INDEPENDENT GEOGRAPHIC ORIGINS OF THE GENUS *AMAZONA* IN THE WEST INDIES

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> "*The distribution of birds is hard to understand but the present pattern is clear enough, although complex. The processes that have produced the present pattern — the evolution and dispersal of birds — are difficult to trace and understand.*" (Darlington 1957)

Abstract.—Nine species of the parrot genus *Amazona* are endemic to the Greater Antilles, Bahamas, and Cayman Islands (*A. leucocephala*, *A. agilis*, *A. collaria*, *A. ventralis*, *A. vittata*) and Lesser Antilles (*A. guildingii*, *A. imperialis*, *A. arausiaca*, *A. versicolor*). Populations of one species, *A. leucocephala*, colonized Cuba, Bahamas, and Cayman Islands resulting in five subspecies. Biogeographic relationships of these Antillean *Amazona* were examined by a reconstruction of their evolutionary history: mitochondrial cytochrome *b* sequence data were analyzed with maximum likelihood, parsimony, and distance methods. Phylogenetic analyses show a distinct divergence of the smaller and mostly green Greater Antillean *Amazona* from the larger, more colorful Lesser Antillean species, and imply that they colonized the West Indies independently. This phylogenetic reconstruction was used to trace potential dispersal routes of ancestral *Amazona* into the West Indies. The species distribution found today in the Lesser Antilles may have been the result of at least two colonization events from South America, one or more of which occurred early in the history of this genus. Data from this study also suggest that there may have been two dispersal events to the Greater Antilles. The Greater Antillean species appear closely related to the small *A. albifrons* of Central America. Evolutionary relationships within the *A. leucocephala* subspecies complex suggest that *A. l. bahamensis* and *A. l. caymanensis* were the first populations of this species to become genetically isolated. Isolation of populations on Cuba (*A. l. palmarum* and *A. l. leucocephala*) occurred later.

Key words: Amazona, *biogeography*, *Caribbean*, *cytochrome* b, *parrots*, *phylogeny*

Resumen.—LOS ORÍGENES GEOGRÁFICOS INDEPENDIENTES DEL GÉNERO *AMAZONA* EN LAS ANTILLAS. Nueve especies de cotorras del género *Amazona* son endémicas en las Antillas Mayores, Bahamas y las islas Caimán (*A. leucocephala*, *A. agilis*, *A. collaria*, *A. ventralis*, *A. vittata*) y las Antillas Menores (*A. guildingii*, *A. imperialis*, *A. arausiaca*, *A. versicolor*). Poblaciones de una especie, *A. leucocephala*, colonizaron Cuba, Bahamas y las islas Caimánn resultando en cinco subespecies. Las relaciones biogeográficas de las especies de *Amazona* de las Antillas fueron examinadas por medio de una reconstrucción de su historia evolutiva: secuencias de citocromo *b* mitocondrial fueron analizadas utilizando métodos de parsimonia, máxima verosimilitud y de distancia. Análisis filogenéticos muestran una marcada divergencia entre las especies de las Antillas Mayores, que tienen menor tamaño corporal y plumaje predominantemente verde, y las especies de las Antillas Menores, que tienen plumajes más coloridos. Esta divergencia implica que los dos grupos colonizaron los Antilles independientemente. Esta reconstrucción filogenética fue utilizada para trazar rutas potenciales de dispersión de las *Amazona* ancestrales por las Antillas. La presente distribución de especies en las Antillas Menores podría ser resultado de por lo menos dos colonizaciones desde Sudamérica, y por lo menos una de éstas ocurrió temprano en la historia del género. Datos de este estudio también sugieren la posibilidad de dos eventos de dispersión a las Antillas Mayores. Las especies de las Antillas Mayores están estrechamente relacionadas con *A. albifrons*, una especie relativamente pequeña de Centroamérica. Relaciones evolutivas dentro del complejo de *A. leucocephala* sugieren que *A. l. bahamensis* y *A. l. caymanensis* fueron las primeras poblaciones de esta especie en aislarse genéticamente. El aislamiento de las poblaciones de Cuba (*A. l. palmarum* y *A. l. leucocephala*) ocurrió más tarde.

Palabras clave: Amazona, biogeografía, Caribe, citocromo b, *cotorras, filogenia*

Résumé.— ORIGINES GÉOGRAPHIQUES INDÉPENDANTES CHEZ LE GENRE *AMAZONA* DANS LES ANTILLES. Neuf espèces de perroquets du genre *Amazona* sont endémiques des Grandes Antilles, des Bahamas et des îles Cayman (*A. leucocephala*, *A. agilis*, *A. collaria*, *A. ventralis*, *A. vittata*) et des Petites Antilles (*A. guildingii*, *A. imperialis*, *A. arausiaca*, *A. versicolor*). Des populations d'une espèce, *A. leucocephala*, ont colonisé Cuba, les Bahamas et les îles Cayman, donnant naissance à cinq sous-espèces. Les relations biogéographiques entre ces amazones antillaises ont été étudiées par la reconstruction de leur histoire évolutive. Les données de séquences du cytochrome *b* mitochondrial ont été étudiées par les méthodes du maximum de vraisemblance, de parcimonie et de distance. Les analyses phylogénétiques montrent une divergence entre les amazones des Grandes Antilles, plus petites et à dominante verte, et les espèces plus grandes et colorées des Petites Antilles, ce qui indiquent qu'elles ont colonisé les Antilles indépendamment. Cette reconstruction phylogénétique a été utilisée pour tracer les routes potentielles de dispersion des amazones ancestrales dans les Antilles. La distribution des espèces observées aujourd'hui dans les Antilles pourrait être le résultat d'au moins deux événements de colonisation depuis l'Amérique du Sud, l'un d'entre eux, ou plusieurs, étant survenu très précocement dans l'histoire du genre. Les données de cette étude suggèrent qu'il pourrait y avoir eu aussi deux événements de dispersion dans Les Grandes Antilles. Les espèces des Grandes Antilles apparaissent étroitement reliées au petit *A. albifrons* d'Amérique Centrale. Les relations évolutives du complexe de sous-espèces de *A. leucocephala* suggèrent que *A. l. bahamensis* et *A. l. caymanensis* ont été les premières populations de cette espèce à avoir été génétiquement isolées. L'isolement des populations de Cuba (*A. l. palmarum* et *A. l. leucocephala*) est survenue plus tard.

