patterns in closely related species is the use of a character set that has an generally slow rate of evolutionary change, like amino acid substitutions detected by allozyme electrophoresis, as the observation of extensive shared polymorphism across taxa suggests. Interestingly, detailed studies of DNA sequences have shown a similar problem: "The presence of pervasive and ancient polymorphism within species, while posing a problem for constructing evolutionary trees, suggests that variation of potential value in evolution may linger for a long time in evolutionary lineages and survive several speciation events" (Coyne and Kreitman 1986).

The phylogenetic hypotheses obtained with different methods in this study varied substantially. Because it is concordant with plumage and biogeographic pattern, I prefer the solution of polymorphism parsimony (Figure 5) as the most compelling phylogenetic hypothesis provided by the available data. The treatment of all alleles as uniquely derived characters did not seem to represent an incorrect assumption, based on the observed pattern of allozyme differentiation, and the

concordance mentioned above.

As currently recognized, neither Geothlypis nor Oporornis appear to be monophyletic. However, allozyme data analyzed with parsimony methods suggest that taxa of both genera together do form a monophyletic group. The paruline taxon that is closest to this clade is Protonotaria, as polymorphism and Wagner parsimony combined suggest, and as was previously reported with genetic distance data (Avise et al. 1980). The plumage pattern of Protonotaria warblers is similar to that of the Yellowthroats and their allies. The predominantly intense yellow and bluish gray pigmentation of Protonotaria citrea puts this species close to Yellowthroats, but the presence of a white tail patch separates it from Geothlypis or Oporornis taxa.

That O. formosus did not join with other species of Oporornis is not surprising on the grounds of plumage variation. However, the other three Oporornis species are similar in plumage (they have gray throats), and yet they did not group together. Possibly plumage pigmentation (gray or yellow) is a misleading character to infer phylogenetic relationships in this genus, as has been suggested by molecular studies of other bird taxa (for instance in brush finches of the Andes, Atlapetes sp., Remsen, pers.com.). O. agilis often appeared as the sister taxon of G. nelsoni in different analyses, perhaps because retention in both taxa of ancestral alleles were interpreted as convergences. The location of O. agilis at the base of the tree appears most likely on the basis of plumage: this species is the only one of the 16 taxa that does not have any black facial marking. Moreover, O. agilis seems to be the more terrestrial member of this assemblage. Its behavior has sometimes been compared to that of waterthrushes (Seiurus spp.), and its song to that of the Ovenbird (Seiurus auricapillus) (Bent 1953). In addition, its

distribution would seem to be relictual because it has more separated winter and breeding ranges than any other species of Oporornis (AOU, 1983), although an understanding of the evolution of migratory patterns in paruline warblers is in need of much more work (see Keast 1980a, 1980b).

The remaining 15 taxa of Geothlypis and Oporornis form two clades. In the first, there are four taxa including birds with a small amount of black in the lores (O. philadelphia, O. tolmiei), birds having black in the lores and around the eye (G. poliocephala), or birds with the black patch extending to a little patch below the eye (G. aequinoctialis). This putative sister group relationship is also supported by other plumage characters, such as white eye marks and gray crowns. G. velata and G. auricularis form the next sister group; they join either with the first clade or with the second, depending on the root. They also have gray crowns, and plumage patterns similar to that of the first clade.

The more derived clade is formed by 9 taxa, including all the remaining species of Geothlypis, plus O. formosus. All these taxa have a well-defined black mask covering the forehead to the auriculars, with some taxa having even more black (ex. G. speciosa). The first group is formed by three taxa. Although G. semiflava and G. chiriquensis always grouped together, it is not a well supported node by plumage characters. The presence of O. formosus in this clade agrees very well with plumage, distribution, and habitat. G. semiflava and O. formosus have very similar plumage coloration, and strong feet, similar habitat preference and contiguous geographic ranges (including their wintering grounds). The only taxon in this clade that retains a predominantly gray crown is G. chiriquensis. Because of its color pattern and distribution, G. chiriquensis is currently classified with the widespread Masked

Yellowthroat (Geothlypis aequinoctialis sensu lato, including also velata and auricularis), but allozyme differences (Escalante-Pliego, in press) and morphological characters (Escalante-Pliego, in prep.) support the recognition of four species. These four taxa do not form a monophyletic assemblage, but show that the current Masked Yellowthroat is instead paraphyletic, with eleven taxa in between. The last clade, formed by six taxa, also agrees well with variation in plumage characters; five of these taxa have a well marked black mask with a light border, either white or yellow, except for G. speciosa (which has black covering the entire head) and G. nelsoni (gray border). The resolution within this clade is not consistent among the different trees obtained. Because G. speciosa has such a reduced range, and has comparatively reduced variability (Escalante-Pliego in press), it is possible that secondary losses have occurred due to more recent genetic bottlenecks.

In comparison to allozymes, plumage shows a different pattern. Temperate breeding taxa have more diagnostic characters, and perhaps higher rates of plumage change (i.e. O. formosus), than tropical breeding taxa, which have presumably been separated for a longer time (i.e. G. aequinoctialis versus G. velata, for instance) and are more conservative in plumage characters. This ecological pattern is also present in the amount of sexual dimorphism, in these and other parulines (Griscom and Sprunt 1957).

The most parsimonious biogeographic scenario, harmonious with this phylogeny, is that yellowthroats evolved from forms occupying open shrubby habitats and that marsh-dwelling is a derived ecological condition. The differentiation of the Geothlypis and Oporornis group perhaps started first in northern South America and Central America,

where winter ranges of migratory taxa, and breeding ranges of sedentary taxa of the basal clade are presently situated. During dry periods of the Pleistocene (Haffer 1974) or even the Pliocene (Webb 1985) ancestral yellowthroats probably extended southward across the Amazon Basin, and westward to the Peruvian Pacific coast; from the coast, the genus may have crossed the Isthmus of Panama on a second route, this time through the northwestern part of South America. Perhaps some of the northward dispersal events in these warblers were part of the faunal movements associated with the Great American Interchange (Stehli and Webb 1985). This postulate agrees with the estimate of time divergence given by the genetic distance data.

The noticeable genetic affinity of G. chiriquensis with the taxa of the Central and North American clade of complete-masked forms, suggests that a genetic bottleneck occurred when the ancestral taxon crossed Central America, an event that was followed by rapid speciation. This sequence of events left a minor trace as allozyme differences detectable in the present-day descendant taxa. That this bottleneck occurred in the ancestral lineage of the derived clade is suggested by the pattern of IDH1 and PEPA loci. A similar pattern where a lineage that nourishes high genetic variability in a continent goes through a bottleneck when it disperses away from it has been postulated for human evolution from Africa on the basis of mitochondrial DNA (Cann et al. 1987).

## Taxonomic implications

A taxonomic treatment concordant with the genealogical history obtained in this study should include all 16 taxa (now in Geothlypis and Oporornis) in a single monophyletic genus Geothlypis. Finer lineage

classification of an enlarged genus Geothlypis into either subgenera or informal species groups should await the testing of this phylogenetic hypothesis with new sets of characters, such as DNA sequences, or vocalizations.

Indeed, a taxonomy consistent with the global reconstruction obtained in this study would have to reduce all parulines (about 100 species in 20 genera) to the level of a monophyletic genus that would be diagnosable with allozyme characters. Such speciose genera are not frequent in birds which are often said to be oversplit (Sibley and Ahlquist 1982), but are common in other vertebrate classes (i.e., Colosthetus frogs with about 75 species).

At this time, in view of the fact that DNA or vocalization information is not available to corroborate or modify my findings, I refrain from suggesting a formal classification of these birds.

## A C K N O W L E D G M E N T S

I extend my appreciation to CONACyT (Consejo Nacional de Ciencia y Tecnología) of México and to the doctoral training program of the American Museum of Natural History for having provided the financial support that made my studies possible. Additional financial assistance for this project was granted by the Frank M. Chapman Memorial Fund of the Department of Ornithology of the American Museum of Natural History, the Graduate Studies Committee of the Ecology and Evolutionary Biology Program of the City University of New York, the Alexander Wetmore Fund of the American Ornithologists' Union, the Society of Sigma Xi Society, and the Association of Field Ornithologists (Alexander Bergstrom grant).

Emergency financial assistance was very generously given by the late Sadie Coats.

To the authorities and officials who helped me to obtain collecting permits I extend my sincere acknowledgement: Secretaría de Desarrollo Urbano y Ecología, Mexico City; Ministerio de Recursos Naturales, Energía y Minas in Costa Rica; Museo de la Universidad Central de Venezuela; State of Florida Game and Fresh Water Fish Commission, and US Fish and Wildlife Service; and Department of Agriculture of the Bahamas.

I thank the members of my doctoral committee for their advice, guidance and support throughout the development of this project: François Vuilleumier, George F. Barrowclough, Robert F. Rockwell, Leslie F. Marcus and Robert S. Voss.

I thank Robert W. Dickerman for having suggested a study of Yellowthroats in Mexico. For excellent companionship in the field, I am grateful to Miriam Torres, Roberto Chavira, Alejandro Said, Ambrosio Ramírez, Fernando Villaseñor, Carlos Escalante, Ernesto Díaz, Javier Salgado, Gabriela Ibañez, Laura Rivera, David Padilla, and Judith Vega, in Mexico; to Miguel Lentino and Jose Luis Jimenez in Venezuela; to Hesiquio Benitez, Ana Isabel Pereyra, Gilbert Barrantes, and Ingrid Ayub in Costa Rica; to Blanca Hernandez Baños and Scott Baker in Florida and the Bahamas. The Sweetings and the Ketchams of Marsh Harbour, generously gave us directions, advice, shelter and food in Abaco. Jay Pitocchelli, Robert M. Zink, and Scott Lanyon provided me with important tissue samples.

I thank many friends for numerous discussions, among them, Bonnie Bain, Parker Cane, Angelo Capparella, Linda S. Ford, Rosemarie Gnam, Carole Griffiths, Nedra Klein, Gavin Naylor, Roderick Page, Town

Peterson, Jay Pitocchelli, Rick Prum, and Jeff Woodbury. Special thanks go to Charles W. Myers and to the Department of Herpetology of the American Museum of Natural History, and to Jorge Llorente and Adolfo Navarro from the Museo de Zoología de la Facultad de Ciencias de la Universidad Nacional Autónoma de México.

## L I T E R A T U R E  C I T E D

Arnold, E. N.
1981. Estimating phylogenies at low taxonomic levels. Z. zool. Syst. Evolut.-forsch 19:1-35.

Avise, J. C., J. C. Patton, and C. F. Aquadro.
1980. Evolutionary genetics of birds. Comparative molecular evolution in New World warblers and rodents. J. Heredity 71:303-310.

AOU.
1983. Check-list of birds of North America. American Ornithologists' Union, 6th ed.

Barrowclough, G. F. and K. Corbin.
1978. Genetic variation and differentiation in the Parulidae. Auk 95:691-702.

Bledsoe, A.
1988. A hybrid Oporornis philadelphia X Geothlypis trichas, with comments on the taxonomic interpretation and evolutionary significance of intergeneric hybridization. Wilson Bull. 100: 1-8.

Bent, A. C.
1953. Life Histories of North American Wood Warblers. U. S. National Museum Bull. 203. Smithsonian Institution. 734 pp.

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

Cann, R. L., M. Stoneking, and A. C. Wilson.
1987. Mitochondrial DNA and human evolution. Nature, 325:31-36.

Chapman, F. M.
1907. The Warblers of North America. Appleton & Company, New York, New York.

Coyne, J. A. and M. Kreitman.
1986.Evolutionary genetics of two sibling species, Drosophila simulans and D. sechellia. Evolution 40:673-691.

Cracraft, J.
1982. Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. Amer. Zool. 22:411-424.

Davis, L. I.
1972. A field guide to the birds of Mexico and Central America. University of Texas Press. Austin, Texas.

DeBry, R. W. and N. A. Slade.
1985. Cladistic analysis of restriction endonuclease cleavage maps within a maximum-likelihood framework. Syst. Zool. 34:21-34.

Donaghue, M. J.
1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Syst. Bot. 9:192-202.

Escalante-Pliego, P.
Genetic differentiation in yellowthroats (Parulinae: Geothlypis). Proceedings of the XX International Ornithological Congress. Christchurch, New Zealand.

Farris, J. S.
1977. Phylogenetic analysis under Dollo's Law. Syst. Zool. 26:77-88.

———.
1978. Inferring phylogenetic trees from chromosome inversion data. Syst. Zool. 27:275-284.

Felsenstein, J.
1979. Alternative methods of phylogenetic inference and their interrelationship. Syst. Zool. 28:49-62.

———.
1982. Numerical methods for inferring evolutionary trees. Quart Rev. Biol. 57:379-404.

———.
1989. PHYLIP (Phylogeny inference package). Version 3.2. Seattle, Washington, USA.

Funk, V. A. and D. R. Brooks.
1990. Phylogenetic systematics as the basis of comparative biology. Smithsonian Contrib. Botany 73:1-45.

Griscom, L. and A. Sprunt, Jr.
1957. The warblers of North America. Devin-Adair Company, New York, New York.

Hackett, S. J.
1989. Effects of varied electrophoretic conditions on detection of evolutionary patterns in the Laridae. Condor 91:73-90.

