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A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves)

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ABSTRACT

The birds in the family Parulidae—commonly termed the New World warblers or wood-warblers—are a classic model radiation for studies of ecological and behavioral differentiation. Although the monophyly of a ‘core’ wood-warbler clade is well established, no phylogenetic hypothesis for this group has included a full sampling of wood-warbler species diversity. We used parsimony, maximum likelihood, and Bayesian methods to reconstruct relationships among all genera and nearly all wood-warbler species, based on a matrix of mitochondrial DNA (5840 nucleotides) and nuclear DNA (6 loci, 4602 nucleotides) characters. The resulting phylogenetic hypotheses provide a highly congruent picture of wood-warbler relationships, and indicate that the traditional generic classification of these birds recognizes many non-monophyletic groups. We recommend a revised taxonomy in which each of 14 genera (*Seiurus*, *Helmitheros*, *Mniotilta*, *Limnothlypis*, *Protonotaria*, *Parkesia*, *Vermivora*, *Oreothlypis*, *Geothlypis*, *Setophaga*, *Myioborus*, *Cardellina*, *Basileuterus*, *Myiothlypis*) corresponds to a well-supported clade; these nomenclatural changes also involve subsuming a number of well-known, traditional wood-warbler genera (*Catharopeza*, *Dendroica*, *Ergaticus*, *Euthlypis*, *Leucopeza*, *Oporornis*, *Parula*, *Phaeothlypis*, *Wilsonia*). We provide a summary phylogenetic hypothesis that will be broadly applicable to investigations of the historical biogeography, processes of diversification, and evolution of trait variation in this well studied avian group.

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1. Introduction

The wood-warblers of the avian family Parulidae have a long history of serving as models for ecological and behavioral studies (e.g., MacArthur, 1958; Morse, 1970; Shutler and Weatherhead, 1990; Price et al., 2000; Martin and Martin, 2001; Freckleton and Harvey, 2006; Lovette and Hochachka, 2006; Rabosky and Lovette, 2008), but there has been no comprehensive analysis of their phylogenetic relationships that includes most of the genera or species

in this otherwise well-studied radiation. Wood-warblers are small, primarily insectivorous birds with a broad diversity of habitat affinities and life-histories. Overall, the breeding distributions of species in this New World group span the Arctic to temperate South America, with centers of diversity in eastern North America, the West Indies, Mexico and Central America, and Andean South America. Most northern-breeding species are migratory, but many island and tropical species are sedentary or undertake only short-distance elevational migrations. The wood-warblers breed exclusively in the New World, and they are not closely allied to the various Old World songbirds (from 10 or more families) that are also commonly termed “warblers.” Modern classifications have generally recognized 112–115 wood-warbler species distributed among 24–26 genera (Sibley and Monroe, 1990; Curson et al., 1994;

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AOU, 1998; Dickinson, 2003), but, as summarized below, recent molecular phylogenetic studies have shown that 10 of these species, representing seven genera, fall outside of a monophyletic “core Parulidae.”

Within the Passeriformes, the Parulidae fall within a highly diverse group of songbirds often referred to as the New World nine-primaried oscines, although this term is somewhat of a misnomer as the tenth primary is reduced but not absent in the wood-warblers and most other members of this radiation (Hall, 2005). In addition to the Parulidae, this larger group includes the traditional families (*sensu* AOU, 1998) Coerebidae (Bananaquit), Thraupidae (tanagers), Emberizidae (emberizid sparrows and buntings), Cardinalidae (cardinals, saltators, and allies), and Icteridae (blackbirds and allies). Recent molecular phylogenetic studies have revealed that many of these traditional families are not monophyletic, leading to a series of revised classifications, some of which are still in progress (e.g., Burns, 1997; Klicka et al., 2003; Klicka et al., 2007; Alström et al., 2008; F.K. Barker, pers. comm.). There is strong molecular phylogenetic support, however, for a monophyletic “core Parulidae” that includes all of the phenotypically typical wood-warbler genera (Lovette and Bermingham, 2002; Klein et al., 2004).

In various recent studies encompassing a broad range of taxonomic and molecular marker sampling, the “core Parulidae” clade is consistently defined by a long basal internode separating it from all other taxa within the nine-primaried radiation (Sibley and Ahlquist, 1990; Klicka et al., 2000; Lovette and Bermingham, 2002; Yuri and Mindell, 2002; Klein et al., 2004; Klicka et al., 2007; Alström et al., 2008). Taxa traditionally classified within the wood-warblers but that are not members of this core Parulidae clade include: (1) the Olive Warbler *Peucedramus taeniatus* of North America, which on the basis of both morphological (e.g., Raikow, 1978) and molecular data (e.g., Sibley and Ahlquist, 1990; Yuri and Mindell, 2002; Ericson and Johansson, 2003) is now placed in its own family and outside of the entire nine-primaried oscine assemblage; (2) the Yellow-breasted Chat *Icteria virens* of North America, the sole member of a lineage with variable placement close to the Icteridae, Parulidae, or Emberizidae (e.g., Lovette and Bermingham, 2002; Yuri and Mindell, 2002; Klein et al., 2004; Klicka et al., 2007); (3) three species of Neotropical chats in the genus *Granatellus* (Lovette and Bermingham, 2002), which fall within a group recently recognized as cardinal-grosbeaks (Klicka et al., 2007); (4) the Wrenthrush *Zeledonia coronata* of southern Central America, which like *Icteria* represents an old lineage that falls outside—but possibly close to—the core Parulidae (Lovette and Bermingham 2002; Klicka et al., 2007); (5) the Green-tailed Warbler *Microligea palustris* and the White-winged Warbler *Xenoligea montana*, two sister-taxa endemic to the island of Hispaniola, which are likely allied to a small group of other relatively old West Indian-endemic lineages such as *Phaenicophilus* (Lovette and Bermingham, 2002; Klein et al., 2004; Klicka et al., 2007); and (6) two species of *Teretistris* warblers endemic to Cuba, which likewise appear to have affinities with other non-parulid taxa from the West Indies (Lovette and Bermingham, 2002; Klein et al., 2004; Klicka et al., 2007). Although the deeper relationships of these various lineages are not yet well resolved, the strong and replicated evidence for a well-supported and monophyletic core Parulidae allows us to focus here on reconstructing phylogenetic relationships within this more recently derived group.

Our understanding of phylogenetic relationships within the core Parulidae clade is variable, because only some subsets of the radiation have been sampled intensively with informative markers. Phylogeographic studies have been conducted on many species or

species complexes (e.g., Bermingham et al., 1992; Klein and Brown, 1994; Lovette et al., 1998; Buerkle, 1999; Lovette et al., 1999; Milá et al., 2000; Zink et al., 2000; Lovette and Bermingham, 2001; Kimura et al., 2002; Lovette, 2004; Markland and Lovette, 2005; Smith et al., 2005; Boulet and Gibbs, 2006; Milá et al., 2007; Colbeck et al., 2008; Grus et al., 2009; McKay, 2009), and several pairs of taxa that commonly hybridize have been investigated in complementary molecular and field studies (e.g., Rohwer et al., 2001; Vallender et al., 2007; Irwin et al., 2009; Brelsford and Irwin, 2009). These investigations at the population/species interface have helped define wood-warbler species and fostered inferences about the biogeographic and ecological contexts of wood-warbler diversification.

At an intermediate phylogenetic level within the Parulidae radiation, three high-diversity groups have been the targets of phylogenetic studies that included all-or nearly all-constituent species. The large genus *Dendroica* has many species that occur in present-day sympatry; a historical pattern of early and rapid *Dendroica* radiation was first detected in phylogenies based on mtDNA markers (Lovette and Bermingham, 1999), with later reconstructions based on both mtDNA and nuclear markers similarly supporting a pattern of density-dependent speciation in this group (Rabosky and Lovette, 2008). Pérez-Emán (2005) reconstructed relationships among the 12 species in the genus *Myioborus* using mtDNA sequence markers, and found that this group likely dispersed from Central America into South America, where most of its subsequent diversification then occurred. Relationships among the 13 species traditionally assigned to the closely allied genera *Oporornis* and *Geothlypis* were recently reconstructed using mtDNA markers by Escalante et al. (2009), who found gene-tree paraphyly between these genera as well as among some populations of *Geothlypis*.

Previous studies that have addressed relationships across the entire core Parulidae radiation include two allozyme-based surveys (Barrowclough and Corbin, 1978; Avise et al., 1980) that found relatively low differentiation among the species they compared, and which hence had modest phylogenetic resolution. Sibley and Ahlquist (1990) included only eight core Parulidae species from six genera in their DNA–DNA hybridization-based phylogeny, in which they form a distinct clade with low internal resolution. More recently, Lovette and Bermingham (2002) included 30 species in 19 core Parulidae genera in reconstructions based on robust sampling of mtDNA loci and one nuclear locus; Klein et al. (2004) reconstructed relationships among 47 core Parulidae species from 15 genera using mtDNA cytochrome *b* sequences; and Lovette and Hochachka (2006) generated a mtDNA-based phylogeny as part of a study of the ecological interactions of 43 North American wood-warbler species from 12 genera. Considered together, these sequence-based studies have helped clarify the relationships of some Parulidae lineages, but they have also suggested that the core Parulidae diversified in successive waves of radiation, that most traditional parulid genera do not represent monophyletic groups, and that a well-informed revision of wood-warbler classification will require reconstructions based on robust sampling of both markers and species.

The goal of the present study is to present a comprehensive phylogenetic treatment of the entire Parulidae radiation based on nearly complete species-level sampling and an informative set of both mitochondrial and nuclear sequence markers. The resulting phylogenetic reconstructions have high utility for revising the generic taxonomy of the Parulidae, for additional model-based explorations of patterns and processes of its diversification, and in comparative analyses that explore the drivers of differentiation in morphological, ecological, and behavioral traits for which this group is well known.

Table 1

Taxa included in this study, museum source information, and a proposed new generic classification of the Parulidae.