Mots-clés: Amazona, *biogéographie*, *Caraïbe*, *cytochrome* b, *perroquets*, *phylogénie*

INTRODUCTION

THE WEST INDIES and its unique avian fauna fascinated early zoogeographers (Du Tertre 1654, 1667; Denny 1847a,b; Léotaud 1866; Sclater 1891; Arldt 1936; Berlioz 1959a,b; as summarized in Wiley 2000). A distinctive feature of the West Indian avifauna is the widespread distribution of the parrot genus *Amazona*; it is better represented than any other parrot genus. Although the source of *Amazona* in the West Indies is believed to be from the mainland the details of their colonization patterns are unclear.

We will first introduce the study area and summarize its geologic history. We then outline hypotheses regarding the colonization of the West Indies by birds and other fauna, and their evidence and limitations relevant to this project. Next, we discuss the history of the genus *Amazona*. Finally, we present new molecular data that we use in this study to fill gaps in the knowledge of the phylogeography of West Indian *Amazona*. These data are corroborated with previous studies on comparative plumage characteristics.

Study Area

Here, we adopt the description of the West Indies (Fig. 1) as those islands that are in the Greater and Lesser Antillean faunal regions (see review in Morgan 2001). The Lesser Antillean faunal region includes the northern-most island of Anguilla to the southern-most island of Grenada. The Greater Antillean faunal region includes the four major islands of Cuba, Hispaniola (Haiti and Dominican Republic), Jamaica, and Puerto Rico and their satellite islands (e.g., Isla de Pinos and Culebra); the Cayman Islands; the Bahamas (all islands of the Bahamas archipelago and the Turks and Caicos Islands); and the Virgin Islands. The Anegada Passage is a 100-km water barrier between the Greater Antilles (Puerto Rican Bank) and the Lesser Antilles (St. Martin Bank). In this discussion, we exclude those islands off the northern coast of South America (Trinidad, Tobago, Isla de Margarita, Aruba, Bonaire, and Curaçao).

Vertebrate Colonization of the West Indies

Many authors have explored the modes and sources of vertebrate colonizations of the West Indies (e.g., Darlington 1957; Bond 1963, 1979; Lack 1976; Ricklefs and Cox 1978; Terborgh *et al*. 1978; Pregill 1981; Morgan and Woods 1986; Kluge 1988; Hedges *et al*. 1992; Hedges 1996; Iturralde-Vinent and MacPhee 1999). The two principal theories that have been used to explain the origins of island species are overwater dispersal and vicariance (fragmentation of habitats). Island vicariance can occur by geologic factors (plate tectonics) or sea level changes that can result in the isolation of ancestral biota (Morgan 1994). We will briefly present arguments for and against vicariance and overwater dispersal as potential colonization modes of the West Indies.

Interest in a vicariant faunal history of the West Indies resulted from emerging evidence of eastward tectonic movement of the Caribbean plate during

* Grand Cayman, Cayman Brac, and Little Cayman

** Not included in this study

Fig. 1. Distribution of *Amazona* in islands where they reside. Extinct species and previous distributions known from prehistoric and historic evidence (as reviewed in Williams and Steadman 2001) include: *A. vittata* (Barbuda and Antigua), *A. vittata gracilipes* (Culebra), *A. violacea* (Guadeloupe), *A.* cf. *violacea* (Marie-Galante), *A. martinicana* (Martinique), *A. leucocephala bahamensis* (Grand Turk, Fortune, Long, Acklins, New Providence, and Crooked islands, Bahamas), and *A. leucocephala hesterna* (Little Cayman, Cayman Islands). There is evidence of *Amazona* (undescribed species) on Montserrat, Grand Turk, and Grenada. These extinct and undescribed species of *Amazona* are not shown, however, the names of these islands are shown in this figure.

the late Cretaceous to early Tertiary (e.g., Malfait and Dinkelmann 1972; see Table 1 for an outline of geologic time intervals discussed here and below), carrying with it a proposed archipelago (Greater Antilles) that initially lay between South and Central America, and its ancestral mainland biota (Croziat *et al.* 1974, Rosen 1976). However, there is no evidence that these early emergent lands survived as permanent islands into the Late Eocene (continent-island vicariance; Iturralde-Vinent and Mac Phee 1999).

More recent tectonic models of the eastward movement of the Caribbean plate (e.g., Pindell *et al.* 1988) stimulated further interest in vertebrate colonization of the West Indies. Two terrestrial connections may have existed at alternate times between Central America and the Greater Antilles during the early Tertiary: 1) Cuba was connected with the Yucatan Peninsula and 2) Jamaica and Honduras were connected by the Nicaraguan Rise (Donnelly 1988). Direct paleontologic evidence of early Eocene terrestrial mammals in Jamaica (e.g., *Hyrachyus*; Domning *et al.* 1997) indicates that emergent land between western Jamaica and the eastern end of the Nicaraguan Rise may have provided a corridor for immigration of such terrestrial biota (as reviewed in Portell *et al.* 2001). Both of these connections were, however, submerged by the middle Tertiary (30 million years before present; mybp), creating overwater distances of approximately 350 km across the Nicaraguan Rise and 150 km between Cuba and the Yucatan Penin-

Table 1. Geologic time scale is given in years before present (approximate dates after Feduccia 1996). Divisions of the geologic time scale are shown here as Eras (Cenozoic and late Mesozoic), Periods (Quaternary, Tertiary, and Late Cretaceous), and Epochs (Paleocene through Holocene).