Haffer, J.
1974. Avian speciation in tropical South America. Publ. Nuttall Ornithol. Club, no. 14, pp. 1-390.

Heads, M.
1985. On the nature of ancestors. Syst. Zool. 34:205-215.

Keast, A.
1980a. Spatial relationships between migratory parulid warblers and their ecological counterparts in the Neotropics. In, Keast, A. and E. S. Morton (eds.). Migrant birds in the Neotropics. Ecology, behavior, distribution, and conservation. Smithsonian Institution Press. Washington, D. C. Pp. 109-130.

———.
1980b. Synthesis: ecological basis and evolution of the Neartic-Neotropical migration system. In, Keast, A. and E. S. Morton (eds.). Migrant birds in the Neotropics. Ecology, behavior, distribution, and conservation. Smithsonian Institution Press. Washington, D. C. Pp. 559-576.

Kluge, A. and S. Farris.
1969. Quantitative Phyletics and the evolution of anurans. Syst. Zool. 18:1-32.

Lowery, G. H., Jr. and B. L. Monroe, Jr.
1968. Parulidae. In Peters, J. L. Check-List of Birds of the World, v. XIV, Cambridge, Massachusetts.

Maddison, W., M. J. Donoghue, and David R. Maddison.
1984. Outgroup analysis and parsimony. Syst. Zool. 33:83-103.

Mikevitch, M. F. and C. Mitter.
1983. Evolutionary patterns in allozyme data: a systematic approach. In, Platnick, N. I. and V. A. Funk. Advances in Cladistics, vol. 2. Columbia University Press, New York. Pp. 169-176.

Miller, A. H., H. Friedmann, L. Griscom, and R. T. Moore.
1957. Distributional Check-list of the birds of Mexico. Part II. Pacific Coast Avifauna No. 33. 435 pp.

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

Page, R.
1990, Temporal congruence and cladistic analysis of biogeography and cospeciation. Syst. Zool. 39: 205-226.

Raikow, R.
1978. Appendicular myology and relationships of the New World Nine-primaried Oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. no. 7.

Richardson, B. J., P. R. Baverstock, and M. Adams.
1986. Allozyme electrophoresis. Academic Press. Sydney, Australia.

Ridgway, R.
1902. The Birds of North and Middle America, vol. II, Bull. U.S. nat. Mus. no.50, Washington.

Sharpe, R. B.
1885. Catalogue of the Birds in the British Museum , vol. X, London.

Sibley, C. G. and J. E. Ahlquist.
1982. The relationships of the Yellow-breasted Chat (Icteria virens) and the alleged slowdown in the rate of macromolecular evolution in birds. Postilla 187, 19 pp.

_____.
1990. Phylogeny and classification of birds. A study in molecular evolution. Yale University Press, New Haven, Connecticut.

Stehli, F. G. and S. D. Webb (eds.).
1985. The great American biotic interchange. Plenum Press, New York and London.

Swofford, D.
1988. FREQPARS.Release 1.0. Illinois Natural Survey. Urbana, Illinois.

_____.
1990. PAUP. Phylogenetic Analysis Using Parsimony. Version 3.0. Illinois Natural Survey. Champaign, Illinois.

_____ and S. H. Berlocher.
1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. Syst. Zool. 36:293-325.

_____ and R. B. Selander.
1989. BIOSYS-1. A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. Urbana, Illinois, USA.

Swofford, D. and G. J. Olsen.
1990. Phylogeny reconstruction. In Molecular systematics, D. M. Hillis and C. Moritz (eds.). Sinauer Associates Inc. Sunderland, Massachusetts.

Tordoff, H. B.
1954. Relationships in the New World Nine-primaried Oscines. Auk

71:273-284.

Wanntorp, H. E., D. R. Brooks, T. Nilsson, S. Nylin, F. Ronquist, S. C. Stearns, and N. Wedell.
1990. Phylogenetic approaches in ecology. Oikos 57: 119-132.

Webb, S. D.
1985. Late Cenozoic mammal dispersals between the Americas. In Stehli, F. G. and S. D. Webb (eds.). The great american biotic interchange. Plenum Press, New York, N. Y. Pp.357-386.

Wright, S.
1978. Evolution and the genetics of populations. Vol. 4. Variability within and among natural populations. University of Chicago Press. Chicago, Illinois.

Wu, Chung-I.
1991. Inferences of species phylogeny in relation to segregation of ancient polymorphisms. Genetics 127:429-435.

TABLE 1. Allelic frequencies for 24 variable loci in 16 species of Geothlypis and Oporornis. Average sample size per species in parenthesis.

| | T A X A | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | GTRI | GBEL | GFLA | GROS | GSEM | GSPE | GNEL | GCHI | GVEL | GAUR | GAEQ | GPOL | OFOR | OAGI | OPHI | OTOL |
| ADA | | | | | | | | | | | | | | | | |
| A | | | | | | . | | | .250 | | .563 | | | | | |
| B | | | | | | | | | .250 | .333 | .438 | | | | | |
| D | | | | | | 1.000 | | | | | | | | | | |
| E | .005 | .009 | | | .026 | | | .111 | .250 | .667 | | | | | | |
| F | | .380 | | | | | | | | | | | | | | |
| G | | | | | | | | .222 | | | | | | | | |
| H | .847 | .463 | 1.000 | .273 | .974 | | .821 | .667 | .250 | | | .972 | .818 | .643 | 1.000 | .906 |
| J | | | | | | | | | | | | | | | | |
| K | | .074 | | | | | | | | | | | | | | |
| M | .147 | .037 | | .727 | | | .179 | | | | | .028 | .182 | .357 | | .094 |
| O | | .037 | | | | | | | | | | | | | | |
| ADH | | | | | | | | | | | | | | | | |
| B | .006 | | | | | | | | | | | | | | | |
| C | | | | | | .857 | | | | | | | | | | |
| D | .994 | 1.000 | 1.000 | 1.000 | 1.000 | .143 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| EAP | | | | | | | | | | | | | | | | |
| A | | | | | | | | | | | | | | .786 | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .214 | 1.000 | 1.000 |
| ESTD | | | | | | | | | | | | | | | | |
| A | | | | .029 | | | .192 | | | | .313 | | | .125 | | .063 |
| B | .995 | 1.000 | 1.000 | .971 | 1.000 | 1.000 | .769 | 1.000 | 1.000 | .833 | .688 | 1.000 | .917 | .813 | 1.000 | .938 |
| C | | | | | | | .038 | | | .167 | | | | .063 | | |
| D | | | | | | | | | | | | | .083 | | | |
| E | .005 | | | | | | | | | | | | | | | |

TABLE 1. (cont.)

| | T A X A | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | GTRI | GBEL | GFLA | GROS | GSEM | GSPE | GNEL | GCHI | GVEL | GAUR | GAEQ | GPOL | OFOR | OAGI | OPHI | OTOL |
| FUM | | | | | | | | | | | | | | | | |
| D | .014 | | | | | | | | | | | | | | | |
| E | .979 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .972 | 1.000 | 1.000 | 1.000 | 1.000 |
| F | | | | | | | | | | | | .028 | | | | |
| G | .007 | | | | | | | | | | | | | | | |
| GDA | | | | | | | | | | | | | | | | |
| D | | | | | | | | | 1.000 | 1.000 | | 1.000 | | | 1.000 | 1.000 |
| E | .990 | .352 | 1.000 | 1.000 | .974 | 1.000 | 1.000 | 1.000 | | | 1.000 | | 1.000 | 1.000 | | |
| F | .005 | | | | | | | | | | | | | | | |
| G | | | | | .026 | | | | | | | | | | | |
| K | .005 | .648 | | | | | | | | | | | | | | |
| GOT1 | | | | | | | | | | | | | | | | |
| C | .982 | 1.000 | 1.000 | 1.000 | .895 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| D | .018 | | | | | | | | | | | | | | | |
| E | | | | | .105 | | | | | | | | | | | |
| GOT2 | | | | | | | | | | | | | | | | |
| A | 1.000 | 1.000 | 1.000 | 1.000 | .974 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| B | | | | | .026 | | | | | | | | | | | |
| GPDH | | | | | | | | | | | | | | | | |
| A | | | | | | | | | | | | | | | | |
| B | | | | | .333 | | | | | | | | | | | |
| C | | | | | | | | | | | | | | | | .031 |
| G | .995 | 1.000 | 1.000 | 1.000 | .667 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .900 | 1.000 | 1.000 | 1.000 | 1.000 | .906 |
| H | .005 | | | | | | | | | | | | | | | |
| I | | | | | | | | | | | .100 | | | | | |

TABLE 1. (cont.)

| | T A X A | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | GTRI | GBEL | GFLA | GROS | GSEM | GSPE | GNEL | GCHI | GVEL | GAUR | GAEQ | GPOL | OFOR | OAGI | OPHI | OTOL |
| G6PD | | | | | | | | | | | | | | | | |
| A | | | | | .053 | | .038 | .389 | | | | .071 | | .083 | | |
| C | .896 | 1.000 | 1.000 | .719 | .947 | 1.000 | .962 | .500 | 1.000 | 1.000 | 1.000 | .929 | .909 | .917 | 1.000 | 1.000 |
| D | | | | | | | | .111 | | | | | .091 | | | |
| E | .104 | | | .281 | | | | | | | | | | | | |
| IDH1 | | | | | | | | | | | | | | | | |
| A | | | | | | | | | | | .063 | .028 | | | | |
| B | | | | | | | | | .250 | | .938 | .917 | | .125 | .200 | .031 |
| C | | | | | | | | | | | | .056 | | | .100 | . |
| D | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .750 | 1.000 | | | 1.000 | .813 | .700 | .969 |
| E | | | | | | | | | | | | | | .063 | | |
| LAP | | | | | | | | | | | | | | | | |
| A | .009 | | | | | | | | | | | | | | | |
| B | .991 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| LDH1 | | | | | | | | | | | | | | | | |
| A | .005 | | | | | | | | | | | | | | | |
| C | .995 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| LDH2 | | | | | | | | | | | | | | | | |
| A | | | | | | | | | | | | | | | | .031 |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .969 |
| MDH1 | | | | | | | | | | | | | | | | |
| A | | | .071 | | | | | | | | | | | | | |
| B | | | | .382 | | | | | | | | | | | | |
| C | 1.000 | 1.000 | .929 | .618 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

TABLE 1. (cont.)

| | T A X A | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | GTRI | GBEL | GFLA | GROS | GSEM | GSPE | GNEL | GCHI | GVEL | GAUR | GAEQ | GPOL | OFOR | OAGI | OPHI | OTOL |
| ME | | | | | | | | | | | | | | | | |
| A | | | | | | | | | | | | | | .500 | | |
| B | | | | | | | | | | | | | | .500 | | |
| C | | | | | | | | | | | 1.000 | 1.000 | | | | .125 |
| D | | | .071 | | | | | | | | | | | | | |
| E | | | | | | | | | | | | | .188 | | | |
| F | .985 | 1.000 | .929 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | | | .813 | | .833 | .875 |
| H | .015 | | | | | | | | | | | | | | | |
| I | | | | | | | | | | | | | | | .167 | |
| NP | | | | | | | | | | | | | | | | |
| B | | | | | | | | | | | | | | | .100 | .031 |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .938 | 1.000 | 1.000 | 1.000 | .900 | .969 |
| D | | | | | | | | | | | .063 | | | | | |
| PEPA | | | | | | | | | | | | | | | | |
| B | | | | | | | .143 | | | | | | | | | |
| C | | | | | | | | | | | | .139 | | | | .031 |
| D | .995 | 1.000 | .929 | 1.000 | 1.000 | 1.000 | .857 | 1.000 | | .167 | .063 | | 1.000 | 1.000 | .900 | .500 |
| E | | | | | | | | | 1.000 | .500 | .938 | .861 | | | .100 | .469 |
| G | | | .071 | | | | | | | | | | | | | |
| H | | | | | | | | | | .167 | | | | | | |
| I | .005 | | | | | | | | | | | | | | | |
| J | | | | | | | | | | .167 | | | | | | |

TABLE 1. (cont.)