Taxon	English Name	Recommended Genus ^a	Museum source Information ^b	Tissue Type ^c	Collection locality
<i>Seiurus aurocapilla</i>	Ovenbird	<i>Seiurus</i>	STRI-PRSAU1	T	Puerto Rico, Patillas
<i>Helmitheros vermivorus</i>	Worm-eating Warbler	<i>Helmitheros</i>	STRI-JAHVE2	T	Jamaica, St. Andrews Parish, John Crow Nat. Park
<i>Seiurus motacilla</i>	Louisiana Waterthrush	<i>Parkesia</i>	STRI-JASMT1	T	Jamaica, Westmoreland Parish, Savanna la Mar
<i>Seiurus noveboracensis</i>	Northern Waterthrush	<i>Parkesia</i>	STRI-HASNO144	T	Honduras, Cayos Cochinos, Cochino Pequeno
<i>Vermivora bachmanii</i>	Bachman's Warbler	<i>Vermivora</i>	AMNH-759214	aDNA	USA, South Carolina St., Charleston, I'on Swamp (1915)
<i>Vermivora chrysoptera</i>	Golden-winged Warbler	<i>Vermivora</i>	CUMV-44030	T	USA, New York St., Tompkins County
<i>Vermivora pinus</i> ^d	Blue-winged Warbler	<i>Vermivora</i>	CUMV-228087252	T	USA, New York St., Tompkins County
<i>Mniotilta varia</i>	Black-and-white Warbler	<i>Mniotilta</i>	STRI-JAMVA2	T	Jamaica, St. Andrews Parish, John Crow Nat. Park
<i>Protonotaria citrea</i>	Prothonotary Warbler	<i>Protonotaria</i>	LSUMNS-B23575	T	USA, Louisiana St., St. Martin Parish
<i>Limnothlypis swainsonii</i>	Swainson's Warbler	<i>Limnothlypis</i>	STRI-JALSW2	T	Jamaica, St. Andrews Parish, John Crow Nat. Park
<i>Parula gutturalis</i>	Flame-throated Warbler	<i>Oreothlypis</i>	LSUMNS-B26458	T	Panama, Chiriqui Province, Boquete
<i>Parula superciliosa</i>	Crescent-chested Warbler	<i>Oreothlypis</i>	FMNH-5730-BMM154	T	Mexico, Est. Michoacan, Cerro de Tancitaro
<i>Vermivora peregrina</i>	Tennessee Warbler	<i>Oreothlypis</i>	STRI-HAVPE62	T	Honduras, Dept. Atlántida, La Ceiba
<i>Vermivora celata</i>	Orange-crowned Warbler	<i>Oreothlypis</i>	UWBM-53827	T	USA, Alaska St., Valdez-Cordova County, Valdez
<i>Vermivora crissalis</i>	Colima Warbler	<i>Oreothlypis</i>	FMNH-395824	T	Mexico, Est. Mexico, Ocuilan
<i>Vermivora luciae</i>	Lucy's Warbler	<i>Oreothlypis</i>	ANSP-GFB1920	T	USA, Arizona, Cochise County
<i>Vermivora virginiae</i>	Virginia's Warbler	<i>Oreothlypis</i>	UNLVBMMH-MBM10245	T	USA, Nevada St., Clark County
<i>Vermivora ruficapilla</i>	Nashville Warbler	<i>Oreothlypis</i>	UWBM-49896	T	USA, Washington St., Yakima County, Mt. Adams
<i>Oporornis agilis</i>	Connecticut Warbler	<i>Geothlypis</i>	UWBM-JK97004	T	USA, Minnesota St., Washington County
<i>Leucopeza semperi</i>	Semper's Warbler	<i>Geothlypis</i>	ANSP-507561	aDNA	St Lucia (collection year undocumented)
<i>Geothlypis aequinoctialis</i>	Masked Yellowthroat	<i>Geothlypis</i>	CUMV-50367	T	Uruguay, Dept. Artigas, Arroyo Mandiyu
<i>Geothlypis poliocephala</i>	Gray-crowned Yellowthroat	<i>Geothlypis</i>	CUMV-36479	aDNA	Mexico, Est. Chiapas, Berrio Zaibol (1966)
<i>Oporornis tolmiei</i>	MacGillivray's Warbler	<i>Geothlypis</i>	UWBM-CD54192	T	USA, Washington, Whatcom, Mt. Baker
<i>Oporornis philadelphia</i>	Mourning Warbler	<i>Geothlypis</i>	CUMV-228087288	T	USA, New York St., Tompkins County
<i>Oporornis formosus</i>	Kentucky Warbler	<i>Geothlypis</i>	STRI-PROF01	T	Puerto Rico, Carite State Forest
<i>Geothlypis semiflava</i>	Olive-crowned Yellowthroat	<i>Geothlypis</i>	CUMV-IJL04130	T	Panama, Prov. Bocas del Toro, Chiriqui Grande
<i>Geothlypis speciosa</i>	Black-poll'd Yellowthroat	<i>Geothlypis</i>	CUMV-33368	aDNA	Mexico, Est. Guanajuato, Lago Yuriria (1964)
<i>Geothlypis beldingi</i>	Belding's Yellowthroat	<i>Geothlypis</i>	CUMV-16802	aDNA	Mexico, Est. Baja California Sur, San Jose del Cabo (1887)
<i>Geothlypis rostrata</i>	Bahama Yellowthroat	<i>Geothlypis</i>	STRI-ABGRO1	T	Bahamas, Abaco Island
<i>Geothlypis flavovelata</i>	Altamira Yellowthroat	<i>Geothlypis</i>	CUMV-11635	aDNA	Mexico, Est. Tamaulipas, Alta Mira (1941)
<i>Geothlypis trichas</i>	Common Yellowthroat	<i>Geothlypis</i>	STRI-JAGTR1	T	Jamaica, St. Andrews Parish, John Crow Nat. Park
<i>Geothlypis nelsoni</i>	Hooded Yellowthroat	<i>Geothlypis</i>	CUMV-29306	aDNA	Mexico, Est. Puebla, Mt. Malinche (1954)
<i>Catharopeza bishopi</i>	Whistling Warbler	<i>Setophaga</i>	STRI-SVCBI5	T	St. Vincent, Cumberland Valley
<i>Dendroica plumbea</i>	Plumbeous Warbler	<i>Setophaga</i>	STRI-DODPL1	T	Dominica, Springfield
<i>Dendroica angelae</i>	Elfin-woods Warbler	<i>Setophaga</i>	LSUMNS-B11325	T	Puerto Rico, Maricao State Forest
<i>Dendroica pharetra</i>	Arrow-headed Warbler	<i>Setophaga</i>	STRI-JADPH6	T	Jamaica, St. Andrews Parish, John Crow Nat. Park
<i>Wilsonia citrina</i>	Hooded Warbler	<i>Setophaga</i>	CUMV-50468	T	USA, New York St., Monroe County
<i>Setophaga ruticilla</i>	American Redstart	<i>Setophaga</i>	STRI-JASRU1	T	Jamaica, St. Andrews Parish, John Crow Nat. Park
<i>Dendroica kirtlandii</i>	Kirtland's Warbler	<i>Setophaga</i>	USNM-B06558-613582	T	USA, Michigan, Oscoda County
<i>Dendroica tigrina</i>	Cape May Warbler	<i>Setophaga</i>	STRI-JADT11	T	Jamaica, St. Elizabeth Parish, Luana Point
<i>Dendroica cerulea</i>	Cerulean Warbler	<i>Setophaga</i>	LSUMNS-B3397	T	USA, Louisiana St., Cameron Parish
<i>Parula americana</i>	Northern Parula	<i>Setophaga</i>	STRI-JAPAM1	T	Jamaica, St. Elizabeth Parish, Luana Point
<i>Parula pitayumi</i>	Tropical Parula	<i>Setophaga</i>	LSUMNS-B2150	T	Panama, Prov. Darien, Cana
<i>Dendroica magnolia</i>	Magnolia Warbler	<i>Setophaga</i>	CUMV-44183	T	USA, New York St., Monroe County
<i>Dendroica castanea</i>	Bay-breasted Warbler	<i>Setophaga</i>	STRI-HA147	T	Honduras, Cayos Cochinos, Cochino Pequeno
<i>Dendroica fusca</i>	Blackburnian Warbler	<i>Setophaga</i>	ANSP-B2011	T	Ecuador, Prov. Esmeraldas
<i>Dendroica petechia</i>	Yellow Warbler	<i>Setophaga</i>	LSUMNS-B20611	T	USA, Louisiana St., Cameron Parish
<i>Dendroica pensylvanica</i>	Chestnut-sided Warbler	<i>Setophaga</i>	CUMV-50271	T	USA, New York St., Tompkins County
<i>Dendroica striata</i>	Blackpoll Warbler	<i>Setophaga</i>	ANSP-B3659	T	USA, Pennsylvania St., Bucks County
<i>Dendroica caerulescens</i>	Black-throated Blue Warbler	<i>Setophaga</i>	STRI-JADCR1	T	Jamaica, St. Andrews Parish, John Crow Nat. Park
<i>Dendroica palmarum</i>	Palm Warbler	<i>Setophaga</i>	LSUMNS-B21581	T	USA, California St., San Bernardino County
<i>Dendroica pityophila</i>	Olive-capped Warbler	<i>Setophaga</i>	STRI-ABDPY1	T	Bahamas, Abaco Island
<i>Dendroica pinus</i>	Pine Warbler	<i>Setophaga</i>	ANSP-B2933	T	USA, New Jersey St., Cumberland County
<i>Dendroica coronata</i>	Yellow-rumped Warbler	<i>Setophaga</i>	STRI-RDDCO1	T	Dominican Republic, Prov. La Vega, Valle Nuevo
<i>Dendroica dominica</i>	Yellow-throated Warbler	<i>Setophaga</i>	LSUMNS-B3386	T	USA, Louisiana St., Cameron Parish
<i>Dendroica discolor</i>	Prairie Warbler	<i>Setophaga</i>	STRI-JADDI2	T	Jamaica, St. Elizabeth Parish, Luana Point
<i>Dendroica vitellina</i>	Vitelline Warbler	<i>Setophaga</i>	STRI-GCDV1129	T	Cayman Islands, Grand Cayman
<i>Dendroica adelaidae</i>	Adelaide's Warbler	<i>Setophaga</i>	STRI-PRDAD2	T	Puerto Rico, Guanica
<i>Dendroica subita</i>	Barbuda Warbler	<i>Setophaga</i>	STRI-BUDAD1	T	Barbuda, Martello Tower
<i>Dendroica delicata</i>	St. Lucia Warbler	<i>Setophaga</i>	STRI-SLDAD10	T	St. Lucia, Babonneau, Anse Sorciere
<i>Dendroica graciae</i>	Grace's Warbler	<i>Setophaga</i>	LSUMNS-B10176	T	USA, Arizona, Santa Cruz County
<i>Dendroica nigrescens</i>	Black-throated Gray Warbler	<i>Setophaga</i>	UWBM-CSW3126/52347	T	USA, Washington St., Lewis County
<i>Dendroica occidentalis</i>	Hermit Warbler	<i>Setophaga</i>	UWBM-CSW2920/46693	T	USA, California St., Sierra County
<i>Dendroica townsendi</i>	Townsend's Warbler	<i>Setophaga</i>	UWBM-CSW2539/41918	T	USA, Washington St., Pend Oreille County

(continued on next page)

Table 1 (continued)