Era	Period	Epoch	Approximate years before present
Cenozoic	Quaternary	Holocene	Recent–10,000
		Pleistocene	10,000–2,000,000
	Tertiary	Pliocene	2,000,000–5,000,000
		Miocene	5,000,000–23,000,000
		Oligocene	23,000,000–34,000,000
		Eocene	34,000,000–55,000,000
		Paleocene	55,000,000–65,000,000
Mesozoic	Late Cretaceous		65,000,000–100,000,000

sula (Fig. 1; Donnelly 1988). The mammalian fossil record and recent geologic evidence are also consistent with the opinion that there was a short-lived corridor (Aves Ridge — continuous or punctuated by short water gaps) between the developing Greater Antilles and northwestern South America (Eocene-Oligocene interval of 35–33 mybp)(as reviewed in Iturralde-Vinent and MacPhee 1999). Subsidence and subdivision of this corridor (island-island vicariance; Iturralde-Vinent and MacPhee 1999) would have occurred, however, before the more recent divergences of avian genera and species in the Miocene, Pliocene, and early Pleistocene (Wetmore 1951, Haffer 1985, Feduccia 1995). A vicariant hypothesis of colonization would not apply to the Lesser Antilles because this volcanic archipelago developed essentially in their current position from the Miocene to Recent (Donnelly 1988).

Early viewpoints of avian colonization in the West Indies suggested occurrences of dispersal events from the mainland (Darlington 1957, Bond 1963, Lack 1976). Bond (1963, 1979) concluded that bird species from South America colonized the West Indies relatively recently, from the south through the Lesser Antilles and Trinidad (by definition, not in Lesser Antilles) and from the west through Jamaica. The source for most of the Greater Antilles was Central America (Darlington 1957; Bond 1963, 1979). Comparisons of plumage characteristics between the West Indian species of the parrot genus *Aratinga* and those from South and Central America indicated two distinct invasions into the Greater Antilles (Marien and Koopman 1955), apparently from the Yucatan Peninsula and the Honduran-Nicaraguan Bulge (Lantermann 1997). Hummingbird distribution patterns in the West Indies suggest that colonization events were from Central America into the Greater Antilles and Bahamas and from South America into the Lesser Antilles (Schuchmann 1980). Several species of bats (e.g., *Natalas* spp.) and non-volant mammalian species also show a similar biogeographic pattern within the West Indies (Morgan and Woods 1986; Morgan 2001; Morgan, pers. com.). A biogeographic break at the Anegada Passage (Fig. 1) appears to exist for many, but not all (see Results and Discussion: Biogeographic junction between the Lesser and Greater Antilles), avian and bat species at the northern end of the Lesser Antilles (Antigua and Barbuda) and the eastern-most extension of the Greater Antillean faunal region (Puerto Rico and Virgin Islands; Bond 1963, Ricklefs and Cox 1972, Morgan 2001).

Phylogenetic data are useful for reconstructing geographic and historic patterns of colonization. Multiple colonizations from different geographic sources will result in a phylogeographic pattern that appears random (polyphyly). A stepping-stone model of colonization, however, involves a single mainland source of dispersal resulting in monophyly of island taxa (as reviewed in Klein and Brown 1994). Recent examinations of inferred phylogenetic relationships have found both polyphyly and monophyly of several avian taxa within the West Indies (Klein and Brown 1994, Seutin *et al.* 1994, Hunt *et al.* 2001).

Fossil and Zooarcheologic History of New World Parrots

Olson (1989) hypothesized that parrots originated in the Southern Hemisphere and became established in the Northern Hemisphere sometime in the early Miocene. The earliest New World parrot fossil, *Conuropsis fratercula*, was found in North America (Nebraska) from the Miocene (late Hemingfordian, 16.1 ± 3.7 mybp) (Wetmore 1926; as reviewed in Wetmore 1956, Olson 1985, Becker 1987). Only Pleistocene parrot fossils, including *Amazona amazonica* (Brazil) and *Amazona farinosa* (Peru), have been found in South America (Brodkorb 1971, Campbell 1976, Cuello 1988). Records from the West Indies include: 1) Pleistocene fossils of the extinct macaw, *Ara tricolor*, in Cuba (Wetmore 1928, 1956; Brodkorb 1971; Arredondo 1984); 2) the extinct *Ara autocthones* in prehistoric kitchen middens on St. Croix, Virgin Islands (Wetmore 1937, 1956); and 3) an undated-parrot rostrum from Barbuda (Williams and Steadman 2001). Remains of *Amazona leucocephala* are reported in several Pleistocene cave deposits on New Providence, Bahamas (Brodkorb 1959, 1971; Olson 1978; Olson and Hilgartner 1982) and Cayman Brac, Cayman Islands (Morgan 1994); a pre-Columbian bone on Crooked Island, Bahamas (Wetmore 1938, Olson and Hilgartner 1982); and a Quaternary tibiotarsus from Cueva del Campamento, Cuba (Díaz Franco 1999).

Our ability to determine the origins of many island vertebrate species and processes of their evolution are confounded by pre-historic and historic human activities: archeologic evidence suggests movement of West Indian vertebrates among the islands (Pregill *et al.* 1988). Parrots in particular were transported between islands by pre-Columbian Indian cultures (Olson 1982), and there is evidence that some were consumed for food (Du Tertre 1654, 1667; as reviewed in Clark 1905a; Wetmore 1917). Localized and complete extinctions of vertebrate species followed Amerindian (4500 to 500 years before present; ybp) and post-Columbian (500 ybp) colonizations (Olson 1978; Olson and Hilgartner 1982; Steadman *et al.* 1984; Morgan and Woods 1986; Pregill *et al.* 1988, 1994; Morgan 1994; James 1995). Early writings (Clark 1905a,b), along with zooarcheologic (Williams and Steadman 2001) and fossil evidence (see above), suggest a formerly more expanded distribution of parrot taxa in the West Indies, but they do not reveal their place of origin.

At least three parrot genera were found in the West Indies: *Ara* (macaw), *Amazona*, and *Aratinga* (parakeet) (Wiley 1991, Williams and Steadman 2001). Although controversial, there is evidence of a fourth genus, *Anodorhynchus* (macaw), in the Lesser Antilles (Snyder *et al.* 1987, Williams and Steadman 2001). An estimated 50–60 endemic species of parrots are thought to have occurred in the region (Williams and Steadman 2001) before human influence. At the time of Columbus's discovery of the West Indies, nearly 28 species were found; only 12 of them (species of *Amazona* and *Aratinga*) remain today (Wiley 1991).