| | T A X A | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | GTRI | GBEL | GFLA | GROS | GSEM | GSPE | GNEL | GCHI | GVEL | GAUR | GAEQ | GPOL | OFOR | OAGI | OPHI | OTOL |
| PEPB | | | | | | | | | | | | | | | | |
| B | .035 | | | | | | | | | | | | | | | |
| C | | | | | | | | | | | | .036 | | | | |
| D | .146 | | .143 | | .042 | | .700 | .250 | | | | .964 | | .083 | .100 | .818 |
| E | .792 | 1.000 | .857 | 1.000 | .958 | 1.000 | .300 | .750 | 1.000 | 1.000 | 1.000 | | | .917 | .900 | .182 |
| F | .014 | | | | | | | | | | | | | | | |
| G | .014 | | | | | | | | | | | | | | | |
| H | | | | | | | | | | | | | .917 | | | |
| I | | | | | | | | | | | | | .083 | | | |
| PEPC | | | | | | | | | | | | | | | | |
| A | | | | | | | | | | | .063 | .028 | | | | .031 |
| B | .052 | | | .029 | .026 | | | | | | .063 | .194 | | .250 | .100 | .031 |
| E | .938 | 1.000 | 1.000 | .971 | .974 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .875 | .778 | 1.000 | .750 | .800 | .938 |
| F | .010 | | | | | | | | | | | | | | | |
| G | | | | | | | | | | | | | | | .100 | |
| PGM1 | | | | | | | | | | | | | | | | |
| D | .142 | .333 | .500 | | | .022 | .036 | | | | | | | | | |
| J | .853 | .667 | .500 | 1.000 | 1.000 | .978 | .964 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .900 | 1.000 |
| K | .005 | | | | | | | | | | | | | | | |
| M | | | | | | | | | | | | | | | .100 | |
| PGM2 | | | | | | | | | | | | | | | | |
| C | .995 | 1.000 | 1.000 | 1.000 | .974 | 1.000 | 1.000 | .833 | 1.000 | 1.000 | .083 | | 1.000 | 1.000 | | |
| D | .005 | | | | | | | | | | | | | | | |
| E | | | | | .026 | | | .167 | | | .917 | .656 | | | .200 | |
| F | | | | | | | | | | | | .313 | | | .800 | 1.000 |
| G | | | | | | | | | | | | .031 | | | | |

TABLE 1 (end)

| | T A X A | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Locus | GTRI | GBEL | GFLA | GROS | GSEM | GSPE | GNEL | GCHI | GVEL | GAUR | GAEQ | GPOL | OFOR | OAGI | OPHI | OTOL |
| PGM3 | | | | | | | | | | | | | | | | |
| A | | .275 | | | | .022 | | | | | | | | | | |
| B | .979 | .725 | 1.000 | 1.000 | 1.000 | .978 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| C | .021 | | | | | | | | | | | | | | | |
| SDH | | | | | | | | | | | | | | | | |
| A | .019 | | | | | | | | | | | | | | | |
| B | | | | .088 | | | | | | | | | | | | |
| E | .981 | 1.000 | 1.000 | .912 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .900 |
| G | | | | | | | | | | | | | | | | .100 |

Key to species (mean sample size per locus in parenthesis). GTRI: *G. trichas* (86.8); GBEL: *G. beldingi* (51.3); GFLA: *G. flavovelata* (5.8); GROS: *G. rostrata* (15.6); GSEM: *G. semiflava* (17.8); GSPE: *G. speciosa* (17.9); GNEL: *G. nelsoni* (12.6); GCHI: *G. chiriquensis* (8.4); GVEL: *G. velata* (1.8); GAUR: *G. auricularis* (2.8); GAEQ: *G. aequinoctialis* (7.4); GPOL: *G. poliocephala* (16.6); OFOR: *O. formosus* (9.7); OAGI: *O. agilis* (7.4); OPHI: *O. philadelphicus* (4.8); OTOL: *O. tolmiei* (15.0).

Table 2. Allele frequencies for 17 variable loci in other samples of paruline and thraupine species.

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | VRUF | PAME | DPET | DCOR | DTOW | DVIR | SRUT | PCIT | HVER |
| ACON1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | | | | | 1.000 | | | | |
| D | | | | | | | | | |
| E | | | | | | | | | |
| F | | | | | | | | | |
| G | 1.000 | | 1.000 | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 |
| H | | 1.000 | | | | | | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| K | | | | | | | | | |
| ACON2 | | | | | | | | | |
| B | | | | | | | | .167 | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .833 | 1.000 |
| ADA | | | | | | | | | |
| C | | | | | | | | | |
| H | | | | | .500 | | | .833 | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| L | | | | | | | | | |
| M | 1.000 | 1.000 | 1.000 | 1.000 | .500 | 1.000 | 1.000 | | 1.000 |
| N | | | | | | | | | |
| P | | | | | | | | | |
| Q | | | | | | | | | |
| R | | | | | | | | .167 | |
| S | | | | | | | | | |
| T | | | | | | | | | |
| ADH | | | | | | | | | |
| D | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| E | | | | | | | | | |
| EAP | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| ESTD | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| C | | | | | | | | | |
| F | | | | | | | | | |
| G | | | | | | | | | |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | VRUF | PAME | DPET | DCOR | DTOW | DVIR | SRUT | PCIT | HVER |
| FUM | | | | | | | | | |
| B | | | | | | | | | |
| C | | | .667 | | | | | | |
| E | 1.000 | 1.000 | .333 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| F | | | | | | | | | |
| G | | | | | | | | | |
| H | | | | | | | | | |
| GDA | | | | | | | | | |
| A | | | | | 1.000 | 1.000 | | | |
| B | | | | | | | | | |
| C | | | | | | | | | |
| D | | | | | | | | | |
| E | 1.000 | 1.000 | 1.000 | | | | 1.000 | 1.000 | |
| H | | | | | | | | | 1.000 |
| I | | | | 1.000 | | | | | |
| J | | | | | | | | | |
| L | | | | | | | | | |
| GOT1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | 1.000 | | | | | | |
| C | 1.000 | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| GPDH | | | | | | | | | |
| D | | | | | | | | | |
| E | | | .167 | | | | | | |
| F | | | | | | | | | |
| G | 1.000 | 1.000 | .833 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| I | | | | | | | | | |
| J | | | | | | | | | |
| IDH1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | .500 | | .250 | | .333 |
| D | 1.000 | 1.000 | 1.000 | 1.000 | .500 | 1.000 | .750 | 1.000 | .667 |
| E | | | | | | | | | |
| F | | | | | | | | | |
| IDH2 | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| LDH1 | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | VRUF | PAME | DPET | DCOR | DTOW | DVIR | SRUT | PCIT | HVER |
| ME | | | | | | | | | |
| F | 1.000 | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| G | | | 1.000 | | | | | | |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| NP | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | | | .500 | | | | | 1.000 | |
| D | .500 | 1.000 | .500 | 1.000 | .500 | .500 | | | 1.000 |
| E | .500 | | | | .500 | .500 | 1.000 | | |
| PEPA | | | | | | | | | |
| A | | | | | | | .500 | | |
| C | | | | | | | | | 1.000 |
| D | 1.000 | | | | | | | | |
| E | | | 1.000 | | | .500 | | | |
| F | | 1.000 | | 1.000 | 1.000 | .500 | .500 | 1.000 | |
| H | | | | | | | | | |
| J | | | | | | | | | |
| PEPC | | | | | | | | | |
| B | | | | | | | | | |
| D | | 1.000 | | | | | | | |
| E | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .833 |
| H | | | | | | | | | .167 |
| PGM1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | | | | | | | | | |
| E | | | | | | | | | |
| F | | | | | | | | | |
| G | | | | | | | | | |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| L | | | | | | | | | |
| N | | | | | | | | | |
| SDH | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | | | | | | | | |
| C | | | | | | | | | |
| D | | | | 1.000 | 1.000 | | 1.000 | | |
| E | | | 1.000 | | | 1.000 | | 1.000 | 1.000 |
| F | | 1.000 | | | | | | | |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | LSWA | SAUR | SNOV | WCIT | WPUS | WCAN | ERUB | MPIC | MMIN |
| ACON1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | | | | | | | | |
| D | | | .333 | | | | | | |
| E | | | | | | | | | |
| F | | | | | | | | | |
| G | | | .667 | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | 1.000 | | | | |
| K | | 1.000 | | | | | | | |
| ACON2 | | | | | | | | | |
| B | | | | | .182 | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | .818 | 1.000 | 1.000 | 1.000 | 1.000 |
| ADA | | | | | | | | | |
| C | | | .667 | | | | | | |
| H | | | .167 | .100 | .955 | .300 | 1.000 | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| L | | | | | | | | | |
| M | 1.000 | | .167 | .700 | .045 | .700 | | 1.000 | 1.000 |
| N | | | | | | | | | |
| P | | | | .200 | | | | | |
| Q | | 1.000 | | | | | | | |
| R | | | | | | | | | |
| S | | | | | | | | | |
| T | | | | | | | | | |
| ADH | | | | | | | | | |
| D | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| E | | | | | | | | | |
| EAP | | | | | | | | | |
| A | | | | .400 | | | | | |
| B | 1.000 | 1.000 | 1.000 | .600 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| ESTD | | | | | | | | | |
| A | | | .167 | .100 | | | | | |
| B | 1.000 | 1.000 | .833 | .900 | .909 | .900 | 1.000 | 1.000 | 1.000 |
| C | | | | | | .100 | | | |
| F | | | | | .045 | | | | |
| G | | | | | .045 | | | | |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | LSWA | SAUR | SNOV | WCIT | WPUS | WCAN | ERUB | MPIC | MMIN |
| FUM | | | | | | | | | |
| B | | | | | | | | | |
| C | | | | | | | | | |
| E | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .750 | 1.000 | 1.000 |
| F | | | | | | | | | |
| G | | | | | | | | | |
| H | | | | | | | .250 | | |
| GDA | | | | | | | | | |
| A | | | | | | | | | |
| B | | .250 | | | | | | | |
| C | | .750 | | | | | | | |
| D | | | | | | | | | |
| E | 1.000 | | | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| L | | | 1.000 | | | | | | |
| GOT1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| GPDH | | | | | | | | | |
| D | | | | | .056 | | | | |
| E | | | | | | | | | |
| F | | | | | | | | | |
| G | 1.000 | 1.000 | 1.000 | 1.000 | .944 | 1.000 | 1.000 | 1.000 | 1.000 |
| I | | | | | | | | | |
| J | | | | | | | | | |
| IDH1 | | | | | | | | | |
| A | 1.000 | | | | | | | | |
| B | | | | | | .100 | | | |
| D | | 1.000 | 1.000 | 1.000 | | .900 | 1.000 | | .750 |
| E | | | | | | | | 1.000 | .250 |
| F | | | | | 1.000 | | | | |
| IDH2 | | | | | | | | | |
| A | | | .167 | | | | | | |
| B | 1.000 | 1.000 | .833 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| LDH1 | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | LSWA | SAUR | SNOV | WCIT | WPUS | WCAN | ERUB | MPIC | MMIN |
| ME | | | | | | | | | |
| F | 1.000 | 1.000 | 1.000 | 1.000 | | .800 | 1.000 | 1.000 | 1.000 |
| G | | | | | | .100 | | | |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | 1.000 | .100 | | | |
| NP | | | | | | | | | |
| A | | 1.000 | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | | | | | | | | |
| D | | | 1.000 | 1.000 | .950 | 1.000 | 1.000 | 1.000 | 1.000 |
| E | | | | | .050 | | | | |
| PEPA | | | | | | | | | |
| A | | | | | | | | | |
| C | | | | | | .600 | | | |
| D | | | | .300 | | .100 | | | |
| E | 1.000 | .750 | .333 | | | | | | |
| F | | .250 | .167 | .700 | | .200 | | .500 | .750 |
| H | | | .333 | | | .100 | 1.000 | .500 | .250 |
| J | | | .167 | | 1.000 | | | | |
| PEPC | | | | | | | | | |
| B | | | | | 1.000 | | | | |
| D | | | | | | | | | |
| E | 1.000 | 1.000 | 1.000 | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 |
| H | | | | | | | | | |
| PGM1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | .250 | | |
| C | | | | | 1.000 | | | | |
| E | | | | | | | | | |
| F | | | | | | | | | |
| G | | | | | | | | | |
| H | | | | | | | | | |
| I | | | | | | 1.000 | | | |
| J | 1.000 | 1.000 | 1.000 | 1.000 | | | .750 | 1.000 | 1.000 |
| L | | | | | | | | | |
| N | | | | | | | | | |
| SDH | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | .200 | | | |
| C | | | | | | | | 1.000 | 1.000 |
| D | | | | | | | | | |
| E | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .800 | 1.000 | | |
| F | | | | | | | | | |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | ELAC | BLUT | BCOR | BCHR | BCUL | BRUF | BBEL | BMEL | BTRI |
| ACON1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | | | | | | | | | |
| D | | | | | | | | | |
| E | | | | | | | | | |
| F | | | | | | .500 | | .250 | .500 |
| G | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .500 | 1.000 | .750 | .500 |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| K | | | | | | | | | |
| ACON2 | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| ADA | | | | | | | | | |
| C | | | | | | | | | |
| H | | | | | .250 | | .250 | .250 | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| L | | | | | | | | | |
| M | 1.000 | 1.000 | 1.000 | 1.000 | .750 | 1.000 | .750 | .750 | 1.000 |
| N | | | | | | | | | |
| P | | | | | | | | | |
| Q | | | | | | | | | |
| R | | | | | | | | | |
| S | | | | | | | | | |
| T | | | | | | | | | |
| ADH | | | | | | | | | |
| D | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| E | | | | | | | | | |
| EAP | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| ESTD | | | | | | | | | |
| A | .167 | | | | | | | | |
| B | .833 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| C | | | | | | | | | |
| F | | | | | | | | | |
| G | | | | | | | | | |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | ELAC | BLUT | BCOR | BCHR | BCUL | BRUF | BBEL | BMEL | BTRI |
| FUM | | | | | | | | | |
| B | | | | 1.000 | | | | | |
| C | | | | | | | | | |
| E | 1.000 | 1.000 | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| F | | | | | | | | | |
| G | | | | | | | | | |
| H | | | | | | | | | |
| GDA | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | | | | .500 | | | | | |
| D | | | | | | | | | |
| E | 1.000 | 1.000 | 1.000 | .500 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| L | | | | | | | | | |
| GOT1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| GPDH | | | | | | | | | |
| D | | | | | | | | | |
| E | | | | | | | | | |
| F | | | 1.000 | | | .250 | | | |
| G | 1.000 | 1.000 | | 1.000 | 1.000 | .750 | 1.000 | 1.000 | 1.000 |
| I | | | | | | | | | |
| J | | | | | | | | | |
| IDH1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| D | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| E | | | | | | | | | |
| F | | | | | | | | | |
| IDH2 | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| LDH1 | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | ELAC | BLUT | BCOR | BCHR | BCUL | BRUF | BBEL | BMEL | BTRI |
| ME | | | | | | | | | |
| F | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| G | | | | | | | | | |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| NP | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | | | | | | | | | .250 |
| D | 1.000 | .500 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .500 | .750 |
| E | | .500 | | | | | | .500 | |
| PEPA | | | | | | | | | |
| A | | | | | | | | | |
| C | | | | | | | | | |
| D | | | | .500 | | | | | |
| E | | | .500 | .500 | .250 | 1.000 | 1.000 | .500 | |
| F | 1.000 | | .500 | | | | | .500 | |
| H | | 1.000 | | | .750 | | | | 1.000 |
| J | | | | | | | | | |
| PEPC | | | | | | | | | |
| B | 1.000 | | | 1.000 | | | | | |
| D | | | | | | | | .500 | |
| E | | 1.000 | 1.000 | | 1.000 | 1.000 | 1.000 | .500 | 1.000 |
| H | | | | | | | | | |
| PGM1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | | | | | | | | | |
| E | | | | | | | | .250 | |
| F | | | | | | | | | |
| G | | | | | | | | | |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .750 | 1.000 |
| L | | | | | | | | | |
| N | | | | | | | | | |
| SDH | | | | | | | | | |
| A | | | | | | | | | |
| B | | | .250 | | .250 | .250 | | | |
| C | | | | | | | | | |
| D | | | | | | | | | |
| E | 1.000 | 1.000 | .750 | 1.000 | .750 | .750 | 1.000 | 1.000 | 1.000 |
| F | | | | | | | | | |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | ZCOR | IVIR | GPEL | CHCH | HGUI | TSOR | TORN | TRUF | PBID |
| ACON1 | | | | | | | | | |
| A | | | | | | | | | 1.000 |
| B | | | | 1.000 | | | 1.000 | .400 | |
| C | | | | | | | | | |
| D | | | | | | | | | |
| E | | | | | | 1.000 | | .600 | |
| F | | | | | | | | | |
| G | 1.000 | | 1.000 | | 1.000 | | | | |
| H | | | | | | | | | |
| I | | 1.000 | | | | | | | |
| J | | | | | | | | | |
| K | | | | | | | | | |
| ACON2 | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| ADA | | | | | | | | | |
| C | | | | | | | | | |
| H | | | .250 | | | | | | |
| I | | | | | .667 | | | | |
| J | | | | | | .500 | | .667 | |
| L | | | | | | .500 | 1.000 | | |
| M | | | .750 | | .333 | | | .333 | 1.000 |
| N | | | | 1.000 | | | | | |
| P | | | | | | | | | |
| Q | | | | | | | | | |
| R | | | | | | | | | |
| S | 1.000 | | | | | | | | |
| T | | 1.000 | | | | | | | |
| ADH | | | | | | | | | |
| D | 1.000 | 1.000 | 1.000 | .875 | 1.000 | .500 | | | |
| E | | | | .125 | | .500 | 1.000 | 1.000 | 1.000 |
| EAP | | | | | | | | | |
| A | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| B | | | | | | | | | |
| ESTD | | | | | | | | | |
| A | | .333 | 1.000 | 1.000 | .167 | | | | |
| B | 1.000 | .667 | | | .833 | 1.000 | 1.000 | 1.000 | 1.000 |
| C | | | | | | | | | |
| F | | | | | | | | | |
| G | | | | | | | | | |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | ZCOR | IVIR | GPEL | CHCH | HGUI | TSOR | TORN | TRUF | PBID |
| FUM | | | | | | | | | |
| B | | | | | | 1.000 | 1.000 | .917 | |
| C | | | | | 1.000 | | | | |
| E | 1.000 | 1.000 | 1.000 | 1.000 | | | | .083 | 1.000 |
| F | | | | | | | | | |
| G | | | | | | | | | |
| H | | | | | | | | | |
| GDA | | | | | | | | | |
| A | | | | | | | | | |
| B | | | | | | | | | |
| C | 1.000 | | | | | | | | |
| D | | | 1.000 | .625 | | 1.000 | 1.000 | 1.000 | |
| E | | | | .375 | 1.000 | | | | 1.000 |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | 1.000 | | | | | | | |
| L | | | | | | | | | |
| GOT1 | | | | | | | | | |
| A | | | | | | 1.000 | | | |
| B | | | | | | | | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | | 1.000 | 1.000 | 1.000 |
| GPDH | | | | | | | | | |
| D | | | | | | | | | |
| E | | | | | | | | | |
| F | | | | | | | | | |
| G | | | | | | | | | |
| I | 1.000 | 1.000 | 1.000 | .500 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| J | | | | .500 | | | | | |
| IDH1 | | | | | | | | | |
| A | | | | | | | | | |
| B | | | 1.000 | .500 | | | | | 1.000 |
| D | 1.000 | | | .500 | 1.000 | 1.000 | 1.000 | 1.000 | |
| E | | 1.000 | | | | | | | |
| F | | | | | | | | | |
| IDH2 | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| LDH1 | | | | | | | | | |
| B | | | | | | | .250 | | |
| C | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .750 | 1.000 | 1.000 |