Taxon	English Name	Recommended Genus ^a	Museum source Information ^b	Tissue Type ^c	Collection locality
<i>Dendroica virens</i>	Black-throated Green Warbler	<i>Setophaga</i>	CUMV-50461	T	USA, New York St., Tompkins County
<i>Dendroica chrysoparia</i>	Golden-cheeked Warbler	<i>Setophaga</i>	CUMV-16384	aDNA	USA, Texas St., Kerr County, (1915)
<i>Basileuterus luteoviridis</i>	Citrine Warbler	<i>Myiothlypis</i>	LSUMNS-B1242	T	Bolivia, Dept. La Paz, Chuspipata
<i>Basileuterus leucophrys</i>	White-striped Warbler	<i>Myiothlypis</i>	ANSP-270394	aDNA	Brazil
<i>Basileuterus flaveolus</i>	Flavescent Warbler	<i>Myiothlypis</i>	LSUMNS-B14692	T	Bolivia, Dept. Santa Cruz, Serranía de Huanchaca
<i>Basileuterus leucoblepharus</i>	White-browed Warbler	<i>Myiothlypis</i>	UWBM-DAB848	T	Argentina, Prov. Corrientes, Manuel Derqui
<i>Basileuterus signatus</i>	Pale-legged Warbler	<i>Myiothlypis</i>	LSUMNS-B1266	T	Bolivia, Dept. La Paz, Chuspipata
<i>Basileuterus nigrocristatus</i>	Black-crested Warbler	<i>Myiothlypis</i>	LSUMNS-B216	T	Peru, Prov. Cajamarca, Machete
<i>Basileuterus fulvicauda</i> ^e	Buff-rumped Warbler	<i>Myiothlypis</i>	LSUMNS-B2240	T	Panama, Prov. Darien, Cana
<i>Basileuterus rivularis</i> ^e	Neotropical River Warbler	<i>Myiothlypis</i>	USNM-LMSB05027	T	Guyana, Waruma River
<i>Basileuterus bivittatus</i> ^f	Two-banded Warbler	<i>Myiothlypis</i>	LSUMNS-B22653	T	Bolivia, Dept. La Paz, Prov. B. Saavedra
<i>Basileuterus roraimae</i> ^f	Two-banded Warbler	<i>Myiothlypis</i>	LSUMNS-B7581	T	Venezuela, Amazonas Territory, Cerro de la Neblina
<i>Basileuterus chrysogaster</i>	Golden-bellied Warbler	<i>Myiothlypis</i>	LSUMNS-B11907	T	Ecuador, Prov. Esmeraldas, El Placer
<i>Basileuterus conspicillatus</i>	White-lored Warbler	<i>Myiothlypis</i>	IAvH-CT-470	T	Colombia, Dep. Magdalena, Sierra Nevada de Santa Marta.
<i>Basileuterus cinereicollis</i>	Gray-throated Warbler	<i>Myiothlypis</i>	IC-835/COP-81179	T	Venezuela, Estado Zulia, Serranía Las Lajas, Sierra de Perijá.
<i>Basileuterus fraseri</i>	Gray-and-gold Warbler	<i>Myiothlypis</i>	LSUMNS-B430	T	Peru, Dept. Piura, Cruz Blanca
<i>Basileuterus coronatus</i> ^{1§}	Russet-crowned Warbler	<i>Myiothlypis</i>	ANSP-499	T	Ecuador, Prov. Carchi
<i>Basileuterus coronatus</i> ^{2§}	Russet-crowned Warbler	<i>Myiothlypis</i>	LSUMNS-B8014	T	Peru, Dept. Pasco, Playa Pampa
<i>Euthlypis lachrymosa</i>	Fan-tailed Warbler	<i>Basileuterus</i>	FMNH-4458	T	Mexico, Est. Jalisco, Puerto los Mazos
<i>Basileuterus rufifrons</i>	Rufous-capped Warbler	<i>Basileuterus</i>	STRI-PABRU28	T	Panama, Prov. Panama, Gamboa
<i>Basileuterus melanogenys</i>	Black-cheeked Warbler	<i>Basileuterus</i>	LSUMNS-B19913	T	Costa Rica, Prov. Cartago, Villa Mills
<i>Basileuterus belli</i>	Golden-browed Warbler	<i>Basileuterus</i>	FMNH-1232–343399	T	Mexico, Est. Jalisco, Las Joyas
<i>Basileuterus culicivorus</i>	Golden-crowned Warbler	<i>Basileuterus</i>	STRI-TRBCU2	T	Trinidad, St. George County, Arima Valley
<i>Basileuterus hypoleucus</i>	White-bellied Warbler	<i>Basileuterus</i>	LSUMNS-B6640	T	Bolivia, Dept. Santa Cruz, Santiago
<i>Basileuterus trifasciatus</i>	Three-banded Warbler	<i>Basileuterus</i>	ANSP-1819	T	Ecuador, Prov. Loja, Cruzpamba
<i>Basileuterus tristriatus</i>	Three-striped Warbler	<i>Basileuterus</i>	LSUMNS-B26444	T	Panama, Prov. Chiriqui, Gualaca
<i>Wilsonia canadensis</i>	Canada Warbler	<i>Cardellina</i>	STRI-WCA59	T	Panama, Prov. Panama, Gamboa
<i>Wilsonia pusilla</i>	Wilson's Warbler	<i>Cardellina</i>	UWBM-47919	T	USA, Washington St., Wahkiakum County, Cathlamet
<i>Cardellina rubrifrons</i>	Red-faced Warbler	<i>Cardellina</i>	LSUMNS-B10178	T	USA, Arizona St.
<i>Ergaticus ruber</i>	Red Warbler	<i>Cardellina</i>	FMNH-394172	T	Mexico, Est. Michoacan, Zirimonero
<i>Ergaticus versicolor</i>	Pink-headed Warbler	<i>Cardellina</i>	UNLVBMMH-MBM10769	T	Guatemala, Dept. Quezaltenango, Quezaltenango, El Baul
<i>Myioborus pictus</i>	Painted Redstart	<i>Myioborus</i>	FMNH-394176	T	Mexico, Est. Oaxaca, San Gabriel Mixtepec
<i>Myioborus miniatus</i>	Slate-throated Redstart	<i>Myioborus</i>	LSUMNS-B29046	T	Panama, Prov. Chiriqui, Gualaca
<i>Myioborus bruniceps</i>	Brown-capped Redstart	<i>Myioborus</i>	UWBM-DAB760	T	Argentina, Prov. Tucuman, San Miguel de Tucuman
<i>Myioborus flavivertex</i>	Yellow-crowned Redstart	<i>Myioborus</i>	IAvH-CT-491	T	Colombia, Dep. Magdalena, Sierra Nevada de Santa Marta.
<i>Myioborus albifrons</i>	White-fronted Redstart	<i>Myioborus</i>	FMNH-431747	T	Venezuela, Prov. Trujillo, Parque Guaramacal
<i>Myioborus ornatus</i>	Golden-fronted Redstart	<i>Myioborus</i>	FMNH-431751	T	Venezuela, Est. Tachira, Betania
<i>Myioborus melanocephalus</i>	Spectacled Redstart	<i>Myioborus</i>	ANSP-B3878	T	Ecuador, Prov. Carchi, Impueran
<i>Myioborus torquatus</i>	Collared Redstart	<i>Myioborus</i>	USNM-B02017-608223	T	Panama, Prov. Bocas del Toro, Los Planes
<i>Myioborus pariae</i>	Yellow-faced Redstart	<i>Myioborus</i>	FMNH-431752	T	Venezuela, Prov. Sucre, Paria
<i>Myioborus albifacies</i>	White-faced Redstart	<i>Myioborus</i>	ANSP-GFB2959	T	Venezuela, Amazonas, Cerro Yutaje
<i>Myioborus cardonai</i>	Saffron-breasted Redstart	<i>Myioborus</i>	FMNH-431753	T	Venezuela, Prov. Bolivar, Cerro Guaiquinima
<i>Myioborus castaneocapilla</i>	Tepui Redstart	<i>Myioborus</i>	UKNMH-4001	T	Guyana, Mt. Roraima
<i>Coereba flaveola</i>	Bananaquit	(outgroup)	STRI-ABCFA1	T	Bahamas, Abaco Island
<i>Granatellus pelzelni</i>	Rose-breasted Chat	(outgroup)	LSUMNS-B18554	T	Bolivia, Prov. Santa Cruz, Velasco
<i>Icteria virens</i>	Yellow-breasted Chat	(outgroup)	UWBM-CDS4131	T	USA, Washington St., Douglas
<i>Microligea palustris</i>	Green-tailed Warbler	(outgroup)	STRI-RDMPA1	T	Dominican Republic, Prov. La Altagracia
<i>Spindalis zena</i>	Puerto Rican Spindalis	(outgroup)	STRI-SZE3	T	Puerto Rico, Patillas
<i>Xenoligea montana</i>	White-winged Warbler	(outgroup)	STRI-RDXM01	T	Dominican Republic, Prov. Pedernales
<i>Zeledonia coronata</i>	Wrenthrush	(outgroup)	LSUMNS-B19939	T	Costa Rica, Prov. San Jose
<i>Teretistris fernandinae</i>	Yellow-headed Warbler	(outgroup)	ANSP-B5548	T	Cuba, Guantanamo Bay

^a Proposed new generic classification based on phylogenetic reconstructions included here.

^b Museum tissue or specimen voucher numbers. Museum abbreviations: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences Philadelphia; COP, Colección Ornitológica Phelps; CUMV, Cornell University Museum of Vertebrates; FMNH, Field Museum of Natural History; IAvH-CT, Instituto Alexander von Humboldt Tissue Collection; LSUMNS, Louisiana State University Museum of Natural Sciences; USNM, U.S. National Museum of Natural History, Smithsonian Institution; STRI, Smithsonian Tropical Research Institute (all samples unvouchered); UKNMH, University of Kansas Natural History Museum; UMBM, University of Minnesota Bell Museum of Natural History; UNLVBMMH, University of Las Vegas Barrick Museum of Natural History; UWBM, University of Washington Burke Museum.

^c T, frozen tissue; aDNA, toe-pad material from museum specimen (year of preparation given in locality column).

^d Species name recently corrected from *pinus* to *cyanoptera* (Olson and Reveal, 2009).

^e Often separated into the genus *Phaeothlypis* (see Lovette (2004)).

^f Form *roraimae* recently proposed as specifically distinct from *bivittatus* (Hilty, 2003).

[§] Trans-Andean populations with high mtDNA divergence.

2. Materials and methods

2.1. Taxon sampling and laboratory methods

We sampled a total of 115 taxa (Table 1), including 107 generally recognized as valid Parulidae species, 6 taxa (*Granatellus pelzelni*, *Icteria virens*, *Microligea palustris*, *Xenoligea montana*, *Zeledonia coronata*, *Teretistris fernandinae*) that have often traditionally been classified in Parulidae but which we now know to fall elsewhere in the nine-primaried oscine radiation (see Section 1), and 2 additional nine-primaried oscine outgroup taxa (*Coereba flaveola* and *Spindalis portoricensis*). In most cases, samples were derived from high-quality tissue materials that allowed the straightforward amplification and sequencing of multiple mtDNA and nuclear loci. For 10 rare or extinct species (Table 1), we sampled older toe-pad tissues from museum skins, and from these samples we obtained only sequences from the mitochondrial NDII gene. These skin samples were taken by shaving a narrow band of toe-pad tissue from the hallux using a new, sterile scalpel, after which they were transferred to our degraded-DNA laboratory.

From the high-quality tissues we generated sequences from a contiguous 4695–4699 bp region of the mitochondrial genome spanning the NDII, COI, COII, ATPase8, and ATPase6 genes and their intervening spacer and tRNA regions, and from the complete cytochrome *b* gene (1143 bp). Of these 5838–5842 mitochondrial bp in total, 5261 represent protein-coding nucleotides. We also generated sequences from six nuclear introns totaling 4602 aligned nucleotides. Four of these nuclear markers are autosomal: rhodopsin intron 1 (*RHO-1*; Primmer et al., 2002), transforming growth factor beta-2 intron 5 (*TGFB2-5*; Primmer et al., 2002), beta-fibrinogen intron 5 (*FGB-5*; Kimball et al., 2009), and myoglobin intron 2 (*MB-2*; Slade et al., 1993). These four loci are each located on a different macrochromosome in the chicken genome (Kimball et al., 2009). The additional two nuclear markers are both on the avian Z sex chromosome: aconitase 1 intron 9 (*ACO1-9*; Barker et al., 2008), and muscle-specific tyrosine kinase intron 4 (*MUSK-4*; Kimball et al., 2009). Our laboratory protocols for DNA extraction, PCR amplification, and sequencing of these mitochondrial and nuclear loci have been described previously (Lovette, 2004; Lovette and Rubenstein, 2007; Lovette et al., 2008; Rabosky and Lovette, 2008).

Samples derived from toe-pad materials were processed separately in a laboratory dedicated to degraded-DNA extraction and PCR-set up that has physical and air-handling isolation from our general-use laboratory. Toe-pad extractions and PCR reactions were assembled and conducted within a laminar-flow clean bench with ISO class V air filtering, and we frequently sterilized surfaces and equipment in the degraded-DNA room with intense 254 nm UV irradiation and 10% sodium hypochlorite (chlorine bleach) solutions. To enhance the probability of detecting any contaminated reactions, we interspersed negative control reactions at both the extraction (1 control:1 tissue-containing extraction) and PCR (also 1:1) stages. When sequencing multiple toe-pad samples from one species, we separated the processing of those different specimens by several weeks to months, over which interval many other samples were processed using the same laboratory facility, equipment, primers, and reagents. Degraded DNA PCR amplifications targeted short (100–500 bp) overlapping regions of the NDII gene. We employed numerous primers flanking or within the NDII coding region, including many designed specifically for individual taxa.

Sequences were checked and assembled using Sequencher™ 4.5 (GeneCodes Corporation, Ann Arbor, MI). Nearly all nucleotides were confirmed by sequencing complementary strands. Heterozygous nucleotides in the nuclear loci were assigned the appropriate IUPAC ambiguity code. All mitochondrial sequences lacked indels

within their protein-coding regions, and hence their alignment was straightforward. All six nuclear loci contained multiple indels, and these regions were first aligned using Clustal X (Thompson et al., 1997), then checked by eye.

2.2. Phylogenetic analysis

We conducted a parsimony-based analysis on the entire dataset using PAUP⁴ 4.0b10 (Swofford, 2002). This analysis employed the full heuristic (TBR-branch swapping) algorithm in which starting trees were obtained by 1000 stepwise random-addition replicates, all characters and character state transformations were weighted equally, and gaps treated as missing data. To assess support for nodes, we performed 1000 bootstrap replicates with 10 stepwise additions of taxa per replicate. The eight taxa known to fall outside the core Parulidae (Table 1) on the basis of previous studies were employed as outgroups.

We likewise reconstructed relationships using Bayesian methods as implemented in MrBayes 3.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) and via maximum likelihood as implemented in RaxML 7.0.4 (Stamatakis, 2006). We ran analyses of the full dataset with combined nuclear and mitochondrial partitions using both methods, and conducted extensive exploratory analyses of individual partitions (nuclear, each of six nuclear introns, and mitochondrial) using MrBayes 3.1.

For each analysis in MrBayes 3.1, we performed at least two independent runs from random starting trees, each with three heated and one unheated chain for $4\text{--}8 \times 10^6$ generations, with trees and parameters sampled every 1000 generations. All analyses employed the default flat Dirichlet priors. We assessed convergence of the analysis by observing the values for the standard deviation of split frequencies between the runs and by examining the potential scale reduction factor calculated for the model parameters within each run. Additionally we examined convergence using the AWTY graphical tools available online (Wilgenbusch et al., 2004). We excluded trees and parameter values judged to be from the pre-convergence “burn-in” phases of the runs.