Current New World Parrots and Amazona

The family Psittacidae includes all the New World species and comprises two distinct monophyletic groups—species with short tails and those with long tails—that emerged during the Eocene (approximately 50 mybp) (Miyaki *et al.* 1998). Species of *Amazona* have short tails and are from 23 to 45 cm in length. They have a naked, prominent cere above a strong and heavy bill, a distinct notch in the upper bill, short-broad rounded wings, and diverse plumages (Snyder *et al.* 1987, Forshaw 1989, Collar 1997, Juniper and Parr 1998).

The genus *Amazona* includes approximately 30 recognized extant species (Forshaw 1989, Collar 1997, Juniper and Parr 1998). The greatest diversity of *Amazona* occurs in South America, and it was also highly successful in colonizing Central America (Forshaw 1989). *Amazona* is one of two parrot genera in the Neotropics where sympatric species co-occur, and in many places three or four species overlap ranges (Collar 1997).

Amazona *of the Greater and Lesser Antilles*

The nine extant West Indian *Amazona* (Fig. 1) include the smaller species in the Greater Antilles, Cayman Islands, and Bahamas (*A. agilis*, *A. collaria*, *A. leucocephala*, *A. ventralis*, *A. vittata*) and the larger species in the Lesser Antilles (*A. arausiaca*, *A. guildingii*, *A. imperialis*, *A. versicolor*; Forshaw 1989, Wiley 1991, Raffaele *et al.* 1998). In the Greater Antilles, Jamaica has two sympatric species (*A. agilis* and *A. collaria*) and in the Lesser Antilles, Dominica has two sympatric species (*A. arausiaca* and *A. imperialis*; Lack 1976, Collar 1997).

Amazona leucocephala is represented by five subspecies in Cuba, the Cayman Islands, and the Bahamas (Fig. 1; reviewed in Wiley 1991). *Amazona leucocephala leucocephala* is found mainly in eastern Cuba and *A. l. palmarum* occurs in western Cuba and off the southwestern coast, on Isla de Pinos (Isla de la Juventud). Two subspecies occur in the Cayman Islands: *Amazona l. caymanensis* on Grand Cayman and *A. l. hesterna* on Cayman Brac and previously on Little Cayman. Currently two populations

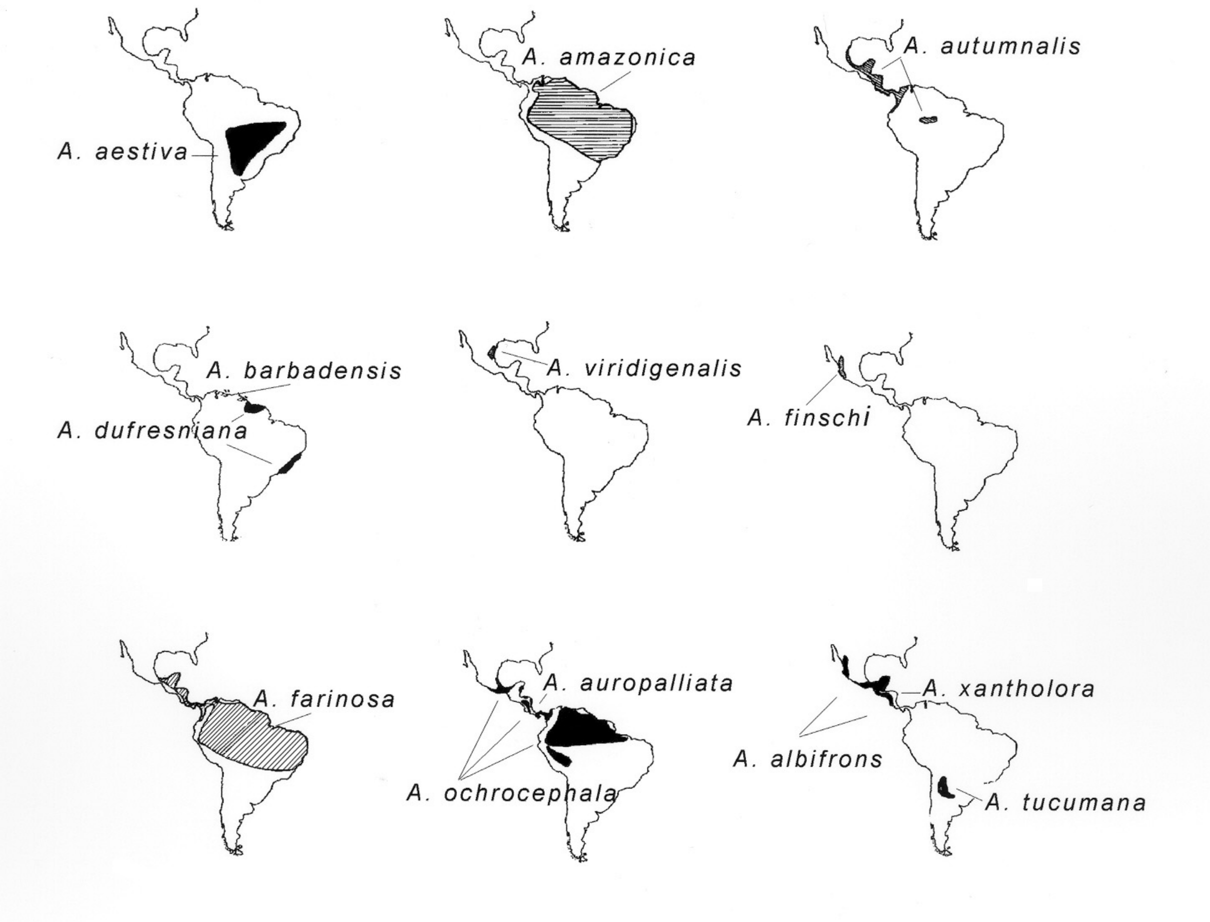

Fig. 2. Mainland distribution of *Amazona* included in this study. Ranges are estimated from Forshaw (1989). *Amazona tucumana* and *A. xantholora* are mentioned in the text but are not included in this study.

of *A. l. bahamensis* survive: one on Abaco (Schröder 1988, Gnam 1991, Gnam and Burchsted 1991) and one on Great Inagua (Snyder *et al.* 1982, Gnam 1990, Gnam *et al.* 1995).