Table 2. (cont.)

| | T A X A | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Locus | ZCOR | IVIR | GPEL | CHCH | HGUI | TSOR | TORN | TRUF | PBID |
| ME | | | | | | | | | |
| F | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| G | | | | | | | | | |
| H | | | | | | | | | |
| I | | | | | | | | | |
| J | | | | | | | | | |
| NP | | | | | | | | | |
| A | | | | | | | | | |
| B | | | 1.000 | | | | | | 1.000 |
| C | 1.000 | | | | | | | | |
| D | | 1.000 | | .375 | 1.000 | | | | |
| E | | | | .625 | | 1.000 | 1.000 | 1.000 | |
| PEPA | | | | | | | | | |
| A | | | | | | | | | |
| C | | | | | | | | | |
| D | | | | | | | | | |
| E | | .833 | | | .100 | | | | |
| F | | .167 | | | | .750 | 1.000 | 1.000 | |
| H | 1.000 | | 1.000 | | .700 | | | | |
| J | | | | 1.000 | .200 | .250 | | | 1.000 |
| PEPC | | | | | | | | | |
| B | | | | | | | | | |
| D | | 1.000 | | | | | | | |
| E | 1.000 | | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| H | | | | | | | | | |
| PGM1 | | | | | | | | | |
| A | | | | | | | 1.000 | 1.000 | |
| B | | | | | | | | | |
| C | | | | | | | | | |
| E | | | | | | | | | |
| F | | | 1.000 | | | | | | |
| G | | | | | | 1.000 | | | |
| H | | | | | | | | | 1.000 |
| I | 1.000 | 1.000 | | | | | | | |
| J | | | | | | | | | |
| L | | | | 1.000 | | | | | |
| N | | | | | 1.000 | | | | |
| SDH | | | | | | | | | |
| A | | | | | | | | | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| C | | | | | | | | | |
| D | | | | | | | | | |
| E | | | | | | | | | |
| F | | | | | | | | | |

Table 2. (end)

Key to species. VRUF = Vermivora ruficapilla ; PAME = Parula americana; DPET = Dendroica petechia; DCOR = D. coronata; DTOW = D. townsendi; DVIR = D. virens; SRUT = Setophaga ruticilla; PCIT = Protonotaria citrea; HVER = Helmitheros vermivorus; LSWA = Limnothlypis swainsoni; SAUR = Seiurus aurocapillus; SNOV = S. noveboracensis; WCIT = Wilsonia citrina; WPUS = W. pusilla; WCAN = W. canadensis; ERUB = Ergaticus ruber; MPIC = Myioborus pictus; MMIN = M. miniatus; ELAC = Euthlypis lachrymosa; BLUT = Basileuterus luteoviridis; BCOR = B. coronatus; BCHR = B. chrysogaster; BCUL = B. culicivorus; BRUF = B. rufifrons; BBEL = B. belli; BMEL = B. melanogenys; BTRI = B. tristriatus; ZCOR = Zeledonia coronata; IVIR = Icteria virens; GPEL = Granatellus pelzeni; CHCH = Chrysothlypis chrysomelas; HGUI = Hemithraupis guira; TSOR = Thlypopsis sordida; TORN = T. ornata; TRUF = T. ruficeps; PBID = Piranga bidentata.

Table 3. Number of polymorphic states invoked for ancestors in most parsimonious tree using the polymorphism parsimony method for Geothlypis and Oporornis taxa, and composite outgroup.

| Allele | polymorphic ancestral states | Allele | polymorphic ancestral states |
|---|---|---|---|
| ADA-a | 3 | ME-c | 2 |
| ADA-b | 2 | ME-f | 3 |
| ADA-e | 4 | NP-b | 3 |
| ADA-h | 7 | NP-d | 2 |
| ADA-m | 8 | PEPA-c | 4 |
| EAP-a | 0 | PEPA-d | 4 |
| ESTD-a | 6 | PEPA-e | 2 |
| ESTD-c | 5 | PEPA-h | 3 |
| FUM-h | 3 | PEPA-j | 3 |
| GDA-d | 3 | PEPBd | 9 |
| GDA-e | 2 | PEPBe | 5 |
| GDA-k | 5 | PEPC-a | 2 |
| GPDH-i | 2 | PEPC-b | 7 |
| G6PDa | 7 | PGM1-d | 1 |
| G6PDd | 1 | PGM2c | 0 |
| G6PDe | 3 | PGM2e | 6 |
| IDH1-a | 3 | PGM2f | 0 |
| IDH1-b | 1 | PGM3a | 2 |
| IDH1-c | 1 | SDH-b | 5 |
| IDH1-d | 1 | | |
| IDH1-e | 0 | | |

Appendix 1. Data matrix for 52 thraupine and paruline taxa. (For abbreviations see tables).

| Taxon | A C O N 1 b | A C O N 1 c | A C O N 1 e | A C O N 1 f | A C O N 1 g | A C O O 2 b | A N D A A a | A D D A A b | A D D A A e | A D D A A h | A D D A H j | A D D A H l | A A A E P m | A A T T D d | A A T T D e | A A T T D a | E E S S M b | E S S F M a | E F F F M b | F G G G M c | G G G G A b | G G G G A e | G O P P A h | G T D D A a | I D D D A c | I D D D A d | I D D D A e | I H H H E k | I H H H E c | I H H H E f | I H H H E g | I M M M P i | P E E E P a | P E E E P b | P E E E P c | P E E E P d | P E E E P e | P E E E P f | P E E E P h | P E E E P j | P E E E P a | P E E E P b | P E E E P d | P E E E P e | P E E E P a | P E E E P d | P E E E P i | P E E E P j | S D D D H b | S D D D H c | S D D D H d | S D D D H e |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| PBID | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| TORN | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| TSOR | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| TRUF | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| CCHR | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| HGUI | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| IVIR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| GPEL | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| ZCOR | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BCHR | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BCUL | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| BRUF | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| BBEL | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| BLUT | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| BMEL | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| BTRI | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| BCOR | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 |
| ELAC | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| PCIT | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| VRUF | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 |
| PAME | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| DPET | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| DCOR | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| DTOW | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| DVIR | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| SRUT | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| HVER | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 |
| LSWA | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| SAUR | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 |
| SNOV | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 |
| WCIT | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| WPUS | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| WCAN | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 |
| ERUB | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| MPIC | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| MMIN | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 |
| GTRI | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |

| Taxon | A C O N 1 - b | A C O N 1 - c | A C O N 1 - e | A C O N 1 - f | A C O N 2 - g | A D A - b | A D A - a | A D A - b | A D A - e | A D A - h | A D A - j | A D H - l | A D H - m | A D P - d | A E P - e | E S D - a | E S D - b | E S D - a | E S D - b | F U M - c | F U M - b | F U M - c | F U M - e | G U M - h | G D A - a | G D A - c | G D A - d | G D A - e | G D A - k | G O A - c | G D A - f | G D A - g | G D A - i | H D A - a | H H 1 - b | H H 1 - c | H H 1 - d | H H 1 - e | M E A - c | M E A - f | M E A - g | M E A - j | N P A - b | N P A - c | N P A - d | N P A - e | P E A - c | P E A - d | P E A - e | P E A - f | P E A - h | P E C - j | P E C - a | P E C - b | P E C - d | P E C - e | P M 1 - a | P M 1 - d | P M 1 - i | P M 1 - j | P D H - b | S D H - c | S D H - d | S D H - e |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| GBEL | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| GFLA | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| GROS | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 |
| GSEM | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| GSPE | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| GNEL | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| GCHI | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| GVEL | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| GAUR | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| GAEQ | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| GPOL | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| OFOR | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| OAGI | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| OPHI | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| OTOL | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 |

Appendix 2. Data matrix for Geothlypis and Oporornis taxa plus composite outgroup.