To optimize the fit of model parameters to the data in the Bayesian and likelihood analyses, parameter estimation for each data partition was performed separately (i.e., unlinked) in the analysis. We determined the appropriate model of evolution for each partition from AIC scores (Posada and Buckley, 2004) using MrModelTest 2.2 (Nylander, 2004). We explored different approaches to data partitioning. For the complete dataset we initially set up 10 partitions (10P) one for each of the six nuclear introns, one for each of the mitochondrial codon positions (for all combined coding regions), and an additional partition for mitochondrial non-coding sites. For some analyses we reduced the six nuclear partitions to three based on similarity of MrModelTest-estimated parameter values (*ACO1-9*, *MUSK-4* and *TGFB2-5* into one partition, *FGB-5* and *MB-2* into a second, and *RHO-1* by itself in a third) in combination with the four mitochondrial partitions (7P). In other analyses we used only two partitions, one each for the nuclear and mitochondrial data.

For likelihood analyses of the complete dataset in RaxML we used the 7P partitioning scheme, assigning a GTR+ Γ model to each (the RaxML author discourages use of GTR+ Γ +I; Stamatakis, 2008) and performed rapid bootstrapping with 1000 pseudoreplicates using the “GTRCAT” approximation. Likelihood ratio-relative rates tests carried out in the software r8s version 1.70 (Sanderson, 2004) confirmed that substitution rates differed between some sister lineages within the warbler phylogram. To generate an ultrametric tree from the best RaxML topology, we used Penalized Likelihood (PL; Sanderson, 2002) as implemented in

the software r8s. This analysis employed the TN algorithm and the log penalty over the additive penalty, due to the former's better performance in estimating internal branches remote from terminal calibration points (Sanderson, 2004). We used the cross-validation procedure to determine an optimal value of the smoothing parameter (=1000), and we checked the uniqueness of each analysis result through use of the "checkgradient" command and by re-running each analysis three times from randomly altered starting conditions.

3. Results

3.1. Summary of molecular results

From most taxa included in this study, we obtained nucleotide sequences comprising approximately one third of the mitochondrial genome, along with those of six intron regions in different nuclear loci. We sequenced only the mitochondrial NDII gene for samples derived from older museum skin materials (Appendix A). Although some of these sequences have been reported as part of our previous phylogenetic investigations of subsets of the parulid radiation, most are new to this study. Appendix A lists all corresponding GenBank Accession Numbers.

3.2. Parsimony analyses

The dataset included 2663 informative characters for parsimony, 598 from the nuclear partition (*ACO1-9*, 186; *FGB-5*, 60; *MUSK-4*, 96; *MB-2*, 86; *RHO-1*, 104; *TGFB2-5*, 66) and 2065 from the mitochondrial partition, with another 1265 variable characters autapomorphic. The heuristic search in PAUP* recovered 20 most parsimonious trees of 22340 steps each with a consistency index of 0.194 with uninformative characters removed. Fig. 1 presents a strict consensus of these shortest trees.

3.3. Bayesian and maximum likelihood analyses

Owing to the size and complexity of our dataset, many analyses using MrBayes failed to reach convergence within the 120 h time limit (corresponding to 4–6 million generations) imposed by the supercomputer cluster on which we ran these analyses; here, we report only the results of those that did apparently reach convergence.

In Bayesian analyses of the complete dataset, only the runs that employed the simplest (2P) partitioning structure reached MCMC convergence (Fig. 2). A separate analysis of the mitochondrial data alone with four partitions (4P) also achieved convergence (Fig. 3). In contrast, the nuclear data alone partitioned six ways by locus did not converge, but the nuclear-only runs did converge (Fig. 4) when the data were subdivided into three partitions [3P]. In exploratory analyses we saw no improvement in convergence when we varied the default value of the temperature setting for the heated chains, nor when we employed starting trees generated in RaxML. By examination of the MrBayes tree files in AWTY, we conservatively estimated pre-convergence "burn-in" cutoffs as follows: 2P all data analysis: 2.5 million generations, 3P nuclear data only analysis: 3 million generations, 4P mitochondrial analysis: 1.6 million generations.

The fully resolved maximum likelihood topology estimated via RaxML (Fig. 5) was nowhere inconsistent with the corresponding topology estimated in the 2P MrBayes analysis. This RaxML tree has a log likelihood score of -114042.91 and contained many nodes with high bootstrap support values.

4. Discussion

4.1. Defining a monophyletic Parulidae

The reconstructions presented here focus on the group we term the "core Parulidae," a group that previous studies with much greater outgroup sampling define (Sibley and Ahlquist, 1990; Klicka et al., 2000; Lovette and Bermingham, 2002; Yuri and Mindell, 2002; Klein et al., 2004; Klicka et al., 2007; Alström et al., 2008) by a long basal internode that separates this group from its relatives within the nine-primaried oscine radiation. Although the taxonomic sampling in the present study is not appropriate for formally testing the monophyly of the core Parulidae, we included in our reconstructions most taxa historically placed in the Parulidae, but which earlier molecular phylogenies showed to fall outside this core clade. In all cases, these lineages (*Icteria*, *Teretistris*, *Microligea*, *Xenoligea*, *Granatellus*, *Zeledonia*) fall outside of the "core Parulidae" group, along with several other non-Parulidae outgroup taxa (*Coereba*, *Spindalis*). We caution, however, that all of these other traditionally "wood-warbler" taxa except *Granatellus* (Klicka et al., 2007) appear to be relatively old lineages without close extant relatives, and the topological arrangement of their long branches in relation to one another and to other clades of nine-primaried oscines varies substantially among the phylogenetic studies in which they have been included. It therefore remains possible that one or more of these taxa form the sister group to the core Parulidae.

It is also unlikely that any taxa traditionally assigned to other avian families actually represent cryptic Parulidae. Most species from other families that have wood-warbler-like traits have been sampled in previous molecular phylogenetic studies (e.g., García-Moreno et al., 2001; Lovette and Bermingham, 2002; Burns et al., 2003; Mauck and Burns, 2009). Furthermore, the present study is part of a comprehensive survey of the phylogenetic relationships of the entire nine-primaried oscine group, with sequence data now collected on all ~200 genera and nearly all ~823 species in that diverse radiation. Preliminary analyses indicate that none of those additional taxa fall unexpectedly within or near the core Parulidae clade (Barker, et al., pers comm.; Lovette, unpublished data).

4.1.1. Molecular systematics of the Parulidae

The reconstructions presented here provide a highly congruent perspective on phylogenetic relationships within the Parulidae. Support metrics for numerous sub-clades within this radiation were high across all datasets and methods of phylogenetic reconstruction (Figs. 1–5). In particular, all analyses that included information from mtDNA loci resulted in nearly identical topologies at all well-supported nodes. Although support values were generally lower in the reconstructions based solely on nuclear intron loci, those trees also shared most nodes with the mtDNA-based reconstructions. These commonalities among analyses are the basis for the taxonomic recommendations below.

4.1.2. Early low-diversity lineages

All reconstructions were congruent in identifying a single species, the Ovenbird (*Seiurus aurocapilla*), as the sole member of the lineage that is sister to the remaining core Parulidae, generally with strong support (Figs. 1–5). This placement of the Ovenbird lineage has also been found in previous phylogenetic studies with less extensive taxonomic and marker sampling (Lovette and Bermingham, 2002; Klein et al., 2004; Lovette and Hochachka, 2006). The English name of this species refers to its dome-shaped terrestrial nest, which differs from that of all other species of parulids. Lovette and Hochachka (2006) suggested that the early

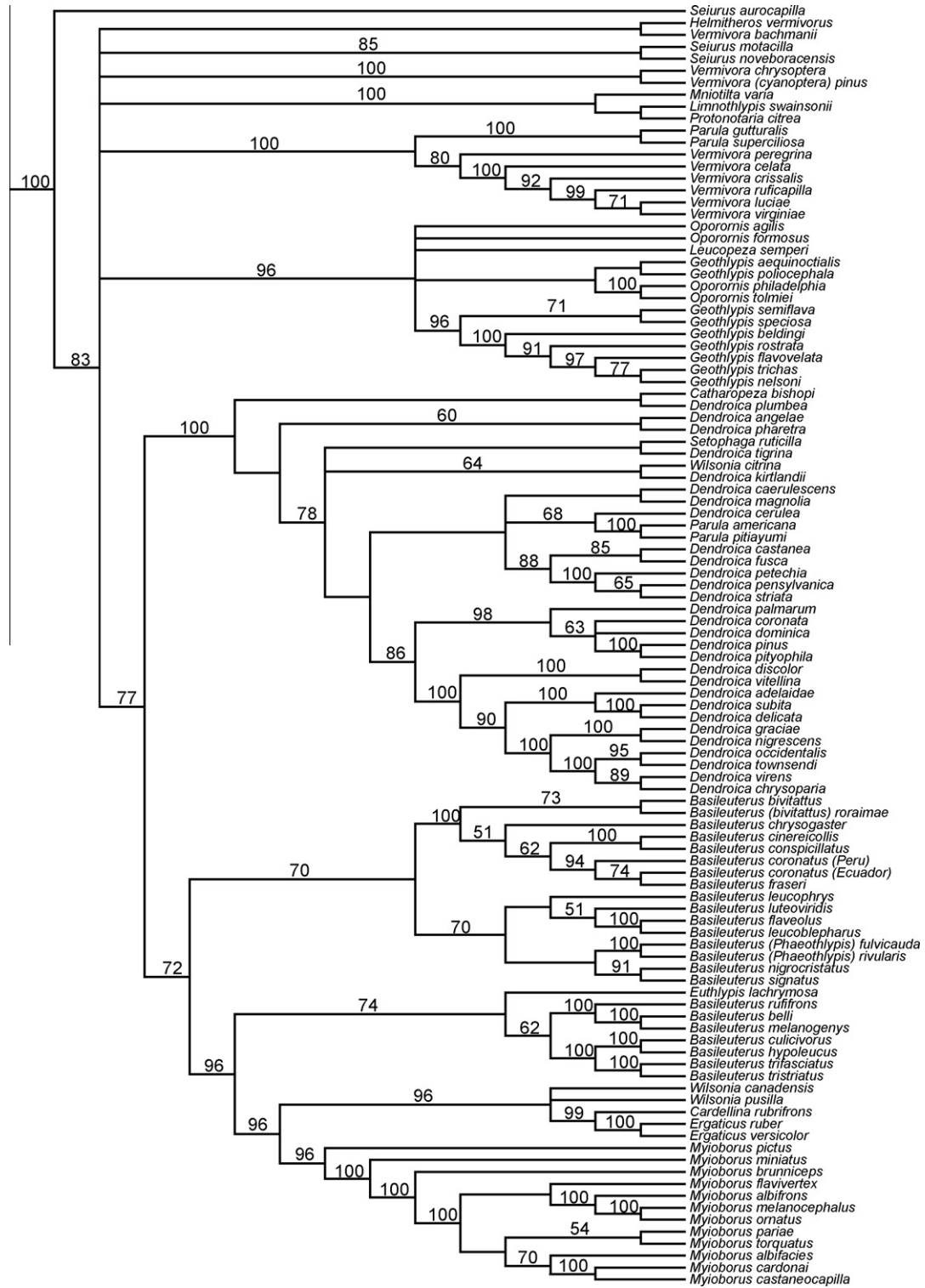


Fig. 1. Maximum parsimony reconstruction of relationships among 107 species of Parulidae. Topology shown here is the strict consensus of the 20 most parsimonious trees of 22340 steps (C.I. = 0.192) recovered from an unweighted parsimony analysis of 10,449 aligned nucleotides of mitochondrial and nuclear intron sequence. Outgroups (not shown) were *Coereba flaveola*, *Granatellus pelzelni*, *Icteria virens*, *Microligea palustris*, *Spindalis portoricensis*, *Xenoligea montana*, *Zeledonia coronata*, and *Teretistris fernandinae*. Numbers adjacent to nodes indicate all bootstrap proportions $\geq 50\%$.

split between the Ovenbird and the remaining Parulidae has involved substantial niche differentiation that limits present-day competition and thereby fosters their spatial overlap during the breeding season.