Archeologic evidence and historic accounts suggest a wide distribution of *Amazona* throughout the Lesser Antilles (see review in Williams and Steadman 2001). For example, an undetermined large species of *Amazona* occurred on Grenada (Du Tertre 1667; as mentioned in Snyder *et al.* 1987 and Butler 1992; reviewed in Williams and Steadman 2001). *Amazona violacea* from Guadeloupe (based on writings of DuTertre 1654, 1667; Labat 1722, 1724, 1742; Brisson 1760; as compiled in Clark 1905a and Wiley 2000) and, perhaps, *A.* cf. *violacea* from Marie-Galante (Williams and Steadman 2001) appeared to share a striking purple plumage with *A. imperialis* of Dominica (Clark 1905a). Apparently, *Amazona violacea* was larger than *A. imperialis* and had a red eye ring (Clark 1905a), however, plumage descriptions of these extinct species of *Amazona* do not clearly determine if they are unique species or the same species. Another extinct species from Martinique, *A. martinicana* (Clark 1905a), was large and resembled *A. versicolor* (St. Lucia) and *A. arausiaca* (Dominica). The plumage of the head was mostly slate-colored with a small amount of red (based on account of Labat 1722; reviewed in Forshaw 1989 and Williams and Steadman 2001). *Amazona martinicana* may have been related to these two species and its colonization was part of a radiation among the more central islands of the Lesser Antilles.

Plumage characteristics and morphometric measurements suggest a close relationship of the Greater Antillean species of *Amazona* (Fig. 1) with the Central American *A. albifrons* and *A. xantholora* (Fig. 2; Lack 1976, Snyder *et al.* 1987, Wiley 1991, Lantermann 1997), which are thought to be sibling species (Paynter 1955). Several authors (Bond 1963, Lack 1976, Snyder *et al.* 1987, Wiley 1991, Lantermann 1997) favor two colonizations of the Greater Antilles from Central America (e.g., Yucatan Peninsula and Honduran-Nicaraguan Bulge). Movement of parrots into the Lesser Antilles (Fig. 1) was probably from South America (Bond 1963, Snyder *et al.* 1987, Lantermann 1997). The relationship among the Lesser Antillean *Amazona* and South American species appears complex based on their plumage patterns (Snyder *et al.* 1987, Forshaw 1989, Collar 1997, Juniper and Parr 1998). Plumage characteristics have proven useful in establishing relationships; however, such analyses have been difficult because the evolution of parrot plumage patterns is not well understood (Snyder *et al.* 1987). Comprehensive studies of species of *Amazona* are few, making comparative analyses difficult (Snyder *et al.* 1987, Lousada and Howell 1996; and see reviews in Gnam 1991, Enkerlin-Hoeflich 1995, Koenig 1999).

Molecular Data

Molecular data provide another means of estimating the relationships of organisms (Avise 2000) because nucleotide sequences carry information about the taxa's historical past (Zuckerandl and Pauling 1965). Mitochondrial DNA sequences (e.g., cytochrome *b* gene) provide a source of characters for studying systematics (Wilson *et al.* 1985) and biogeography (as reviewed in Avise 2000).

We attempt to provide the best estimate of the relatedness of the West Indian *Amazona* with several mainland species by reconstructing a phylogeny using cytochrome *b* sequence data. We combine this analysis with current distribution patterns of *Amazona* to propose a hypothesis of their historic movements into the West Indies. Finally, we evaluate plumage characteristics from mainland and island species to determine whether they support the molecular phylogeny presented here.

MATERIALS AND METHODS

Samples and Permits

We provide a list of all individuals sampled for this study in Table 2, which includes sample types, source of samples, voucher identification (deposited with George Amato, Wildlife Conservation Society of New York), permit identification numbers, sequence length, and GenBank accession numbers. Permits (Convention for International Trade of Endangered Species, CITES I & II) were obtained and regulations were followed for the importation of samples obtained from outside the United States (Littell 1993). The U.S. Fish and Wildlife Service was consulted for appropriate procedures regarding the transfer of samples within the United States.

Samples were collected from wild and captive birds. Ornithologists from established institutions collected samples from wild birds (Table 2). We collected feathers from *A. leucocephala palmarum* in Cuba (Isla de Pinos) and *A. l. caymanensis* in the Cayman Islands (Grand Cayman). On Isla de Pinos, juvenile parrots were removed from nests by Cuban scientists from the Empresa Nacional para la Protección de la Flora y Fauna. Two to three contour pinfeathers were extracted with sterile forceps from each individual and placed in 80% ethanol. Previous studies indicated that removal of a primary wing pinfeather does not affect nestling survival (Stangel and Lennartz 1988) but we chose to take smaller contour feathers to decrease discomfort to the nestling parrots. In the Cayman Islands, with assistance from F. Burton and the National Trust of the Cayman Islands, we collected individual feathers (*A. leucocephala caymanensis*) from road kills (wild birds) and private aviary collections (captive birds).

Samples (captive birds) from zoological institutions and private aviaries were predominately feathers, although several blood samples, and one liver and one skin sample (deceased birds) were used. No birds were harmed or sacrificed for collection of any samples.

Categorization of samples from captive birds include: 1) wild-caught birds that were transferred to a zoological institution within the same country or island, 2) wild-caught birds that were transferred from their place of origin to a zoological institution of a different country or island, and 3) pet or avicultural birds (Table 2). Reputable scientists made taxonomic identifications of the captive birds (categories one and two), and supervised the collection of samples for this study.