Abbreviations are as follows: CompOutg: composite outgroup; GTRI: *G. trichas*; GBEL: *G. beldingi*; GFLA: *G. flavovelata*; GROS: *G. rostrata*; GSEM: *G. semiflava*; GSPE: *G. speciosa*; GNEL: *G. nelsoni*; GCHI: *G. chiriquensis*; GVEL: *G. velata*; GAUR: *G. auricularis*; GAEQ: *G. aequinoctialis*; GPOL: *G. poliocephala*; OFOR: *O. formosus*; OAGI: *O. agilis*; OPHI: *O. philadelphia*; OTOL: *O. tolmiei*.

| Node | a | b | e | h | m | a | a | c | h | d | e | k | i | a | d | e | a | b | c | d | e | c | f | b | d | c | d | e | h | j | d | e | a | b | d | c | e | f | a | b |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| CompOutg | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 9 | 9 | 1 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 9 | 9 | 0 | 1 | 0 | 9 | 9 | 9 | 9 | 1 |
| GTRI | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 |
| GBEL | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | |
| GFLA | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | |
| GROS | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| GSEM | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 |
| GSPE | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 |
| GNEL | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 |
| GCHI | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 |
| GVEL | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| GAUR | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| GAEQ | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| GPOL | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | |
| OFOR | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| OAGI | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| OPHI | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 |
| OTOL | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | |

Appendix 3. Plumage data matrix.

| Taxa | Characters | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| *G. trichas* | 1 | 0 | 3 | 2 | 0 |
| *G. beldingi* | 1 | 0 | 3 | 2 | 0 |
| *G. flavovelata* | 1 | 0 | 3 | 2 | 0 |
| *G. rostrata* | 1 | 0 | 3 | 2 | 0 |
| *G. semiflava* | 1 | 0 | 3 | 0 | 0 |
| *G. speciosa* | 1 | 0 | 3 | 0 | 0 |
| *G. nelsoni* | 1 | 0 | 3 | 1 | 1 |
| *G. chiriquensis* | 1 | 0 | 2 | 1 | 0 |
| *G. velata* | 1 | 1 | 2 | 1 | 1 |
| *G. auricularis* | 1 | 0 | 2 | 1 | 0 |
| *G. aequinoctialis* | 1 | 0 | 2 | 1 | 0 |
| *G. poliocephala* | 1 | 1 | 1 | 1 | 0 |
| *O. formosus* | 1 | 0 | ? | 1 | 1 |
| *O. agilis* | 0 | 2 | 0 | 1 | 0 |
| *O. philadelphia* | 0 | 1 | 1 | 1 | 0 |
| *O. tolmiei* | 0 | 1 | 1 | 1 | 0 |

Character states:

1: throat color (0=gray, 1=yellow)

2: white eye marks (0=none, 1=arcs, 2=ring)

3: mask (0=none, 1=reduced, 2=extending to forehead and cheeks, 3=extending to mid-crown, cheeks and auriculares)

4: margin behind mask (0=olive green, 1=gray, 2=yellow)

5: yellow eyebrow (0=absent, 1=present)

Appendix 4. Fitch-Margoliash trees in reduced format with branch lengths, using three different outgroups.

With Icteria:

((polioceph:0.16706,aequinoct:0.15194):0.03354,((auricular:0.05972,velata:0.06128):0.06600,(tolmiei:0.09272,(philadelp:0.07916,((speciosa:0.16344,(beldingi:0.09381,(((formosus:0.10709,nelsoni:0.06291):0.01079,(chiriquen:0.05961,(semiflava:0.05455,(flavovela:0.05613,trichas:0.02487):0.00544):0.00940):0.00747):0.00909,rostrata:0.09546):0.01180):0.00305):0.00689,agilis:0.15087):0.04681):0.01226):0.00418):0.01994,Icteria:0.44107).

With Basileuterus:

((((auricular:0.05967,velata:0.06133):0.06651,((polioceph:0.16953,aequinoct:0.14947):0.04979,tolmiei:0.08887):0.00563):0.01133,philadelp:0.07984):0.03099,(agilis:0.15323,(((((nelsoni:0.06299,formosus:0.10701):0.01060,(((flavovela:0.05613,trichas:0.02487):0.00549,semiflava:0.05449):0.00933,chiriquen:0.05966):0.00764):0.01191,rostrata:0.09256):0.00844,beldingi:0.09498):0.00435,speciosa:0.16321):0.00431):0.02010,Basileute:0.16654).

With ComOutg:

(((((aequinoct:0.15001,polioceph:0.16899):0.04976,tolmiei:0.08910):0.00522,(auricular:0.05958,velata:0.06142):0.06679):0.01162,philadelp:0.07957):0.02413,((speciosa:0.16340,((((formosus:0.10701,nelsoni:0.06299):0.01088,((semiflava:0.05452,(trichas:0.02501,flavovela:0.05599):0.00542):0.00940,chiriquen:0.05959):0.00734):0.01079,rostrata:0.09391):0.01009,beldingi:0.09424):0.00355):0.00637,agilis:0.15133):0.02529,ComOutg:0.16167).

Appendix 5. Trees obtained with FREQPARS, using either Basileuterus or Icteria as outgroups.

((((((((((trichas,rostrata)formosus)agilis)nelsoni)speciosa)chiriquen
sis)((flavovelata,beldingi)semiflava)(velata,auricularis))philadelphia)
tolmiei)(poliocephala,aequinoctialis))Icteria)

(((((((((trichas,rostrata)formosus)agilis)nelsoni)speciosa)chiriquens
is)((flavovelata,beldingi)semiflava)((((poliocephala,aequinoctialis)tol
miei) philadelphia)(velata,auricularis))Basileuterus)

Fig. 1. Geothlypis and Oporornis phylogenetic trees obtained with maximum likelihood using different outgroups. A: with Icteria; B: with Basileuterus; C: with composite outgroup. Solid lines represent branches in which confidence intervals are positive; thin lines represent branches with negative lower bounds, where rearrangements may be acceptable.

Fig. 2. Consensus of shortest trees obtained with Wagner parsimony in 52 taxa of parulines and thraupines. The node where "other Parulines" join trees represents a major polytomy where the remaining 26 parulines join the cladogram (with minimun additional structure), including the putative closely related Basileuterus. Detail on the Geothlypis and Oporornis clade is discussed in text. On the left, strict consensus node descriptors are (state change, and consistency index of character in the tree in parentheses): 1 = ADA-h (0->1, 0.077); 2 = NP-c (0->1, 0.200); 3 = NP-d (1->0, 0.111); 4 = PEPA-d (0->1, 0.125); 5 = ACON1-g (0->1, 0.111); 6 = EAP-a (1->0, 0.333); 7 = EAP-b (0->1, 1.000); 8 = GDA-e (0->1, 0.083); 9 = GPDH-g (0->1, 0.500); 10 = GPDH-i (1->0, 0.500); 11 = NP-d (0->1, 0.111); 12 = PGM1-j (0->1, 0.500); 13 = SDH-b (1->0, 0.167); 14 = SDH-e (0->1, 0.143). On the right, numbers indicate percent of trees in which that node occurred in shortest trees.

Fig. 3. Phylogenetic trees for Geothlypis and Oporornis taxa obtained with two methods of discrete data analysys and a composite outgroup. A: Wagner parsimony, unique shortest

tree of 91 steps long (CI=0.440, RI=0.528). B: Dollo parsimony, strict consensus of 4 shortest trees, 120 steps long (CI=0.333, RI=0.801).

Fig. 4. Shortest tree (L=130) obtained with polymorphism parsimony for *Geothlypis* and *Oporornis* taxa, and a composite outgroup.

Fig. 5. Phylogeny based on plumage color pattern. Characters were polarized using *Basileuterus* and other parulines as outgroups.

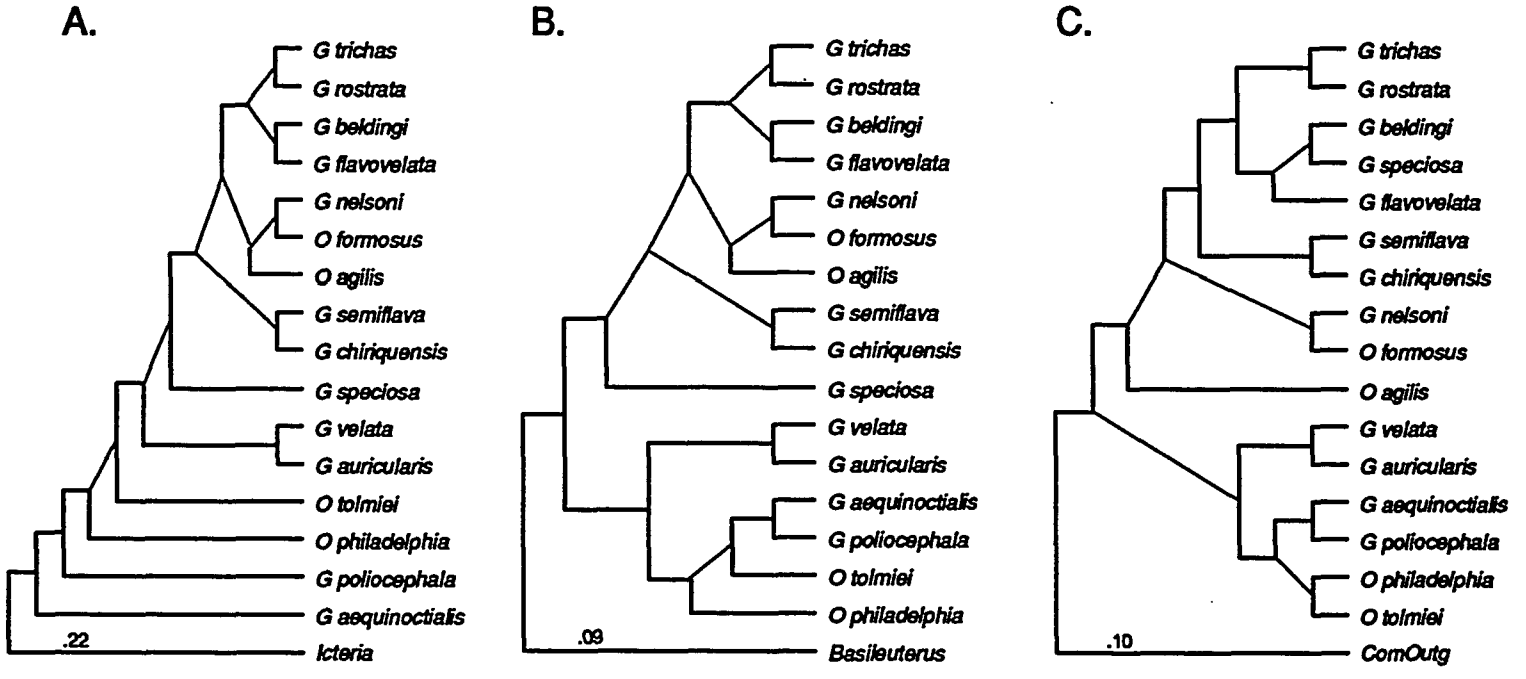

A.
G trichas
G rostrata
G beldingi
G flavovelata
G nelsoni
O formosus
O agilis
G semiflava
G chiriquensis
G speciosa
G velata
G auricularis
O tolmiei
O philadelphia
G poliocephala
G aequinoctialis
.22
Icteria
B.
G trichas
G rostrata
G beldingi
G flavovelata
G nelsoni
O formosus
O agilis
G semiflava
G chiriquensis
G speciosa
G velata
G auricularis
G aequinoctialis
G poliocephala
O tolmiei
O philadelphia
.09
Basileuterus
C.
G trichas
G rostrata
G beldingi
G speciosa
G flavovelata
G semiflava
G chiriquensis
G nelsoni
O formosus
O agilis
G velata
G auricularis
G aequinoctialis
G poliocephala
O philadelphia
O tolmiei
.10
ComOutg

Fig. 1.

Fig. 2.