Six low-diversity lineages, all with long branches, are rooted near the base of the core Parulidae tree, most clearly in the reconstructions based on all markers (Figs. 4 and 5). Notably short internodes separate these lineages from one another, and topological

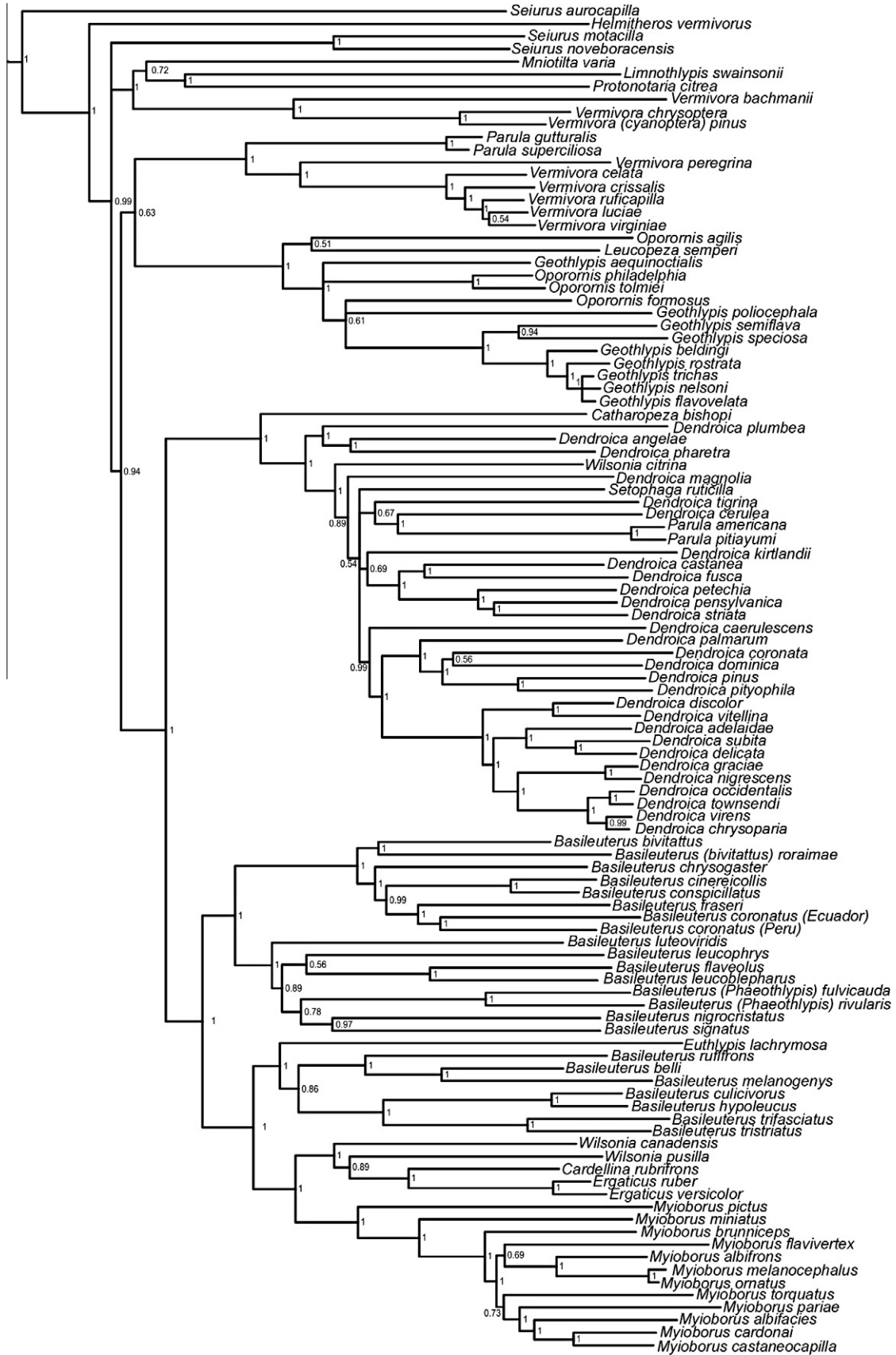


Fig. 2. Relationships among species of Parulidae estimated by a Bayesian analysis of 10,449 aligned nucleotide bases divided into two partitions (nuclear, mitochondrial), each with an unlinked GTR+I+ Γ model. The topology shown here is a 50% majority rule consensus of 7252 post burn-in trees from four runs in MrBayes 3.1. Mean tree likelihood = -116368. Numbers adjacent to nodes indicate posterior probability values. Topology is rooted to eight outgroup taxa (not shown) as in Fig. 1.

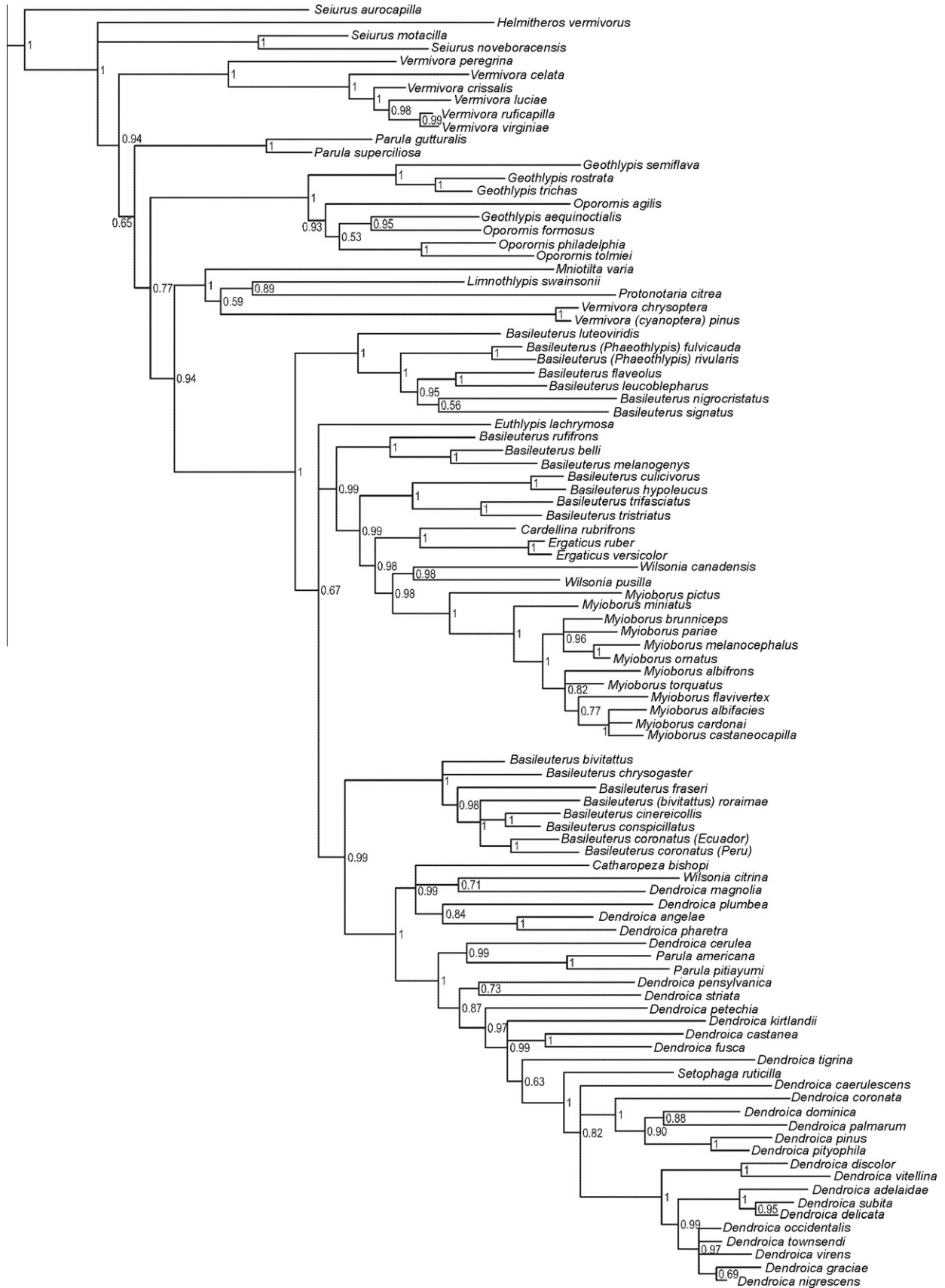


Fig. 3. Relationships among species of Parulidae estimated by a Bayesian analysis of 4602 aligned bases from six nuclear introns, subdivided into three partitions according to similarity of their model parameters as estimated in MrModelTest2.0 (ACO1-9, MUSK-4, TGF2-5; FGB-5, MB-2; RHO-1) each receiving an unlinked GTR+ Γ model. The topology shown here is a 50% majority rule consensus of 6002 post burn-in trees (mean tree likelihood = -23221) from two independent runs in MrBayes 3.1. Numbers adjacent to nodes indicate posterior probability values. Topology is rooted to eight outgroup taxa (not shown) as in Fig. 1.

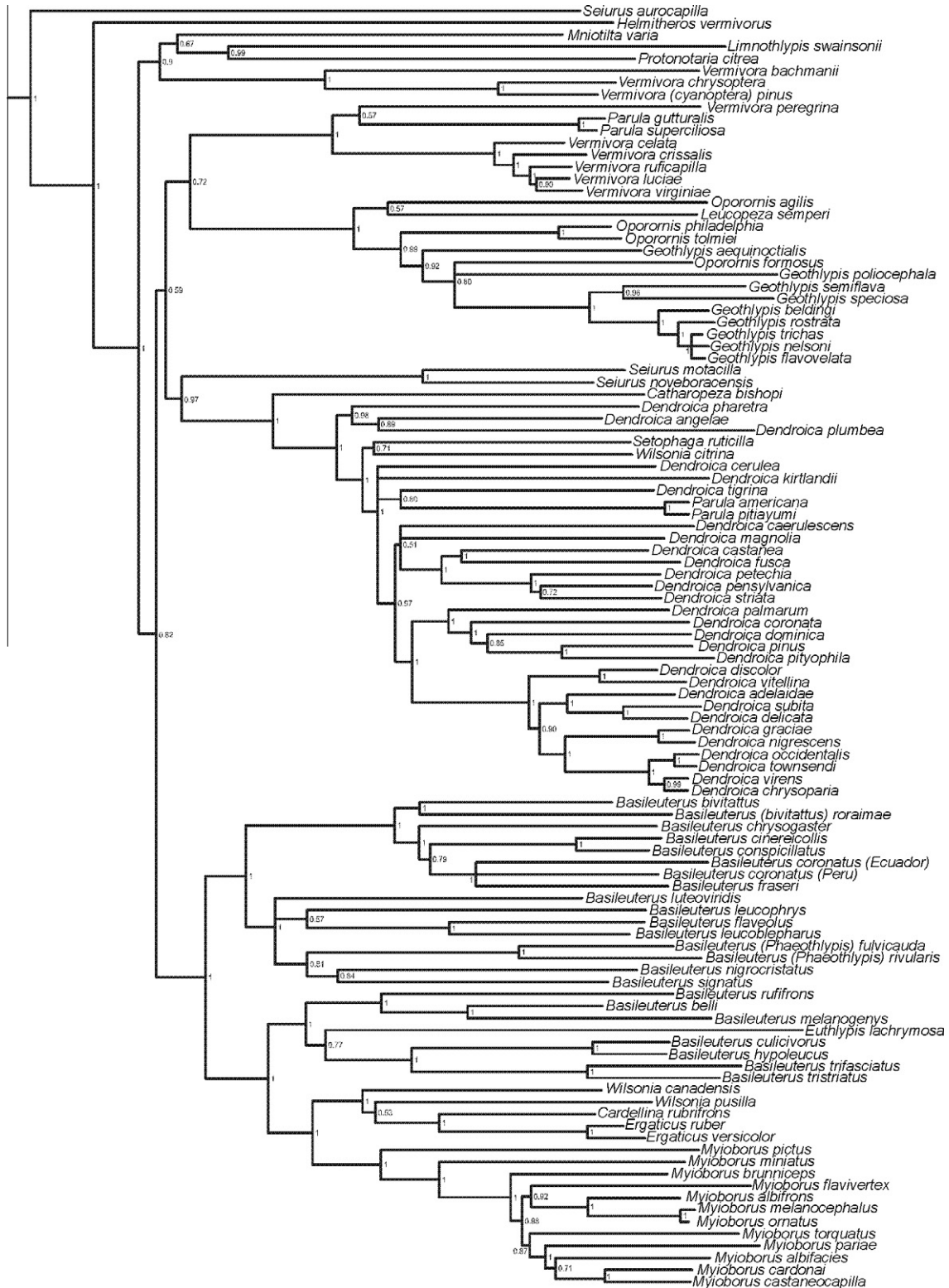


Fig. 4. Relationships among species of Parulidae estimated by a Bayesian analysis of 5847 aligned bases of mitochondrial sequence divided into four partitions (one for each codon position in coding genes, and one for non-coding data), each receiving an unlinked GTR+I+ Γ model. Topology shown here is a 50% majority rule consensus of 8002 post burn-in trees (mean tree likelihood = -90027) from two independent runs in MrBayes 3.1. Numbers adjacent to nodes indicate posterior probability values. Topology is rooted to eight outgroup taxa (not shown) as in Fig. 1.