In the Bahamas, the Bahamas National Trust (supervised by M. Isaacs and E. Carey) transferred *A. l. bahamensis* captive birds (category 2) from their island of origin. Wardens transported parrots from Great Inagua to the Ardasta Zoo (New Providence) for a captive-breeding program. The single captive bird from Abaco was removed from a nest and transferred to Rand Nature Center on Grand Bahama. The Great Inagua parrot is distinct from the Abaco parrot: there are more white feathers on

Table 2. Species list, sample information, DNA sequence information, permit documentation (i.e., Convention on International Trade of Endangered Species, CITES; Endangered Species Act, ESA), voucher identification, and GenBank accession numbers.

Short/Long sequences* (# of individuals)	Species/ taxonomic names	Date received	Permits		Sample	Collectors, affiliations, origin of sample, voucher identifications and GenBank accession # [1,2,3,4,5]
			Export	Import		
Long (3); Short (1)	*A. aestiva* (Linnaeus) 1758	1994	***	***	S/B/Se	B. Ritchie, N. Pritchard, D. Pesti, F. Niagro; Department of Medical Microbiology and School of Veterinary Medicine, University of Georgia, GA (UGA); (captive birds 3); UGA ID# BLFR1056 (AY283469), BLFR2009 (AY 283472), BLFR78-72 (AY 283448), BLFR78-73 (AY283497)
Long (1); Short (1)	*A. agilis* (Linnaeus) 1758	1996	CITES II: JM533	**	F	S. Koenig, C. Levy; Gosse Bird Club and Ministry of Agriculture (GBC and MA), Kingston, Jamaica; (captive birds 1); BBPA1 [AMCC#110724] (AY283515), BBPA2 (AY283489)
Long (1); Short (3)	*A. albifrons* (Sparrman) 1788	1996	CITES II: 12582	**	F	E. Enkerlin Hoeflich; Instituto Tecnológico y de Estudios Superiores de Monterrey (ITESM); Corrillo Pto., Quintana Roo, Mexico; (wild birds); AMAL2 (AY283450), AMAL3 (AY283449), AMAL4 (AY283506), AMAL5 (AY283492)
Short (1)	*A. amazonica* (Linnaeus) 1766	1995	CITES II: 95/291	**	F	M. Isaacs, E. Carey; Ministry of Agriculture (MA), Bahamas; P. Weeks, L. Gapes; Ardasta Zoo (AZ), Bahamas National Trust (BNT), Nassau, Bahamas; (captive bird 2); ORWI1 (AY283516)
Long (2); Short (2)	*A. arausiaca* (Muller) 1776	1995	No certificate #	CITES I: 795191	F	A. Christian; Ministry of Agriculture and Botanical Gardens (MA and BG); Roseau, Dominica; (captive birds 1); Leg Band ID# RETH102 (AY283464), RETH006 (AY283465), RETH004 (AY283445), RETH009 (AY283446)
Short (1)	*A.*[*ochrocephala*] *auropalliata* (Lesson) 1842	1994	***	***	F	R. Bellon; New Jersey Bird Club, NJ; (captive bird 3); YENA1 (AY283447)
Long (3)	*A. autumnalis* (Linnaeus) 1758	1996	CITES II: 12582	**	F	E. Enkerlin Hoeflich; ITESM; Tamaulipas, Mexico; (wild birds); RELO1 (AY283456), RELO2 [AMCC#110732] (AY283455)
		1994	***	***	S	B. Ritchie, N. Pritchard, D. Pesti, F. Niagro; UGA; (captive bird 3); UGA ID # RELO116 (AY283453)
Long (2)	*A. barbadensis* (Gmelin) 1788	1993	***	***	L	S. Rabinowitz, G. Amato; Wildlife Conservation Society of New York (WCS); Margarita Island, Venezuela; (wild birds); BARB1 [AMCC#110761] (AY283463), BARB2 [AMCC #110734] (AY283462)
Long (2)	*A. collaria* (Linnaeus) 1758	1996	CITES II: JM533	**	F	S. Koenig, C. Levy; GBC and MA, Kingston, Jamaica; (captive birds 1); YBPA2 [AMCC#110735] (AY283494), YBPA4 [AMCC#110762] (AY283493)
Long (1)	*A. dufresniana* (Shaw) 1812	1993	***	***	F	D. Rimlinger; The Zoological Society of San Diego (ZSSD) CA; (captive bird 2); BLCH1 [AMCC#110736] (AY283454)
Long (1)	*A. farinosa* (Boddaert) 1783	1997	***	***	F	JRE, H. de Espinosa; Smithsonian Tropical Research Institute, Balboa, Panama, Chiriqui, Western Panama (captive bird 3); STRI-X-21 (AY283475; AY194413)

Table 2. (Continued).