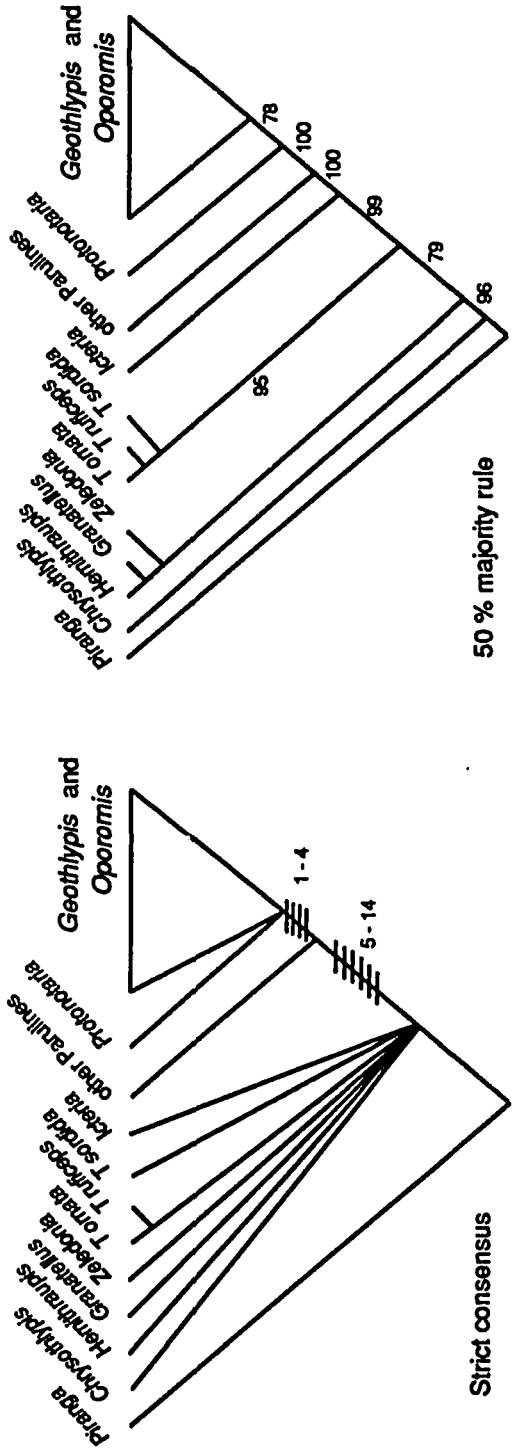

Geothlypis and Oporornis
78
100
100
99
79
96
95
Protonotaria
other Parulines
Icteria
T sordida
T ruficeps
T ornata
Zeledonia
Granatellus
Hemithraupis
Chrysothlypis
Piranga
50 % majority rule
Geothlypis and Oporornis
1 - 4
5 - 14
Protonotaria
other Parulines
Icteria
T sordida
T ruficeps
T ornata
Zeledonia
Granatellus
Hemithraupis
Chrysothlypis
Piranga
Strict consensus

Fig. 3.

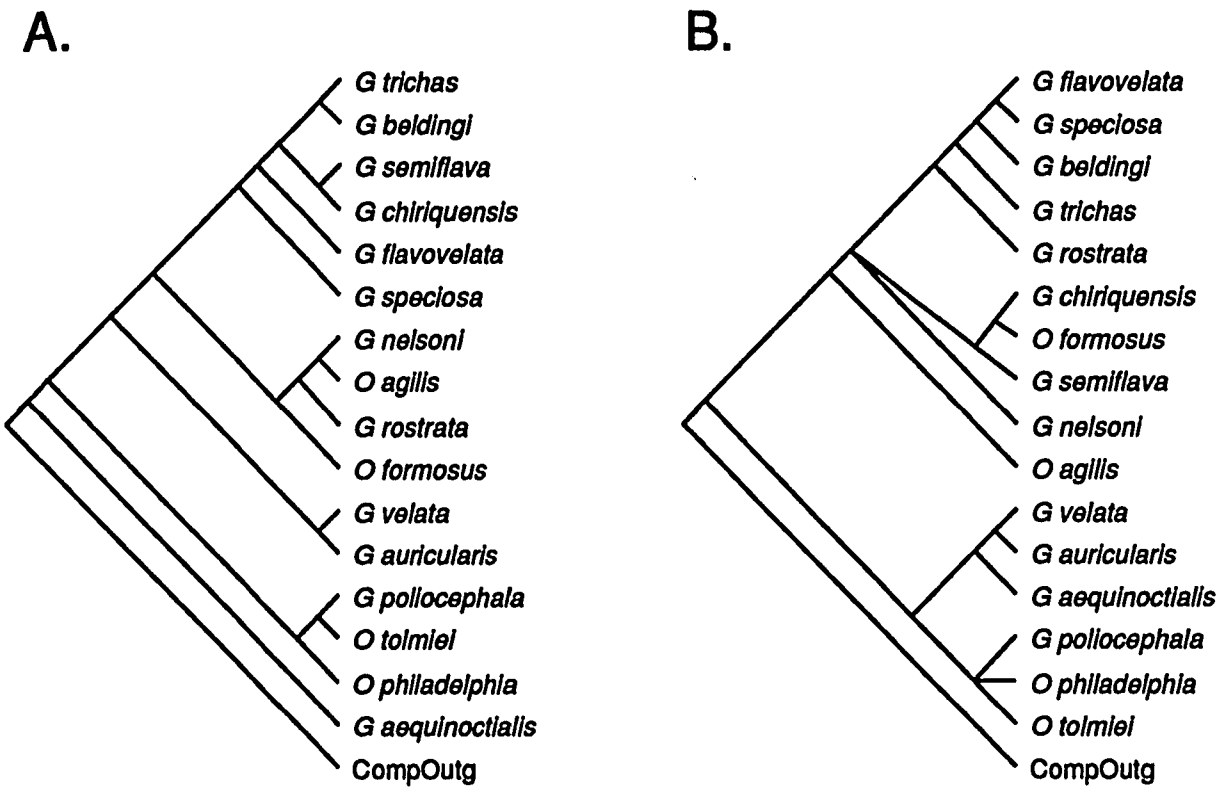

A.
G trichas
G beldingi
G semiflava
G chiriquensis
G flavovelata
G speciosa
G nelsoni
O agilis
G rostrata
O formosus
G velata
G auricularis
G poliocephala
O tolmiei
O philadelphia
G aequinoctialis
CompOutg
B.
G flavovelata
G speciosa
G beldingi
G trichas
G rostrata
G chiriquensis
O formosus
G semiflava
G nelsoni
O agilis
G velata
G auricularis
G aequinoctialis
G poliocephala
O philadelphia
O tolmiei
CompOutg

Fig. 4.

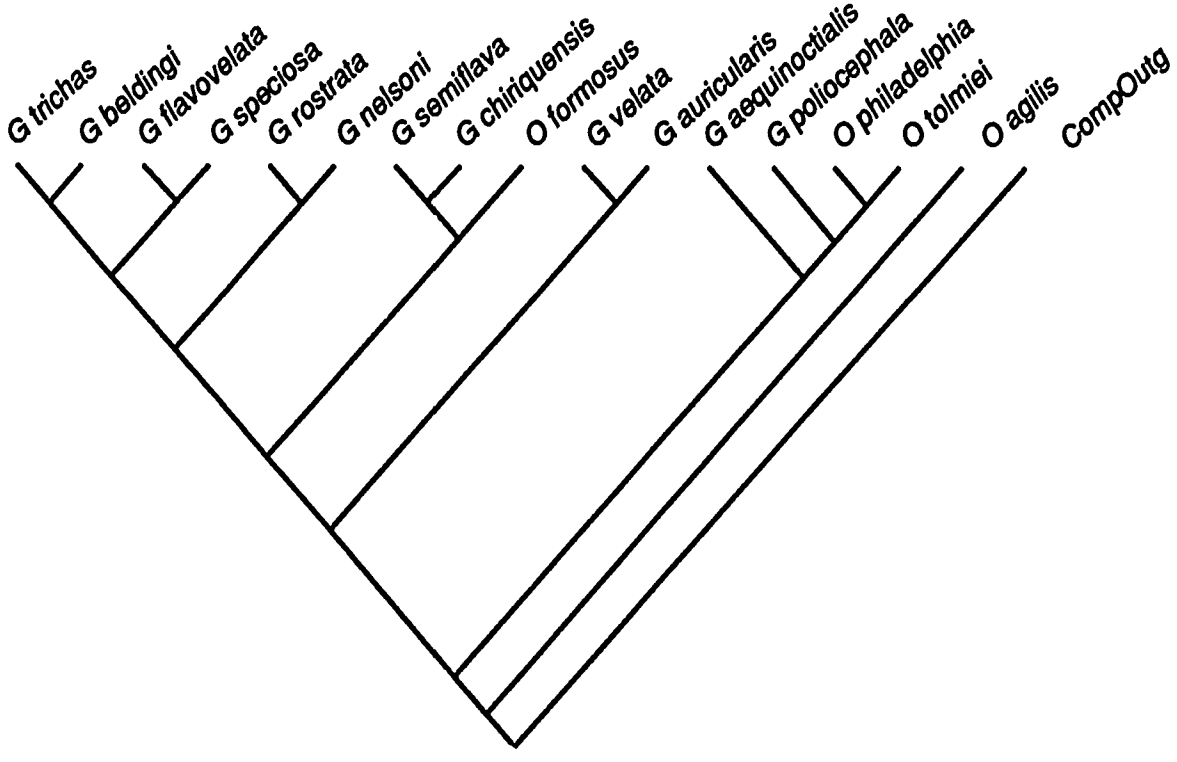
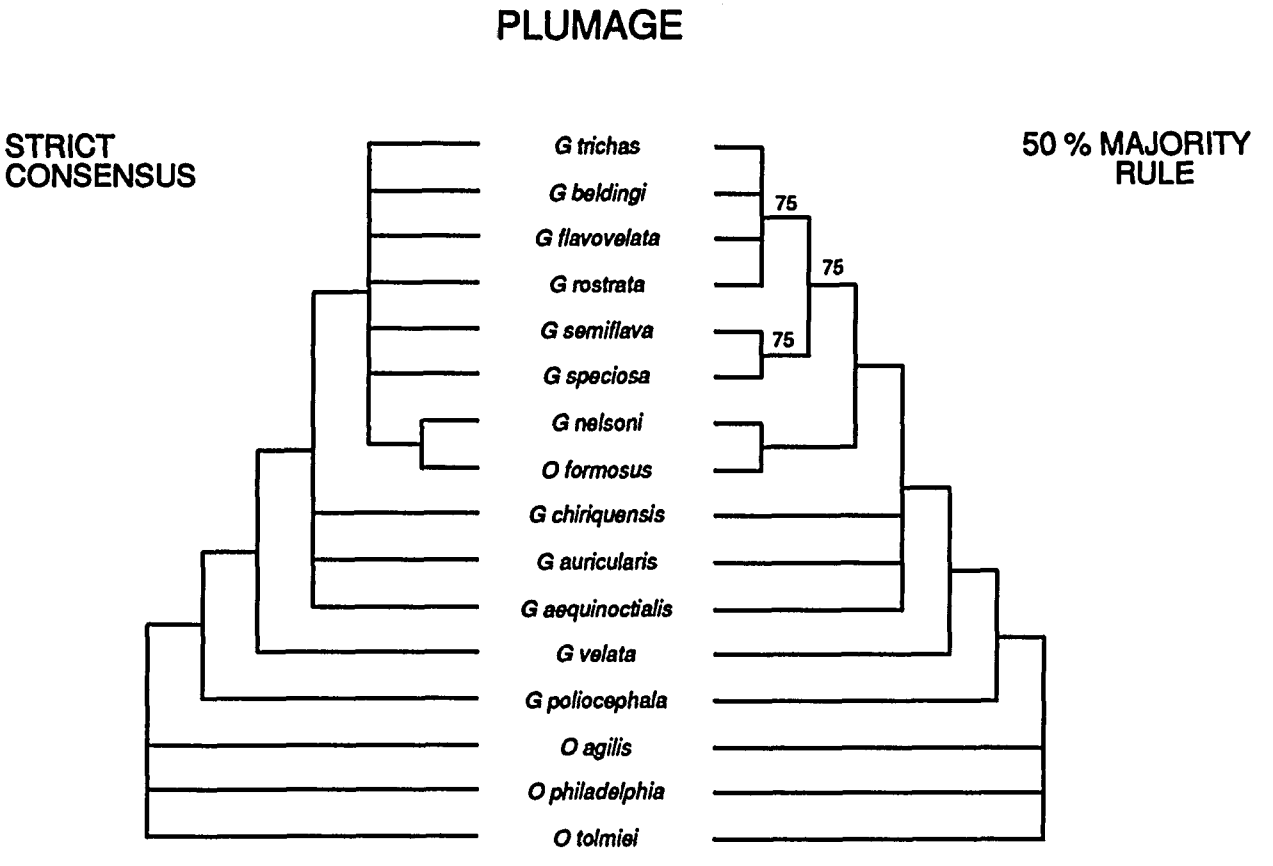

G trichas
G beldingi
G flavovelata
G speciosa
G rostrata
G nelsoni
G semiflava
G chiriquensis
O formosus
G velata
G auricularis
G aequinoctialis
G poliocephala
O philadelphia
O tolmiei
O agilis
CompOutg

Fig. 5.


PLUMAGE
STRICT CONSENSUS
50 % MAJORITY RULE
G trichas
G beldingi
G flavovelata
G rostrata
G semiflava
G speciosa
G nelsoni
O formosus
G chiriquensis
G auricularis
G aequinoctialis
G velata
G poliocephala
O agilis
O philadelphia
O tolmiei
75
75
75

# GENERAL CONCLUSIONS

The allozyme information obtained in this study was useful in analyzing genetic differentiation at two biological levels, populations and species. At the population level, populations of temperate taxa showed less allozyme differentiation than tropical taxa, suggesting that tropical species in this group are perhaps older evolutionarily. The trend in morphological differentiation in populations of Baja California Yellowthroats (G. beldingi) was found to be parallel to that in allozyme differentiation. In contrast, in Masked Yellowthroats (G. aequinoctialis) there was more allozyme differentiation among populations than in either plumage or external morphology.