support for their relative placement is correspondingly low or unstable across reconstructions (Figs. 1–5). Four of these lineages each include a single species that has long been recognized as a

monotypic genus (*Helminthos vermivorus*, *Mniotilta varia*, *Limnothlypis swainsonii*, and *Protonotaria citrea*) on the basis of its morphological distinctiveness. Among these, *Limnothlypis* has been



Fig. 5. Relationships among 110 species of Parulidae estimated via a RaxML maximum likelihood analysis of 5847 mitochondrial and 4602 intron nucleotides. This fully resolved topology ($-Ln = -114042.91$) represents our recommended tree for phylogenetically informed analyses of ecological and evolutionary variation in this group. Asterisks above or adjacent to nodes indicate bootstrap support values >95% (1000 pseudoreplicates). Tree was rendered ultrametric by penalized likelihood using the software r8s, employing a log penalty and a smoothing parameter of 1000 as determined by cross-validation. To generate the scale bar at top, the root (which links the clade depicted here with eight non-Parulidae taxa from allied families within the nine-primaried oscine radiation) was arbitrarily set to 100 time units. Colored boxes in the background indicate the clades for which we advocate the revised generic names given at right. Monotypic lineages for which we advocate the traditional generic names are uncolored.

merged into *Helmitheros* in some past classifications (Griscom and Sprunt, 1957; Mayr and Short, 1970; Howell and Webb, 1995), but the phylogenetic reconstructions presented here are all congruent in showing that these two taxa are highly distinct, with *Limnothlypis* and *Protonotaria* more likely to be sister species. The phylogenetic reconstructions also help clarify the enigmatic relationships of the Black-and-white Warbler *Mniotilta varia*, a species with several unique morphological features related to its bark-clinging foraging behavior. Despite suggestions (e.g., Mayr and Short, 1970; Parkes, 1978) that *Mniotilta* likely falls close to or within the *Dendroica* group, and despite well-documented viable hybrids between *Mniotilta* and two species of *Dendroica* (Parkes, 1978; Vallender et al., 2009), our phylogenetic results indicate that *Mniotilta* represents an old lineage that is highly distinct from the *Dendroica* group.

Two of these early lineages include species that are not closely allied to others traditionally grouped with them as congeners. The two waterthrush species (*Seiurus noveboracensis* and *S. motacilla*) are well-supported as sister-taxa in all reconstructions, as expected on the basis of their close morphological and behavioral similarity to one another. As noted above, however, they do not form a clade with *S. aurocapilla*, the third species traditionally placed in *Seiurus*. The phylogenetic separation of the two waterthrushes from the Ovenbird and their general phylogenetic distinctiveness from all other parulid species supports the retention of the Ovenbird as the sole member of *Seiurus*, of which it is the type species, and the assignment of the two waterthrushes to the genus *Parkesia*, which was recently described for them (Sangster, 2008a).

A similar situation involves three species traditionally assigned to *Vermivora*, which together represent the final low-diversity group that roots near the base of the core Parulidae clade. This group includes two close sister-taxa, the Blue-winged (*V. pinus* or *cyanopectera*) and Golden-winged warblers (*V. chrysoptera*), which have a geographically extensive mosaic hybrid zone (Vallender et al., 2007), plus the more genetically and phenotypically differentiated Bachman's Warbler (*V. bachmanii*), a species that is likely extinct (Hamel, 1995). These three species are clustered with high support in most reconstructions, including those based on mtDNA (Figs. 2, 4 and 5); the exception seen in the maximum parsimony topology (Fig. 1) likely results from the small number of DNA characters we obtained for *bachmanii*, which was represented in our dataset only by NDII sequences. This clade of three species contains *pinus/cyanopectera* (see Olson and Reveal (2009)), the type species of *Vermivora*, but it does not group with the six additional species traditionally placed in *Vermivora* Swainson, 1827 (see below).

4.1.3. *Vermivora/Leiothlypis* and *Parula/Oreothlypis*

A group comprising two species currently assigned to *Parula* (*gutturalis* and *superciliosa*) and six traditionally assigned to *Vermivora* (*peregrina*, *celata*, *ruficapilla*, *virginiae*, *crissalis*, and *luciae*) form a well-supported clade in all but the nuclear-only reconstruction (Fig. 3), in which the species of *Parula* are separated by a short and weakly supported internode. Within this group, the two *Parula* species are sister-taxa, and together they are likely sister to the well-supported cluster of *Vermivora* species; these species now in *Parula* were merged into *Vermivora* in some previous classifications (e.g., Lowery and Monroe, 1968), and Webster's (1997) investigation of wood-warbler skeletal characters found that them to be linked to *Vermivora* by their shared trait of a long retroarticular processes.

Within this clade of *Vermivora*, *V. peregrina* is sister to, and well-differentiated from, a shallow clade containing the remaining five species. This group of five species shows a notably low magnitude of interspecific genetic differentiation and is probably of relatively

recent origin, yet field experiments have shown that in sympatry two of these species compete ecologically and are behaviorally isolated despite their recent phylogenetic separation (Martin and Martin, 2001).

The phylogenetic structure within this group parallels that of previous studies that have examined subsets of these taxa using a variety of molecular markers (Avise et al., 1980; Zink et al., 2000; Lovette et al., 2003; Lovette and Bermingham, 2002; Klein et al., 2004; Lovette and Hochachka, 2006). Because the type species of *Vermivora* is not a member of this clade, Sangster (2008b) recently described the new genus *Leiothlypis* for the six taxa in this group currently assigned to *Vermivora*. He further suggested that the genus *Oreothlypis* be reinstated for *Parula gutturalis* and *P. superciliosa*, because these two taxa are not closely allied to the type species of *Parula* (= *americana*). The results presented here are consistent with these nomenclatural changes, but we suggest instead that because all eight species form a well-supported group, merging them all into *Oreothlypis* is a marginally preferable alternative.

4.1.4. *Geothlypis* and allies (*Oporornis*, *Leucopeza*)

Fourteen species traditionally assigned to the genera *Oporornis*, *Geothlypis*, and *Leucopeza* form a clade with a long and universally highly supported basal internode. Our reconstructions of relationships within this group are generally concordant with those of Escalante et al. (2009), who explored relationships within this group at both the population and species levels using mtDNA markers. Substantial paraphyly in their mtDNA reconstructions indicated that *G. aequinoctialis*, which has four subspecies with disjoint ranges in Central and South America, may represent several well-differentiated species-level taxa (Escalante et al., 2009); our sample from Uruguay represents only the southernmost of these forms (*G. aequinoctialis velata*). A congruent cluster of *Geothlypis* taxa with very low mitochondrial differentiation is also evident in both Escalante et al. (2009) and the present study. This complex includes one species with a breeding distribution that spans much of North America (*G. trichas*), and four taxa with restricted and peripheral ranges relative to *trichas*: a form endemic to the northern Bahamas (*G. rostrata*), one endemic to the Baja California peninsula of Mexico (*G. beldingi*), and two found in small regions of continental Mexico (*G. flavovellata* and *G. nelsoni*). An additional species (*G. speciosa*), endemic to a small area of central Mexico, is phylogenetically distinct from this group; the higher distinctiveness of *speciosa* is notable because it is currently endangered, declining, and of high conservation concern (BirdLife International, 2008).

In both the reconstructions of Escalante et al. (2009) and in the present study, the Kentucky Warbler (*Oporornis formosus*) groups with the *Geothlypis* species, rendering *Oporornis* paraphyletic. The Mourning (*O. philadelphia*) and MacGillivray's (*O. tolmiei*) warblers, which hybridize across a zone of contact in western Canada (Irwin et al., 2009), are sister-taxa. The Connecticut Warbler (*O. agilis*) lineage consistently falls basal to the remaining *Oporornis* and *Geothlypis* (Figs. 1–5; see also Escalante et al. (2009)).

The most surprising finding in our reconstructions of this group is its inclusion of Semper's Warbler (*Leucopeza semperi*), a morphologically enigmatic species endemic to the West Indian island of St. Lucia that likely became extinct in the mid-1900s (Keith, 1997). The relationships of *Leucopeza* have long been described as confusing (Ridgway, 1902; Bond, 1956, 1963; Curson et al., 1994; Lovette and Bermingham, 2002), and this is the first molecular phylogenetic information on its affinities. Our power to resolve its precise placement is limited by the fact that we have only NDII sequences from *Leucopeza*, but it appears to be either the sister taxon to *O. agilis* or a deep lineage that split from the ancestor of the remaining *Geothlypis* group at about the same time as did the *agilis*

lineage (Figs. 1, 2, 4 and 5). How the incipient *Leucopeza* population initially colonized the Lesser Antilles remains perplexing, because no other species within the *Oporornis* group currently breeds on any of the oceanic West Indian islands, although the migratory *G. trichas* overwinters in the Greater Antilles and the non-migratory *G. rostrata* is endemic to the land-bridge islands of the northern Bahamas.

Given the high support for the clade comprising all *Oporornis*, *Geothlypis*, and *Leucopeza*, and the strong evidence (Escalante et al., 2009) that the species traditionally assigned, respectively, to *Oporornis* and *Geothlypis* are not monophyletic, we follow Escalante et al. (2009) in recommending that all of these taxa be merged into the genus *Geothlypis* Cabanis, 1847, which has priority.

4.1.5. *Setophaga* and allies (*Dendroica*, *Catharopeza*, some *Wilsonia*, some *Parula*)

A large and well-supported group of 34 species contains all forms currently placed in the genus *Dendroica*, two of four species of *Parula*, one of three species of *Wilsonia*, and the monotypic genera *Catharopeza* and *Setophaga*. The relationships of many of these taxa have been explored in previous phylogenetic studies (e.g., Bermingham et al., 1992; Lovette and Bermingham, 1999, 2002; Klein et al., 2004; Lovette and Hochachka, 2006; Rabosky and Lovette, 2008), but this is the first set of reconstructions based on multilocus sequences that includes a complete sampling of all species in this group.

The early splits within this clade all involve relatively old West Indian lineages, with the Whistling Warbler (*Catharopeza bishopi*), a species endemic to the island of St. Vincent, sister to the remaining taxa. The close affinities of *Catharopeza* to *Dendroica* have long been recognized (Lowery and Monroe, 1968; Kepler and Parkes, 1972; AOU, 1998), and this placement of *Catharopeza* parallels that in our previous molecular phylogenetic hypotheses for the *Dendroica* group (Lovette and Bermingham, 1999, 2002). Three *Dendroica* species endemic to disjunct regions of the West Indies (*D. plumbea* of Dominica/St. Lucia; *D. pharetra* of Jamaica; *D. angelae* of Puerto Rico) form the next sub-clade within this group and may represent the relicts of a previously more widespread island radiation (Ricklefs and Cox, 1972).

A series of short and generally weakly supported internodes groups a slightly more recent radiation of all other *Dendroica* lineages, along with one species traditionally assigned to *Wilsonia*, two to *Parula*, and the monotypic *Setophaga*. Elsewhere, we have suggested that the compressed internodes at the base of this group indicate that the continental members of this clade had a non-randomly high speciation rate early in their history (Lovette and Bermingham, 1999), with a later slowing of diversification consistent with a scenario of density-dependent speciation mediated by ecological interactions (Rabosky and Lovette, 2008). Relationships among several sets of closely related species within this large clade are congruent with previous reconstructions of those species complexes based primarily on mtDNA markers (Bermingham et al., 1992; Lovette and Bermingham, 1999, 2001, 2002; Klein et al., 2004; Markland and Lovette, 2005; Lovette and Hochachka, 2006; Rabosky and Lovette, 2008).

The placement of *Parula americana*, *P. pitiayumi*, *Setophaga ruticilla*, and *Wilsonia citrina* well within this fairly bushy clade confirms previous suggestions about their general affinities to the *Dendroica* group (e.g., Parkes, 1978; Lovette and Bermingham, 2002; Klein et al., 2004), but also raises a series of nomenclatural challenges. We recommend including all 34 members of this group in a single genus, because the internode at the base of this clade is long and universally well-supported, whereas few other deep internodes within this radiation have strong support and the overall topology has a comb-like structure (Figs. 1–5). The generic

names *Dendroica* Gray, 1842, *Wilsonia* Bonaparte, 1838, and *Parula* Bonaparte, 1838, are all particularly well-known among ecologists and the bird-watching general public, but the generic name *Setophaga* Swainson, 1827 has nomenclature priority for this combined group. We therefore recommend that all species in this group be assigned to *Setophaga*.