Short/Long sequences* (# of individuals)	Species/ taxonomic names	Date received	Permits		Sample	Collectors, affiliations, origin of sample, voucher identifications and GenBank accession # [1,2,3,4,5]
			Export	Import		
Long (1)	*A. finschi* (Sclater) 1864	1994	***	***	B	B. Ritchie, N. Pritchard, D. Pesti, F. Niagro; UGA; (captive bird 3); UGA ID # LILC2016 [AMCC#110741] (AY283461)
Long (2)	*A. guildingii* (Vigors) 1837	1993	***	***	B	S. Rabinowitz, G. Amato; WCS; St. Vincent; (captive birds 2); STVI1 (AY283459), STVI2 (AY283460)
Long (2)	*A. imperialis* Richmond 1899	1995	No certificate. #	CITES I: 795191	F	A. Christian; MA and BG; Roseau, Dominica; (captive birds 1); Leg Band # IMPE051 (AY283457), IMPE110 [AMCC#110743] (AY283458)
Long (1)	*A. leucocephala bahamensis* (Bryant)	1995	CITES I: 89/698	CITES I: 735115	F	RG; American Museum of Natural History (AMNH), NY; (wild bird; Abaco); BAPA(A)RG, AMNH#18276, (AY283480)
Long (1)		1993	CITES I: 95/168	CITES I: 796145	F	R. Oliver; Rand Nature Ctr. BNT, Freeport, Bahamas; (captive bird 2; Abaco); BAPA(A)RO (AY283481)
Long (2); Short (1)	*A. leucocephala bahamensis* (Bryant)	1995	CITES I: 95/168;292	CITES I: 796145	F	M. Isaacs, E. Carey; MA; P. Weeks, L. Gapes; AZ and BNT, Bahamas; (captive birds 2; Inagua); BAPA(I)1 (AY283484), BAPA (I)2 (AY283513), BAPA(I)3 (AY283482)
Long (3)	*A. leucocephala caymanensis* (Cory)	1995	CITES I: 001006	CITES 1: 798252	F	F. Burton; National Trust Cayman Islands, Grand Cayman Island (GCI); (wild birds); CAMA(RK5-91) (AY283490), CAMA1 (AY283483), CAMA3-3B (AY283500)
Short (2)		1995	US Captive Bred	ESA-PRT: 774895	B	J. Maly; Maly Parrot Farm, Kingwood, TX; (captive birds 3); Leg ID # CAMA084 (AY283495), CAMA91-95 (AY283501)
Short (2)		1995	CITES I: 001006	CITES 1: 798252	F	O. Watler; GCI; (captive birds 3); CAMA(O)1 (AY283504), CAMA(O)5 (AY283505)
Long (2)	*A.* [*leucocephala*] *leucocephala* (Linnaeus 1758)	1993	***	***	F	D. Rimlinger; ZSSD, CA; (captive birds 2); CUAM (L)1 [AMCC#110744] (AY283487), CUAM(L)2 (AY283488)
Long (4); Short (5)	*A. leucocephala palmarum* Todd	1995	CITES I: 00272	CITES I: 799196	PF	PW, XG, RG, JW; Los Indios, Isla de Pinos, Cuba; (wild birds); CUAM(P)1 (nest 3813) (AY283509), CUAM(P)6 (nest 3898) (AY283511), CUAM(P)2 (nest 1878) (AY283478), CUAM(P)3 (nest 3303) (AY283476), CUAM(P)4 (nest 3825) (AY283477), CUAM(P)5 (nest 3335) (AY283479), CUAM(P)7 (nest 3321) (AY283512), CUAM(P)21 (AY283510), CUAM(P)14 (AY283508)
Long (2)	*A. ochrocephala* (Gmelin) 1788	1994	***	***	B; F	B. Ritchie, N. Pritchard, D. Pesti, F. Niagro; UGA; (captive bird 3); UGA ID # YEHE2014 (AY283467); O. Sanfur; NJ; (captive bird 3); YEFR1 [AMCC#110763] (AY283471)
Long (1); Short (1)	*A.* [*ochrocephala*] *oratrix* Ridgway 1887	1996	CITES II: 12582	**	F #1 & 2	E. Enkerlin Hoeflich; ITESM; Ebano, Mexico; (wild bird); (same individual) DBYE (F1) (AY283470), DBYE (F2) (AY283503)
Long (1)	*A. ochrocephala tresmariae* Nelson	1996	CITES II: 12582	**	F	E. Enkerlin Hoeflich; ITESM; Islas Marias, Mexico; (wild bird); AOTR2 (AY283468)
Long (3)	*A. ventralis* (Muller) 1776	1988	***	***	BF	B. Ritchie; UGA; Atlanta Zoo, GA; (captive bird 2); AMVE1 (AY283473)

Table 2. (Concluded).

Short/Long sequences* (# of individuals)	Species/ taxonomic names	Date received	Permits		Sample	Collectors, affiliations, origin of sample, voucher identifications and GenBank accession # [1,2,3,4,5]
			Export	Import		
		1996	***	***	F	M. Herzog, A. Smith; Puerto Rican Parrot Project (PRPP), US Fish and Wildlife Service, (USFWS), PR; (captive birds 2); Leg Band ID# AMVE154 (AY283486), AMVE164 [AMCC #110752] (AY283474)
Long (1)	*A. versicolor* (Muller) 1776	1996	CITES I: 0088	CITES I: 795190	F	D. Anthony; Ministry of Agriculture and Forestry Department, Castries, St. Lucia; (captive bird 1); STLU(OS) [AMCC #110753] (AY283466)
Short (2)	*A. viridigenalis* (Cassin) 1853	1995	CITES I: 12582	CITES I: 38288/9	F	E. Enkerlin Hoeflich; ITESM; Ebano, Mexico; (wild birds); GRCH5 [AMCC#110755] (AY283451), GRCH125 (AY283452)
Long (2); Short (3)	*A. vittata* (Boddaert) 1783	1995	***	***	F	M. Herzog; PRPP, USFWS, PR; (captive birds 1); Leg Band ID# PRPA008 (AY283507), PRPA061 [AMCC#110756] (AY283491), PRPA103 (AY283502), PRPA107 (AY283485), PRPA502 (AY283514)
	Outgroups:					
Long (1)	*Pionus menstruus* (Linnaeus) 1766	1996	***	***	F	K. and R. Gifford; ME; (captive bird 3); PIME1 (AY283496)
Long (1)	*Poicephalus gulielmi*	1994	***	***	F	PW; (captive bird 3); PUMB1 [AMCC#110759] (AY283498)
Long (1)	*Deroptyus accipitrinus* (Linnaeus) 1758	1996	***	***	F	NJ Bird Club; (captive bird 3); DEAE1 (AY283499)

Sample type: B = Blood, BF = Blood Feather, F = Feather, L = Liver, S = Skin, and Se = Serum.

[1] In some cases: leg band number, institution identification number, or nest number.

[2] Voucher DNAs and samples are placed with G. Amato, Wildlife Conservation Society, NY and the American Museum of Natural History, NY: Ambrose Monnel Cryo Collection [AMCC#xxxxxx]

[3] Wild bird samples were collected from the field.

[4] Captive bird samples include: (captive bird 1) wild-caught birds transferred to a zoological institution of the same country or island; (captive bird 2) wild-caught birds transferred from their place of origin to a zoological institution of a different country or island; (captive bird 3) pet or avicultural birds.