The use of allozyme information to reconstruct phylogenies has limitations. The results of this study showed that paruline species share polymorphisms not only among closely related species, but also among genera. For instance, alleles found in different parulines species, and in some thraupine taxa assayed in this study, do not form consistent character phylogenies. Alleles that are common in some lineages are rare in others, but some rare alleles seem to keep lurking in many species' genomes after several speciation events. Although the possibility of mis-identification of these shared alleles cannot be ruled out, the small amount of genetic differentiation among taxa strongly suggests that ancestral polymorphism is the more parsimonious explanation for this pattern, rather than extensive convergence of electromorphs, or recurrent mutations for similar alleles in different lineages. This pattern represents the "worst-case" scenario for phylogenetic reconstruction in cladistic analysis. If ancestors were polymorphic, local demographic phenomena in the branches of the

phylogeny could produce more noise than signal. such as parallel losses, and the phylogenetic information contained in this data set would be very difficult to retrieve. However, an adequate analysis of allozyme data with more pertinent assumptions may reveal a more likely phylogenetic hypothesis underlying this kind of data. The one obtained here, allowing polymorphic ancestors, was the most concordant with patterns of plumage and biogeography.

Another limitation of allozyme electrophoresis is the reduced number of loci that can be sampled in practice. On the other hand, an appealing advantage of allozyme electrophoresis is that it allows one to examine large numbers of individuals relatively fast and inexpensively. This is very important if populations and taxa share polymorphic characters.

Additional data from other characters, such as song or DNA sequences, could be informative and thus could be used to test the phylogenetic hypothesis obtained with allozymes. A set of characters with larger rates of change, like mitochondrial DNA, could be especially informative in nodes where there seems to have been rapid speciation, as when the genus reinvaded Central America from the northwestern side of South America. However, in order to detect whether the problem of ancestral polymorphism found in allozymes is also present at the DNA level, it is important to examine more individuals per taxa than has been done until now and, if possible, to analize several gene sequences of mitochondrial and nuclear genomes.

# L I T E R A T U R E  C I T E D


Amadon, D.
1959. The significance of sexual differences in size among birds. Proc. Amer. Phil. Soc. 103:531-536.

AOU.
1983. Check-list of birds of North America. American Ornithologists' Union, 6th ed.

Aquadro, C. F. and J. C. Avise.
1982. Evolutionary genetics of birds. VI. A reexamination of protein divergence using varied electrophoretic conditions. Evolution 36:1003-1019.

Arnold, E. N.
1981. Estimating phylogenies at low taxonomic levels. Z. zool. Syst. Evolut.-forsch 19:1-35.

Avise, J.
1974. Systematic value of electrophoretic data. Syst. Zool. 23:465-481.

_____, J. C. Patton, and C. F. Aquadro.
1980. Evolutionary genetics of birds. Comparative molecular evolution in New World Warblers and rodents. J. Heredity 71:303-310.

Baldwin, S. P., H. C. Oberholser, and L. G. Worley.
1931. Measurements of birds. Sci. Pub. Cleveland Mus. Nat. Hist. 2. 121 pp.

Barrowclough, G. F.
1980. Genetic and phenotypic differentiation in a wood warbler (genus Dendroica) hybrid zone. Auk 97: 655-668.

_____.
1983. Biochemical studies of microevolutionary processes. In Perspectives in ornithology. A. H. Brush and G. A. Clark, Jr. (eds.). Cambridge Univ. Press, New York, N.Y. pp.223-261.

_____ and K. W. Corbin.
1978. Genetic variation and differentiation in the Parulidae. Auk 95:691-702.

_____, and N. K. Johnson
1988. Genetic structure of North American birds. Pp. 1630-1645 in H. Ouellet (ed.) Proc. XIX International Ornithological Congress, Univ. Ottawa Press, Ottawa, Ontario, Canada.

_____, N. K. Johnson, and R. M. Zink.
1985. On the nature of genic variation in birds. Current Ornithology 2:135-154.

Behle, W. H.
1950. Clines in the yellow-throats of western North America. Condor 52:193-219.

Bent, A. C.
1953. Life histories of North American wood warblers. U. S. National Museum Bull. 203. Smithsonian Institution. 734 pp.

Bledsoe, A.
1988. A hybrid Oporornis philadelphia X Geothlypis trichas, with comments on the taxonomic interpretation and evolutionary significance of intergeneric hybridization. Wilson Bull. 100:1-8.

_____ and R. J. Raikow.
1990. A quantitative assessment of congruence between molecular and non-molecular estimates of phylogeny. J. Mol. Evol. 30:247-259.

Bock, W.
1962. The pneumatic fossa of the humerus in the Passeres. Auk 79:425-443.

Braun, M. J. and T. A. Parker, III.
1985. Molecular, morphological, and behavioral evidence concerning the taxonomic relationships of "Synallaxis" gularis and other synallaxines. Pp. 333-346 in Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely and F. G. Buckley, eds.). Ornithological Monographs No. 36.

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

Cann, R. L., M. Stoneking, and A. C. Wilson.
1987. Mitochondrial DNA and human evolution. Nature, 325:31-36.

Capparella, A. C.
1987. Effects of riverine barriers on genetic differentiation of amazonian forest undergrowth birds. PhD. thesis. Louisiana State University and Agricultural and Mechanical College.

_____.
1988. Genetic variation in Neotropical birds: Implications for the speciation process. Pp. 1658-1664 in H. Ouellet (ed.) Proc. XIX International Ornithological Congress, Univ. Ottawa Press, Ottawa, Ontario, Canada.

_____ and S. M. Lanyon.
1985. Biochemical and morphometric analysis of the sympatric, neotropical, sibling species Mionectes macconnelli and M. oleagineus. Pp. 347-355 in Neotropical Ornithology (P. A. Buckley, M. S. Foster, E. S. Morton, R. S. Ridgely and F. G. Buckley, eds.). Ornithological Monographs No. 36.

Chapman, F. M.
1907. The Warblers of North America. Appleton & Company, New York, New York.

Coyne, J. A. and M. Kreitman.
1986.Evolutionary genetics of two sibling species, Drosophila simulans and D. sechellia. Evolution 40:673-691.

Cracraft, J.
1982. Geographic differentiation, cladistics, and vicariance biogeography: reconstructing the tempo and mode of evolution. Amer. Zool. 22:411-424.

Davis, L. I.
1972. A field guide to the birds of Mexico and Central America. University of Texas Press. Austin, Texas.

DeBry, R. W. and N. A. Slade.
1985. Cladistic analysis of restriction endonuclease cleavage maps within a maximum-likelihood framework. Syst. Zool. 34:21-34.

Donaghue, M. J.
1984. The logic and limitations of the outgroup substitution approach to cladistic analysis. Syst. Bot. 9:192-202.

Escalante-Pliego, P.
Genetic differentiation in yellowthroats (Parulinae: Geothlypis). Proceedings of the XX International Ornithological Congress. Christchurch, New Zealand. In press.

Evans, P. G. H.
1988. Electrophoretic variability of gene products. Pp. 105-162 in Cooke, F., and P. A. Buckley (eds.). Avian genetics. Academic Press, London.

Farris, J. S.
1977. Phylogenetic analysis under Dollo's Law. Syst. Zool. 26:77-88.

———.
1978. Inferring phylogenetic trees from chromosome inversion data. Syst. Zool. 27:275-284.

Felsenstein, J.
1979. Alternative methods of phylogenetic inference and their interrelationship. Syst. Zool. 28:49-62.

———.
1982. Numerical methods for inferring evolutionary trees. Quart. Rev. Biol. 57:379-404.

———.
1989. PHYLIP (Phylogeny inference package). Version 3.2. Seattle, Washington, USA.

Funk, V. A. and D. R. Brooks.
1990. Phylogenetic systematics as the basis of comparative biology. Smithsonian Contrib. Botany 73:1-45.

George, W. G.
1962. The classification of the Olive Warbler, Peucedramus taeniatus. Amer. Mus. Novit. 2103:1-41.

Gerwin,, J. A. and R. M. Zink.
1989. Phylogenetic patterns in the genus Heliodoxa (Aves: Trochilidae): an allozymic perspective. Wilson Bulletin 101:525-544.

Gibson, A. R. A. J. Baker, and A. Moeed.
1984. Morphometric variation in introduced populations of the Common Myna (Acridotheres tristis): an application of the jackknife to principal component analysis. Syst. Zool. 33:408-421.

Gill, F. B. and J. A. Gerwin.
1989. Protein relationships among Hermit Hummingbirds. Proceedings of the Academy of Natural Sciences of Philadelphia 141:409-421.

Grinnell, J.
1928. A distributional summation of the ornithology of Lower California. Univ. Calif. Publ. Zool. 32:1-300.

Griscom, L. and A. Sprunt, Jr.
1957. The warblers of North America. Devin-Adair Company, New York, New York.

Hackett, S. J.
1989. Effects of varied electrophoretic conditions on detection of evolutionary patterns in the Laridae. Condor 91:73-90.

_____ and K. V. Rosenberg.
1990. Comparison of phenotypic and genetic differentiation in South American Antwrens (Formicaridae). Auk 107:473-489.

Haffer, J.
1974. Avian speciation in tropical South America. Publ. Nuttall Ornithol. Club, no. 14, pp. 1-390.

Harris, H. and D. A. Hopkinson.
1976. Handbook of enzyme electrophoresis in human genetics. Oxford: North Holland Publications Company.

Heads, M.
1985. On the nature of ancestors. Syst. Zool. 34:205-215.

Johnson, N. K.
1980. Character variation and evolution of sibling species in the Empidonax difficilis-flavescens complex (Aves:Tyrannidae). Univ. Calif. Publ. 112:1-151.

_____ and J. A. Marten.
1988. Evolutionary genetics of flycatchers II. Differentiation in the Empidonax difficilis complex. Auk 105:177-191.

Johnston, R. F.
1972. Ecological differentiation in North American birds. In, Allen, R. T. and F. C. James (eds.). A Symposium in Systematics, Occ. Pap. Univ. Arkansas Mus. 4:101-132.

Jönsson, P. E. and T. Alerstam.
1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. Biol. J. Linn. Soc. 41:301-314.

Keast, A.
1980a. Spatial relationships between migratory parulid warblers and their ecological counterparts in the Neotropics. In, Keast, A. and E. S. Morton (eds.). Migrant birds in the Neotropics. Ecology, behavior, distribution, and conservation. Smithsonian Institution Press. Washington, D. C. Pp. 109-130.

_____.
1980b. Synthesis: ecological basis and evolution of the Neartic-Neotropical migration system. In, Keast, A. and E. S. Morton (eds.). Migrant birds in the Neotropics. Ecology, behavior, distribution, and conservation. Smithsonian Institution Press. Washington, D. C. Pp. 559-576.

Kluge, A. and S. Farris.
1969. Quantitative phyletics and the evolution of anurans. Syst. Zool. 18:1-32.

Lewontin, R. C.
1974. Detecting population differences in quantitative characters as opposed to gene frequencies. Amer. Nat. 123:115-124.

Livezey, B. L. and P. S. Humphrey.
1984. Sexual dimorphism in continental steamer-ducks. Condor 86:368-377.

Lowery, G. H., Jr. and B. L. Monroe, Jr.
1968. Parulidae. In Peters, J. L. Check-List of Birds of the World, v. XIV, Cambridge, Massachusetts.

Maddison, W., M. J. Donoghue, and David R. Maddison.
1984. Outgroup analysis and parsimony. Syst. Zool. 33:83-103.

Marcus, L. F.
1990. Traditional morphometrics. In, Rohlf, F. J. and F. L. Bookstein. Proceedings of the Michigan Morphometrics Workshop, Spec. Publ. Univ. Michigan Mus. Zool. 2: 77-118.

Mayr, E. and L. L. Short.
1970. Species taxa of North American birds. Nuttall Ornithological Club. no. Cambridge, Massachusetts.

Mikevitch, M. F. and C. Mitter.
1983. Evolutionary patterns in allozyme data: a systematic approach. In, Platnick, N. I. and V. A. Funk. Advances in Cladistics, vol. 2. Columbia University Press, New York. Pp. 169-176.

Miller, A. H., H. Friedmann, L. Griscom, and R. T. Moore.
1957. Distributional check-list of the birds of Mexico. Part II. Pacific Coast Avifauna 33:1-436.

Morse, D. H.
1989. American warblers. An ecological and behavioral perspective. Harvard Univ. Press. Cambridge, Massachusetts.

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

_____, T. Maruyama, and R. Chakraborty.
1975. The bottleneck effect and genetic variability in populations. Evolution 29: 1-10.

Nevo, E., A. Beiles, and R. Ben-Shlomo.
1984. The evolutionary significance of genetic diversity: ecological, demographic and life history correlates. Pp. 13-213 in Evolutionary Dynamics of Genetic Diversity. (G. S. Mani, ed.). New York, NY, USA.

Page, R.
1990, Temporal congruence and cladistic analysis of biogeography and cospeciation. Syst. Zool. 39: 205-226.

Raikow, R.
1978. Appendicular myology and relationships of the New World nine-primaried oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. no. 7.

Richardson, B. J., P. R. Baverstock, and M. Adams.
1986. Allozyme electrophoresis. Sydney, Australia, Academic Press.