4.1.6. *Basileuterus*, *Myioborus*, and allies (*Ergaticus*, *Cardellina*, some *Wilsonia*)

All reconstructions support a large clade primarily of species resident in Central and South America. This group includes all species traditionally assigned to the genera *Basileuterus* (including *Phaeothlypis* and *Euthlypis*), *Myioborus*, *Cardellina*, and *Ergaticus*, and two of the three species of *Wilsonia*. Only the four of these taxa with the northernmost breeding ranges are medium- or long-distance migrants. Many of the sedentary species with broad geographic distributions in the Neotropics are known to contain high phylogeographic structure at the population level (e.g., Lovette, 2004; Pérez-Emán, 2005).

Within this Neotropical assemblage, only *Myioborus* forms a monophyletic group consistent with its traditional generic classification. The phylogenetic relationships of *Myioborus* were explored in detail by Pérez-Emán (2005), and the reconstructions here are highly congruent with his previous mtDNA-based phylogenies. The broader sampling of other warbler taxa included here further confirms that all species of *Myioborus* Baird, 1865, form a well-supported monophyletic group, within which the Painted Redstart (*M. pictus*) is the sister taxon to all remaining *Myioborus*.

Myioborus is in turn sister to a smaller clade containing the two species assigned to *Ergaticus*, the monotypic *Cardellina*, and two of the three *Wilsonia* species, the Wilson's Warbler (*W. pusilla*) and Canada Warbler (*W. canadensis*). As described above, the third (and type) species of *Wilsonia* (= *citrina*) is not closely allied to this clade, instead falling within the *Setophaga/Dendroica* radiation. The relative topology of these five taxa varies among our reconstructions (Figs. 1–5), but whereas the two *Ergaticus* species are clearly close sister-taxa, the two *Wilsonia* group together as sister species only in the reconstruction based on the nuclear loci (Fig. 3). In terms of classification, we recommend merging all five of these taxa into a single genus; under this approach the name *Cardellina* Bonaparte, 1850, has priority for them.

The diverse assemblage of species traditionally placed in the genus *Basileuterus* also appears not to form a monophyletic group, with one subset of these taxa forming instead the sister clade to the combined *Myioborus/Cardellina* group in all but the nuclear-only reconstructions (Figs. 1–5). This first *Basileuterus* sub-group includes the Fan-tailed Warbler (*E. lachrymosa*), which is traditionally placed in the monotypic genus *Euthlypis* but which has long been thought to be allied to *Basileuterus* (Ridgway, 1902; Curson et al., 1994). This group has a center of diversity in Central America and Mexico, where four species are restricted (*lachrymosa*, *belli*, *melanogenys*, *ignotus*). Three additional taxa (*rufifrons*, *culicivorus*, *tristriatus*) are found in both Central and South America; in all three cases, phylogeographic reconstructions based on mtDNA markers indicate that the basal haplotypes among these conspecific populations are found in Central America, and that these taxa have only recently colonized South America across the Isthmus of Panama (Lovette, unpublished data). Two additional species in this group are restricted to South America, but each is closely allied to a more broadly distributed species: *hypoleucus* of southern South America is phylogenetically close to the widespread and phenotypically similar *culicivorus* (Hellmayr, 1935; contra Lowery and Monroe 1968). More surprisingly, although *trifasciatus* of Ecuador

and Peru is also morphologically similar to *culicivorus* (Ridgely and Tudor, 1989), the phylogenetic reconstructions indicate that *trifasciatus* is sister to the widespread species *tristriatus*. Because *culicivorus* is the type species for *Basileuterus*, retaining *Basileuterus Cabanis, 1848*, as the generic name for this clade is warranted.

A second and larger group of species also traditionally assigned to *Basileuterus* forms the well-supported clade that is sister to the combined *Basileuterus/Myioborus/Cardellina* clade in all but the nuclear-only reconstructions (Figs. 1–5). This group of species represents a South American radiation that likely followed from an earlier colonization of that continent, as all but one species in this clade remain restricted to South America. Two sister-taxa (*fulvicauda* and *rivularis*) embedded within this clade have often been placed in the genus *Phaeothlypis*; one of these (*fulvicauda*) is the sole species within this larger group with a population that has reverse-colonized north into Central America (Lovette, 2004). These and a few other species in this group occupy a series of disjunct lowland areas of South America, but most of the species in this clade have diversified in montane regions, with some being highly range-restricted and others having long but narrow and elevationally restricted distributions. Our knowledge of species boundaries in this clade is still evolving, and the current classifications are almost certainly an underestimate of the species-level taxa within this radiation. Retaining the species in this clade within *Basileuterus* would render that genus paraphyletic; consequently, there is a need for an appropriate generic name. For this group we recommend the resurrection of *Myiothlypis Cabanis, 1850*, of which the type species is *nigrocristata*. Because *Basileuterus* is masculine but *Myiothlypis* feminine, this change requires changing the gender of some of the specific names in this group.

4.1.7. Non-sampled taxa

We included in our analyses samples from nearly all species-level taxa in the core Parulidae as recognized in recent taxonomies (e.g., Lowery and Monroe, 1968; Sibley and Monroe, 1990; AOU, 1998; Dickinson, 2003). Species limits within some complexes of closely allied taxa of Parulidae remain controversial, and the splitting of some such taxa could add additional species not represented in our topologies. However, these potential future changes at terminal branches are not likely to influence the classification proposed here.

Three taxa generally recognized as valid species were not included here. The first of these taxa, *Basileuterus griseiceps*, is endemic to the Serranía de Turimiquire in northeastern Venezuela (Hilty, 2003). None of our attempts to amplify NDII sequences from toe pads of this species were successful. This species is little-known (Libro Rojo Sharpe, 2008; Hernández et al., 2009), and its plumage traits are ambiguous regarding its affinities to any of the other species traditionally placed in *Basileuterus* (Curson et al., 1994; Ridgely and Tudor, 1989), although it may be closest to *leucoblepharus* (Todd, 1929; Hellmayr, 1935; Olson, 1975). On these biogeographic and morphological criteria it seems most likely to fall within the South American group that we recognize here as *Myiothlypis*, and we recommend placing it *incertae sedis* within that genus pending better information on its precise relationships.

We were likewise unable to amplify mtDNA from old specimens of *Basileuterus basilicus*, a species endemic to the Sierra Nevada de Santa Marta in northern Colombia. The affinities of this species are unclear, but its plumage traits indicate that it is possibly allied to *Basileuterus tristriatus* (Hellmayr, 1935; Ridgely and Tudor, 1989), and we therefore recommend retaining it *incertae sedis* in *Basileuterus*.

A final species, *Basileuterus ignotus*, was not included here for logistical reasons. This taxon is endemic to the highlands near the Panama–Colombia border, and has most often been treated as a distinct species (e.g., AOU, 1998), but sometimes as a disjunct form of *Basileuterus melanogenys* (Lowery and Monroe, 1968; Wetmore et al., 1984). Preliminary analyses (Lovette, unpublished data) based on mitochondrial sequences support the traditional close sister-relationship between *melanogenys* and *ignotus*.

4.2. Phylogenetic and nomenclatural summary

One impetus for generating a comprehensive phylogeny for the wood-warblers was to facilitate comparative studies that require an explicit phylogenetic hypothesis. At present, the topology of our maximum-likelihood reconstruction of all molecular data partitions (Fig. 5) represents our best hypothesis of relationships within the Parulidae, and we recommend its use for comparative purposes, while recognizing that some nodes within that tree remain weakly supported.

Based on the reconstructions presented here, we have recommended above a revised classification for the Parulidae that recognizes 14 genera in a linear classification consistent with the relationships depicted in our summary tree (Table 1; Fig. 5): *Seiurus*, *Helmitheros*, *Mniotilta*, *Limnothlypis*, *Protonotaria*, *Parkesia*, *Vermivora*, *Oreothlypis*, *Geothlypis*, *Setophaga*, *Myioborus*, *Cardellina*, *Basileuterus*, *Myiothlypis*. Collectively, these changes would subsume nine genera that are currently broadly recognized: *Catharopeza*, *Dendroica*, *Ergaticus*, *Euthlypis*, *Leucopeza*, *Oporornis*, *Parula*, *Phaeothlypis*, *Wilsonia*. Although these taxonomic changes follow the rules of nomenclatural priority and the fundamental criterion that genera should represent well-supported monophyletic groups, we acknowledge that they will be somewhat controversial given the wide usage of some of the traditional generic names.

Although *Parula*, the type genus of the family Parulidae, is here considered to be a junior synonym of *Setophaga*, this does not require a change of the family name Parulidae (see Article 40.1, International Code of Zoological Nomenclature (ICZN, 1999).

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Appendix A

Genbank Accession Numbers for sequences included in this study^a.