Ridgely, R. S. and G. Tudor.
1989. The Birds of South America. Vol 1. University of Texas Press, Austin, Texas, USA.

Ridgway, R.
1902. The Birds of North and Middle America, vol. II, Bull. U.S. nat. Mus. no.50, Washington.

Rising, J. D.
1987. Geographic variation of sexual dimorphism in size of Savannah Sparrows (Passerculus sandvichensis): a test of hypothesis. Evolution 41:514-524.

Rogers, J. S.
1972. Measures of genetic similarity and genetic distance. Studies in Genetics. Univ. Texas Publ. 7213: 145- 153.

SAS Institute Inc.
1987. SAS/STAT for personal computers, version 6.03. SAS Institute Inc. Cary, North Carolina, USA.

Selander, R. K.
1972. Sexual selection and dimorphism in birds. In Campbell, (ed.). Sexual selection and the descent of man 1871-1971. Aldine Publ. Co. Chicago, Illinois. Pp. 180-230.

_____, M. H. Smith, S. Y. Yang, W. E. Johnson, and J. B. Gentry.
1971. Biochemical polymorphism and systematics in the genus Peromyscus. I. Variation in the old-field mouse (Peromyscus polionotus). Studies in Genetics VI. University of Texas Publication 7103: 49-90.

Sharpe, R. B.
1885. Catalogue of the Birds in the British Museum , vol. X, London.

Shine, R.
1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quart. Rev. Biol. 64:419-461.

Sibley, C. G. and J. E. Ahlquist.
1982. The relationships of the Yellow-breasted Chat (Icteria virens) and the alleged slowdown in the rate of macromolecular evolution in birds. Postilla 187, 19 pp.

_____.
1990. Phylogeny and classification of birds. A study in molecular evolution. Yale University Press, New Haven, Connecticut.

Slatkin, M.
1985. Rare alleles as indicators of gene flow. Evolution 39:53-65.

Stehli, F. G. and S. D. Webb (eds.).
1985. The great American biotic interchange. Plenum Press, New York and London.

Swofford, D.
1988. FREQPARS.Release 1.0. Illinois Natural Survey. Urbana, Illinois.

_____.
1990. PAUP. Phylogenetic Analysis Using Parsimony. Version 3.0. Illinois Natural Survey. Champaign, Illinois.

_____ and S. H. Berlocher.
1987. Inferring evolutionary trees from gene frequency data under the principle of maximum parsimony. Syst. Zool. 36:293-325.

_____ and R. B. Selander.
1989. BIOSYS-1. A computer program for the analysis of allelic variation in population genetics and biochemical systematics. Release 1.7. Urbana, Illinois, USA.

_____ and G. J. Olsen.
1990. Phylogeny reconstruction. In Molecular systematics, D. M. Hillis and C. Moritz (eds.). Sinauer Associates Inc. Sunderland, Massachusetts.

Tamayo, J. L. and R. C. West.
1964. The hydrography of Central America. In, Handbook of Middle American Indians. Vol. 1. Natural Environment and Early Cultures. Univ. Texas Press. Austin, Texas, USA.

Templeton, A.
1980. Modes of speciation and inferences based on genetic distances. Evolution 34: 719-729.

Tordoff, H. B.
1954. Relationships in the New World nine-primaried oscines. Auk 71:273-284.

Wanntorp, H. E., D. R. Brooks, T. Nilsson, S. Nylin, F. Ronquist, S. C. Stearns, and N. Wedell.
1990. Phylogenetic approaches in ecology. Oikos 57: 119-132.

Webb, S. D.
1985. Late Cenozoic mammal dispersals between the Americas. In Stehli, F. G. and S. D. Webb (eds.). The great american biotic interchange. Plenum Press, New York, N. Y. Pp.357-386.

Wright, S.
1978. Evolution and genetics of populations, vol. 4. variability within and among natural populations. University of Chicago Press, Chicago.

Wu, Chung-I.
1991. Inferences of species phylogeny in relation to segregation of ancient polymorphisms. Genetics 127:429-435.

Zink, R. M.
1988. Evolution of Brown Towhees: allozymes, morphometrics and species limits. Condor 90: 72-82.

_____, and J. T. Klicka.
1990. Genetic variation in the Common Yellowthroat and some allies. Wilson Bull. 102: 514-520.

_____, and J. V. Remsen, Jr.
1986. Evolutionary processes and patterns of geographic variation in birds. Current Ornithology 4: 1-69.

_____, D. F. Lott, and D. W. Anderson.
1987. Genetic variation, population structure and evolution of California Quail. Condor 89: 395-405.

# CURRICULUM VITAE: Bertha Patricia Escalante-Pliego

September 1991

PERSONAL DATA: Born: 7 April 1957
Birthplace: Mexico DF, Mexico

ADDRESS: Museo de Zoología, Facultad de Ciencias,
Universidad Nacional Autónoma de México,
Apartado Postal 70-399, México DF 04510, MEXICO

EDUCATION:

B.A. Biology, Facultad de Ciencias, Universidad Nacional Autónoma de México. October 1984.

M.A. Maestría en Ciencias (Biología), Facultad de Ciencias, Universidad Nacional Autónoma de México. August 1985.

Ph.D. Ecology and Evolutionary Biology, The City University of New York, expected September 1991. Dissertation: "Phylogenetic relationships of *Geothlypis* (Aves: Parulinae)." (Research advisor: Dr François Vuilleumier).

Professional experience:

1978-1985 Instructor and assistant in approximately 18 curses at college level (Ornithology, Field Biology, Anatomy, Zoology).

1980-1985 Curator. Collection of Birds. Museo de Zoología "Alfonso L. Herrera", Facultad de Ciencias, U.N.A.M.

1986-1987 Curatorial Assistant. Department of Herpetology. American Museum of Natural History.

1987-1988 Research Assistant. Statistical analysis and allozyme electrophoresis. Department of Mammalogy and Department of Herpetology. American Museum of Natural History.

OTHER PROFESSIONAL RESPONSIBILITIES:

1988- Board of Directors of the International Council for Bird Preservation, Panamerican Section (ICBP-PACS), since 1988.

1991- Co-Principal Investigator. National Science Foundation Grant No. INT-9014757 "Support of students at the Museo de Zoologia" with Dr. Frank B. Gill, Academy of Natural Sciences of Philadelphia.

1991 Co-convener, symposium on the Modernization of Ornithological Collections in the Neotropics. Quito, Ecuador; to be held in November 1991.

FIELD EXPERIENCE:

1980-81 Sierra de los Tuxtlas, Veracruz, Mexico

1982-1984 Nayarit, Veracruz, and Guerrero (Mexico)

1987 Central and northeastern Mexico (Jalisco, Michoacán, Tamaulipas)

1988 Baja California and western Mexico.

1989 Territorio Amazonas, and Miranda, Venezuela; Costa Rica; Florida, USA; and Abaco, Bahamas.

1990 Guerrero and Oaxaca, Mexico.

PUBLICATIONS:

Llorente, J., P. Escalante, et al.
1984. Las colecciones cientificas de la Facultad de Ciencias: Acervo del Museo de Zoologia "Alfonso L. Herrera".. 48 pp.

Escalante, P.
1988. Aves de Nayarit. Universidad Autónoma de Nayarit. 230 pp.

Escalante, P. & F. Vuilleumier.
1989. Directorio de Colecciones Ornitológicas en los países de la América Neotropical. Amer. Mus. Nat. Hist., 20 pp.

Voss, R. S., L. Marcus & P. Escalante.
1990. Morphological evolution in muroid rodents I. Conservative patterns of craniometric covariance and their ontogenetic basis in the neotropical genus *Zygodontomys*. Evolution, 44:1568-1587.

Barrowclough, G. F. & P. Escalante.
1990. Notes on the birds of the Sierra de Unturán, southern Venezuela. Bull. B.O.C. 110:167-169.

Navarro S., A., M. Torres y P. Escalante.
1991. Catálogo de la Colección de Aves del Museo de Zoología de la Facultad de Ciencias de la UNAM.

Escalante, P.
Genetic differentiation in yellowthroats (Parulinae: *Geothlypis*). Proc. XXth Intern. Ornithol. Congress. Christchurch, New Zealand. In press.

Escalante, P., A. G. Navarro & A. T. Peterson.
Geographic, ecological and historical analysis of land bird diversity in Mexico. In: Biological Diversity of Mexico. (Fa & Ramamoorthy, eds.). Oxford Univ. Press. In press.

Llorente, J., O. Flores, A. Navarro, P. Escalante et al.
Inventario faunístico del Parque Ecológico Estatal de Omiltemi, Guerrero. Technical report. In press.

Navarro, S., A., A. T. Peterson and P. Escalante.
New species of swift from the Sierra Madre del Sur of Mexico. Wilson Bull. In press.

———.
New distributional information on Mexican birds. I. The Sierra de Atoyac, Guerrero. Bull. B.O.C. In press.

MANUSCRIPTS IN PREPARATION:

Barrowclough, G. F.& P. Escalante.
An annotated list of the birds of Cerro Tamacuari, Federal Territory of Amazonas, Venezuela.

Escalante, P.
———.
Genetic and phenotypic differentiation of the Masked Yellowthroats *(Geothlypis aequinoctialis)* in South America: conservative plumage and cryptic species in the complex.

Escalante, P., M. Arnold and C. W. Myers.
Allozymic and morphometric differentiation in an explosively polymorphic group of dart-poison frogs in the Bocas del Toro Archipelago of Panama (*Dendrobates pumilio*).

Escalante, P.and A. T. Peterson.
Geographic variation and species limits in middle American Woodnymphs *(Thalurania)*.

Navarro S., A. and P. Escalante.
Distribución altitudinal de la avifauna en la Sierra de Atoyac, Guerrero.

Peterson, A. T., P. Escalante P. and A. Navarro S.
Genetic variation and differentiaton in mexican populations of Common Bush-tanagers and Chesnut-capped Brush-finches.

PAPERS PRESENTED AT MEETINGS:

Llorente, J. and P. Escalante.
1984. Insular Biogeography of Submontane Humid Forests in Mexico. 1st. Mesoamerican Biogeography Symposium. Merida, Yucatan.

Escalante, P. and J. Llorente.
1985. Riqueza y endemismo de aves y mariposas como criterio para determinar áreas de reserva en el estado de Nayarit". Congreso Forestal Mundial y 1er. Simposio Internacional de Fauna Silvestre. México, D. F. Proceedings.

Escalante, P.
1987. Diferenciación morfométrica de los Tapaojitos (*Geothlypis* spp.) del Centro de México". III Congreso de Ornitología Neotropical. Cali, Colombia. Nov.

Escalante, P. & G. F. Barrowclough.
1989. Bird Fauna from Tamacuari and Unturán Mountains in the Tepui-Area of southern Venezuela. American Ornithologists' Union, 107th meeting. August. Pittsburgh, Pensylvania, EEUU.

Escalante, P.
1990. Phylogenetic analysis of allozymes in the genus *Geothlypis*. AOU/COS, June 1990. Los Angeles, California, EEUU.

Escalante, P.
1990. Genetic differentiation in Yellowthroats (Parulinae: *Geothlypis*). XXth Intern. Ornithol. Congress., Christchurch, New Zealand.

Escalante, P.
1991. Segregation of ancient polymorphism and reconstruction of Geothlypis warblers phylogeny. American Ornithologists' Union, 109th meeting, August 1991. Montreal, Canada.

RESEARCH INTEREST:

Molecular Systematics

Conservation Genetics

Cloud forests avian biogeography

Morphometrics

SOCIETY MEMBERSHIPS:

American Ornithologist's Union
Cooper Ornithological Society
Wilson Ornithological Society
Association of Field Ornithologists
Society for the study of evolution
Society of Systematic Biology
International Council for Bird Preservtation. Mexican Section and Board of Directors.

GRANTS/FELLOWSHIPS:

| | |
|---|---|
| 1979-1980 | College education fellowship from PSPA (Programa de Formación de Personal Académico) at Universidad Nacional Autonoma de Mexico. |
| 1985-1988 | International Program, fellowship for doctoral studies from CONACyT (Consejo Nacional de Ciencia y Tecnología, Mexico). |
| 1987 | PSPA, Universidad Nacional Autónoma de México, grant for field work in Mexico. |
| 1987, 1988, 1989 | Frank M. Chapman Memorial Fund, American Museum of Natural History. Projects in relation with dissertation research. |
| 1987 | Undergraduate-Graduate Program of the American Museum of Natural History. Dissertation research. |
| 1987 | Alexander Bergstrom Memorial Fund, Association of Field Ornithologists. Dissertation research. |
| 1987 | Alexander Wetmore Fund, American Ornithologist's Union Research Awards. Dissertation research. |
| 1988 | Sigma Xi. Dissertation research. |
| 1989-1991 | Doctoral training program of the American Museum of Natural History, fellowship to continue doctoral studies. |
| 1987-1989 | Graduate Studies Committee, Ph.D. Program in Biology. City University of New York, grant for dissertation research. |

GRADUATE COURSES:

Evolution, Biostatistics, Biogeography, Ornithology, Morphometrics and evolutionary biology, Systematics, Population Genetics, Community Ecology, Animal Behavior, Field class in Animal Behavior.