Taxon	Intron Loci ^b						mtDNA Regions ^c	
	ACO1–9	FGB-5	MUSK-4	MB-2	TGFB2–5	RHO-1	cytb	other mtDNA
<i>Seiurus aurocapilla</i>	GU931829	GU931936	GU932150	GU932257	GU932430	GU932513	GU932365	GU932043
<i>Helmitheros vermivorus</i>	GU931823	GU931930	GU932144	GU932251	GU932424	GU932507	GU932361	GU932037
<i>Seiurus motacilla</i>	GU931830	GU931937	GU932151	GU932258	GU932431	GU932514	GU932366	GU932044
<i>Seiurus noveboracensis</i>	GU931831	GU931938	GU932152	GU932259	GU932432	GU932515	GU932367	GU932045
<i>Vermivora bachmani</i>								GU932360
<i>Vermivora chrysoptera</i>	GU931832	GU931939	GU932153	GU932260	GU932433	GU932516	GU932368	GU932046
<i>Vermivora pinus</i>	GU931833	GU931940	GU932154	GU932261	GU932434	GU932517	GU932369	GU932047
<i>Mniotilta varia</i>	GU931825	GU931932	GU932146	GU932253	GU932426	GU932509	AF383006	GU932039
<i>Protonotaria citrea</i>	GU931826	GU931933	GU932147	GU932254	GU932427	GU932510	GU932362	GU932040
<i>Limnothlypis swainsonii</i>	GU931824	GU931931	GU932145	GU932252	GU932425	GU932508	AF383005	GU932038
<i>Parula gutturalis</i>	GU931827	GU931934	GU932148	GU932255	GU932428	GU932511	GU932363	GU932041
<i>Parula superciliosa</i>	GU931828	GU931935	GU932149	GU932256	GU932429	GU932512	GU932364	GU932042
<i>Vermivora peregrina</i>	GU931919	GU932026	GU932240	GU932347	GU932496	GU932579	GU932420	GU932133
<i>Vermivora celata</i>	GU931916	GU932023	GU932237	GU932344	GU932493	GU932576	GU932417	GU932130
<i>Vermivora crissalis</i>	GU931917	GU932024	GU932238	GU932345	GU932494	GU932577	GU932418	GU932131
<i>Vermivora luciae</i>	GU931918	GU932025	GU932239	GU932346	GU932495	GU932578	GU932419	GU932132
<i>Vermivora virginiae</i>	GU931921	GU932028	GU932242	GU932349	GU932498	GU932581	GU932422	GU932135
<i>Vermivora ruficapilla</i>	GU931920	GU932027	GU932241	GU932348	GU932497	GU932580	GU932421	GU932134
<i>Oporornis agilis</i>	GU931891	GU931998	GU932212	GU932319	GU932468	GU932551	GU932398	GU932105
<i>Leucopoeza semperi</i>								GU932358
<i>Geothlypis aequinoctialis</i>	GU931890	GU931997	GU932211	GU932318	GU932467	GU932550	GU932397	GU932104
<i>Geothlypis poliocephala</i>	DQ233484							
<i>Oporornis tolmiei</i>	GU931894	GU932001	GU932215	GU932322	GU932471	GU932554	GU932400	GU932108
<i>Oporornis philadelphia</i>	GU931893	GU932000	GU932214	GU932321	GU932470	GU932553	GU932399	GU932107
<i>Oporornis formosus</i>	GU931892	GU931999	GU932213	GU932320	GU932469	GU932552	AF383017	GU932106
<i>Geothlypis semiflava</i>	GU931896	GU932003	GU932217	GU932324	GU932473	GU932556	GU932402	GU932110
<i>Geothlypis speciosa</i>								DQ233487
<i>Geothlypis beldingi</i>								DQ233481
<i>Geothlypis rostrata</i>	GU931895	GU932002	GU932216	GU932323	GU932472	GU932555	GU932401	GU932109
<i>Geothlypis flavovellata</i>								DQ233482
<i>Geothlypis trichas</i>	GU931897	GU932004	GU932218	GU932325	GU932474	GU932557	AF383003	GU932111
<i>Geothlypis nelsoni</i>								DQ233483
<i>Catharopoeza bishopi</i>	GU931865	GU931972	GU932186	GU932293	GU932462	GU932545	GU932392	GU932079
<i>Dendroica plumbea</i>	GU931884	GU931991	GU932205	GU932312	GU932465	GU932548	GU932395	GU932098
<i>Dendroica angelae</i>	GU931860	GU931967	GU932181	GU932288	GU932461	GU932544	GU932391	GU932074
<i>Dendroica pharetra</i>	GU931881	GU931988	GU932202	GU932309	GU932463	GU932546	GU932393	GU932095
<i>Wilsonia citrina</i>	GU931871	GU931978	GU932192	GU932299	EU815821	EU815797	EU815695	GU932085
<i>Setophaga ruticilla</i>	GU931870	GU931977	GU932191	GU932298	EU815820	EU815796	EU815694	GU932084
<i>Dendroica kirtlandii</i>	GU931874	GU931981	GU932195	GU932302	EU815806	EU815782	EU815681	GU932088
<i>Dendroica tigrina</i>	GU931886	GU931993	GU932207	GU932314	EU815815	EU815791	AF256505	GU932100
<i>Dendroica cerulea</i>	GU931863	GU931970	GU932184	GU932291	EU815800	EU815776	EU815676	GU932077
<i>Parula americana</i>	GU931868	GU931975	GU932189	GU932296	EU815818	EU815794	EU815692	GU932082
<i>Parula pityayumi</i>	GU931869	GU931976	GU932190	GU932297	EU815819	EU815795	EU815693	GU932083
<i>Dendroica magnolia</i>	GU931875	GU931982	GU932196	GU932303	EU815807	EU815783	EU815682	GU932089
<i>Dendroica castanea</i>	GU931862	GU931969	GU932183	GU932290	EU815799	EU815775	EU815675	GU932076
<i>Dendroica fusca</i>	GU931872	GU931979	GU932193	GU932300	EU815804	EU815780	AY340208	GU932086
<i>Dendroica petechia</i>	GU931880	GU931987	GU932201	GU932308	EU815812	EU815788	EU815687	GU932094
<i>Dendroica pensylvanica</i>	GU931879	GU931986	GU932200	GU932307	EU815811	EU815787	EU815686	GU932093
<i>Dendroica striata</i>	GU931885	GU931992	GU932206	GU932313	EU815814	EU815790	EU815688	GU932099
<i>Dendroica caerulescens</i>	GU931861	GU931968	GU932182	GU932289	EU815798	EU815774	EU815674	GU932075
<i>Dendroica palmarum</i>	GU931878	GU931985	GU932199	GU932306	EU815810	EU815786	EU815685	GU932092
<i>Dendroica pityophila</i>	GU931883	GU931990	GU932204	GU932311	EU932464	GU932547	GU932394	GU932097
<i>Dendroica pinus</i>	GU931882	GU931989	GU932203	GU932310	EU815813	EU815789	AF383027	GU932096
<i>Dendroica coronata</i>	GU931864	GU931971	GU932185	GU932292	EU815801	EU815777	EU815677	GU932078
<i>Dendroica dominica</i>	GU931867	GU931974	GU932188	GU932295	EU815803	EU815779	EU815679	GU932081
<i>Dendroica discolor</i>	GU931866	GU931973	GU932187	GU932294	EU815802	EU815778	EU815678	GU932080
<i>Dendroica vitellina</i>	GU931889	GU931996	GU932210	GU932317	GU932466	GU932549	GU932396	GU932103
<i>Dendroica adelaidae</i>	GU931858	GU931965	GU932179	GU932286	GU932459	GU932542	GU932389	GU932072
<i>Dendroica subita</i>	GU931857	GU931964	GU932178	GU932285	GU932458	GU932541	AF256504	GU932071
<i>Dendroica delicata</i>	GU931859	GU931966	GU932180	GU932287	GU932460	GU932543	GU932390	GU932073
<i>Dendroica graciae</i>	GU931873	GU931980	GU932194	GU932301	EU815805	EU815781	EU815680	GU932087
<i>Dendroica nigrescens</i>	GU931876	GU931983	GU932197	GU932304	EU815808	EU815784	EU815683	GU932090
<i>Dendroica occidentalis</i>	GU931877	GU931984	GU932198	GU932305	EU815809	EU815785	EU815684	GU932091
<i>Dendroica townsendi</i>	GU931887	GU931994	GU932208	GU932315	EU815816	EU815792	EU815690	GU932101
<i>Dendroica virens</i>	GU931888	GU931995	GU932209	GU932316	EU815817	EU815793	EU815691	GU932102
<i>Dendroica chrysoparia</i>								EU815773
<i>Basileuterus luteoviridis</i>	GU931853	GU931960	GU932174	GU932281	GU932454	GU932537	GU932385	GU932067
<i>Basileuterus leucophrys</i>	GU932359							
<i>Basileuterus flaveolus</i>	GU931849	GU931956	GU932170	GU932277	GU932450	GU932533	AF382994	GU932063
<i>Basileuterus leucoblepharus</i>	GU931852	GU931959	GU932173	GU932280	GU932453	GU932536	GU932384	GU932066
<i>Basileuterus signatus</i>	GU931856	GU931963	GU932177	GU932284	GU932457	GU932540	GU932388	GU932070
<i>Basileuterus nigrocristatus</i>	GU931854	GU931961	GU932175	GU932282	GU932455	GU932538	GU932386	GU932068
<i>Basileuterus fulvicauda</i>	GU931851	GU931958	GU932172	GU932279	GU932452	GU932535	AY340213	GU932065

(continued on next page)

Appendix A (continued)

Taxon	Intron Loci ^b						mtDNA Regions ^c	
	ACO1-9	FGF-5	MUSK-4	MB-2	TGFB2-5	RHO-1	cytb	other mtDNA
<i>Basileuterus rivularis</i>	GU931855	GU931962	GU932176	GU932283	GU932456	GU932539	GU932387	GU932069
<i>Basileuterus bivittatus</i>	GU931842	GU931949	GU932163	GU932270	GU932443	GU932526	GU932376	GU932056
<i>Basileuterus roraimae</i>	GU931843	GU931950	GU932164	GU932271	GU932444	GU932527	GU932377	GU932057
<i>Basileuterus chrysogaster</i>	GU931844	GU931951	GU932165	GU932272	GU932445	GU932528	GU932378	GU932058
<i>Basileuterus conspicillatus</i>	GU931846	GU931953	GU932167	GU932274	GU932447	GU932530	GU932380	GU932060
<i>Basileuterus cinereicollis</i>	GU931845	GU931952	GU932166	GU932273	GU932446	GU932529	GU932379	GU932059
<i>Basileuterus fraseri</i>	GU931850	GU931957	GU932171	GU932278	GU932451	GU932534	GU932383	GU932064
<i>Basileuterus coronatus 1</i>	GU931847	GU931954	GU932168	GU932275	GU932448	GU932531	GU932381	GU932061
<i>Basileuterus coronatus 2</i>	GU931848	GU931955	GU932169	GU932276	GU932449	GU932532	GU932382	GU932062
<i>Euthlypis lachrymosa</i>	GU931841	GU931948	GU932162	GU932269	GU932442	GU932525	GU932375	GU932055
<i>Basileuterus rufifrons</i>	GU931838	GU931945	GU932159	GU932266	GU932439	GU932522	AF383012	GU932052
<i>Basileuterus melanogenys</i>	GU931837	GU931944	GU932158	GU932265	GU932438	GU932521	GU932372	GU932051
<i>Basileuterus belli</i>	GU931834	GU931941	GU932155	GU932262	GU932435	GU932518	GU932370	GU932048
<i>Basileuterus culicivorus</i>	GU931835	GU931942	GU932156	GU932263	GU932436	GU932519	AF383106	GU932049
<i>Basileuterus hypoleucus</i>	GU931836	GU931943	GU932157	GU932264	GU932437	GU932520	GU932371	GU932050
<i>Basileuterus trifasciatus</i>	GU931839	GU931946	GU932160	GU932267	GU932440	GU932523	GU932373	GU932053
<i>Basileuterus tristriatus</i>	GU931840	GU931947	GU932161	GU932268	GU932441	GU932524	GU932374	GU932054
<i>Wilsonia canadensis</i>	GU931914	GU932021	GU932235	GU932342	GU932491	GU932574	GU932415	GU932128
<i>Wilsonia pusilla</i>	GU931915	GU932022	GU932236	GU932343	GU932492	GU932575	GU932416	GU932129
<i>Cardellina rubrifrons</i>	GU931911	GU932018	GU932232	GU932339	GU932488	GU932571	AF383026	GU932125
<i>Ergaticus ruber</i>	GU931912	GU932019	GU932233	GU932340	GU932489	GU932572	GU932413	GU932126
<i>Ergaticus versicolor</i>	GU931913	GU932020	GU932234	GU932341	GU932490	GU932573	GU932414	GU932127
<i>Myioborus pictus</i>	GU931909	GU932016	GU932230	GU932337	GU932486	GU932569	GU932411	GU932123
<i>Myioborus miniatus</i>	GU931906	GU932013	GU932227	GU932334	GU932483	GU932566	AF383015	GU932120
<i>Myioborus brunniceps</i>	GU931900	GU932007	GU932221	GU932328	GU932477	GU932560	GU932405	GU932114
<i>Myioborus flavivertex</i>	GU931904	GU932011	GU932225	GU932332	GU932481	GU932564	AY968876	GU932118
<i>Myioborus albifrons</i>	GU931899	GU932006	GU932220	GU932327	GU932476	GU932559	GU932404	GU932113
<i>Myioborus ornatus</i>	GU931907	GU932014	GU932228	GU932335	GU932484	GU932567	GU932409	GU932121
<i>Myioborus melanocephalus</i>	GU931905	GU932012	GU932226	GU932333	GU932482	GU932565	GU932408	GU932119
<i>Myioborus torquatus</i>	GU931910	GU932017	GU932231	GU932338	GU932487	GU932570	GU932412	GU932124
<i>Myioborus pariae</i>	GU931908	GU932015	GU932229	GU932336	GU932485	GU932568	GU932410	GU932122
<i>Myioborus albifacies</i>	GU931898	GU932005	GU932219	GU932326	GU932475	GU932558	GU932403	GU932112
<i>Myioborus cardonai</i>	GU931902	GU932009	GU932223	GU932330	GU932479	GU932562	GU932406	GU932116
<i>Myioborus castaneocapilla</i>	GU931903	GU932010	GU932224	GU932331	GU932480	GU932563	GU932407	GU932117
<i>Coereba flaveola</i>	GU931922	GU932029	GU932243	GU932350	GU932499	GU932582	GU932423	GU932136
<i>Granatellus pelzelni</i>	GU931923	GU932030	GU932244	GU932351	GU932500	GU932583	AF382995	GU932137
<i>Icteria virens</i>	GU931924	GU932031	GU932245	GU932352	GU932501	GU932584	AF383028	GU932138
<i>Microligea palustris</i>	GU931925	GU932032	GU932246	GU932353	GU932502	GU932585	AF383021	GU932139
<i>Spindalis zena</i>	GU931926	GU932033	GU932247	GU932354	GU932503	GU932586	AF383018	GU932140
<i>Xenoligea montana</i>	GU931927	GU932034	GU932248	GU932355	GU932504	GU932587	AF383022	GU932141
<i>Zeledonia coronata</i>	GU931928	GU932035	GU932249	GU932356	GU932505	GU932588	AF382998	GU932142
<i>Teretistris fernandinae</i>	GU931929	GU932036	GU932250	GU932357	GU932506	GU932589	AF382999	GU932143

^a Accession numbers with the GU prefix are new to this study; others have been previously deposited.

^b Locus abbreviations: ACO1-9, aconitase 1 intron 9; FGF-5, beta-fibrinogen intron 5; MUSK-4, muscle-specific tyrosine kinase intron 4; MB-2, myoglobin intron 2; TGFB2-5, transforming growth factor beta-2 intron 5; RHO-1, rhodopsin intron 1.

^c Cytb, cytochrome b. For most taxa "other mtDNA" is the region spanning the NDII, COL, COII, ATPase8, and ATPase6 genes and their intervening spacer and tRNA regions. For taxa with no other accession numbers, "other mtDNA" is the NDII gene only.

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