[5] GenBank Accession # (AYxxxxxx)

* Long DNA sequences are 1101 base pairs in length and short DNA sequences are 596 base pairs in length.

** U.S. import permits are not required for species listed as CITES II.

*** No U.S. permits required for intrastate or interstate exchange of samples. The *A. farinosa* sample and DNA were processed and are located at the Smithsonian Tropical Research Institute, Balboa, Panama.

Table 3. The name of the primer includes the designation for the light (L) chain and heavy (H) chain of the cytochrome *b* gene. The approximate position relative to the 3′ end of the chicken mitochondrial DNA sequence is given herein as the primer name (Desjardins and Morais 1990). Various combinations of these primers were used to amplify the cytochrome *b* fragments and determine their nucleotide sequence. Several primers were numbered in original publications according to their approximate position in the human mitochondrial DNA sequence (second number; Anderson *et al.* 1991): L14990 = L14841, L15311 = L15162, L15506 = L15362, L15656 = L15507, H15104 = H14955, H15298 = H15149, H15710 = H15561, and H16062 = H15915.

Primer name	Nucleotide sequence (5′ to 3′)	Source
Light Chain		
L14990	CCATCCAACATCTCAGCATGATGAAA	Kocher *et al*. 1989, Helm-Bychowski and Cracraft 1993
L15311	CTACCATGAGGACAAATATC	Irwin *et al*. 1991, Helm-Bychowski and Cracraft 1993
L15506	CTCACCTTCCTACACGAAACAGG	Helm-Bychowski and Cracraft 1993
L15656	AACCTACTAGGAGACCCAGA	Helm-Bychowski and Cracraft 1993
L15562	GACAAAATCCCATTCCACCC	This study
L15762	ATCCTACGCTCAATCCCCAACAAACTG	This study
L15866	CCTTCCGCCCCCTCTCACAACTC	This study
L15417	GGTGGCTTCTCAGTGGACAACCCAA	This study
L15985	TAACCTACTTCACCATCCTACTA	This study
L15039	ACTGACACAAATCCTAACAG	This study
L15288	AGCAACTGCCTTCGTAGGATA	This study
L15010	ACTTCGGATCTCTCCTAGG	This study
L15219	CTTCATCTGCATCTACCT	This study
Heavy Chain		
H15104	GAGTCAGCCATATTGGACGTCTCGGC	Helm-Bychowski and Cracraft 1993
H15298	GCCCCTCAGAATGATATTTGTCCTCA	Kocher *et al.* 1989, Helm-Bychowski and Cracraft 1993
H15710	GTAGGCGAATAGGAAGTATC	Helm-Bychowski and Cracraft 1993
H15917	ATGAAGGGATGTTCTACTGGTTG	Edwards *et al*. 1991
H16062	GGAGTCTTCAGTCTCTGGTTTACAAGAC	Edwards and Wilson 1990, Edwards *et al*. 1991
H15622	GGTTGGGGGAGAATAGGGCTA	This study
H15543	GGGTGGAATGGGATTTTGTC	This study
H15735	CAGTTTGTTGGGGATTGAGCGTAGGAT	This study
H15844	GAGTTGTGAGAGGGGGCGGAAGG	This study
H15360	GGGTTAGTGTTGGGTTGTCCACTGA	This study
H15968	TAGGAGTAGTAGGATGGTGAAGTA	This study
H15219	TGTGTTTCAGGTTTCTTTGTAGA	This study
H16054	TTTACAAGACCAATGTTTT	This study
H16029	AAACTACTAGAGTTTAGTTT	This study

the forehead and below the eye (Carraway and Carraway 1979; RSG, pers. observ.).

Samples from avicultural and pet birds (category 3) were verified by POW and JRE, either by direct examination (*A. leucocephala caymanensis*, *Pionus menstruus*, *Deroptyus accipitrinus*, *Poicephalis gulielmi*) or photographs (*A. farinosa*, *A. ochrocephala* spp., *A.* [*ochrocephala*] *auropalliata*) of the parrot plumages. Samples obtained from the University of Georgia were taken from clinic birds at the School of Veterinary Medicine and Branson Ritchie (a leading parrot veterinarian in the U.S.) verified species identification.

Sample Preparation, Amplification of Cytochrome b*, and Determination of Nucleotide Sequences*

Feather processing for each species and subspecies was done on separate days. Epithelial tissue was aseptically removed from the distal end of feathers (Leeton *et al.* 1993). Genomic DNA was extracted from skin, blood, and liver cells following the protocol of Arctander (1988). Cytochrome *b* (cyt *b*) coding regions were amplified (Medlin *et al.* 1988) from extracted genomic DNA (50 ng) using the oligonucleotide primers listed in Table 3. A negative control was included for each set of reactions. DNA sequence data were obtained by standard methods (Sanger *et al.* 1977) with the Taq-Dye Deoxy Prism^{TM} Terminator Cycle Sequencing kit (FS-Mix) and an ABI 373 automated DNA Sequencer (Applied Biosystems, Perkin Elmer, Norwalk, CT) using 10ng of amplified DNA and 0.01 µM cyt *b* primers (Table 3).

Chromatograms were initially aligned by eye in

Table 4. Character status summary of the data sets for assessing phylogenetic relationships among *Amazona* spp. OTU = operational taxonomic units.

Data set	Number of OTUs	Characters				
		Excluded	Included	Constant	Variable uninformative	Variable informative
Long	47	114	1101	718	123	260
Short	72	619	596	410	43	143
Amino Acid	47	0	366	91	76	199

the sequence editor, SeqEd^{TM} (1.03s, Applied Biosystems). Ambiguities of homologous nucleotides were resolved by comparing overlapping sequences from heavy and light chains, and from different sequencing primer fragments. Final alignment of cyt *b* sequences was done with the multiple-alignment program Clustal W (Thompson *et al.* 1994) and verified with the inferred amino acid sequence.

Feather quills, although a poor source for DNA, are less problematic in amplification of "numts" (transposition of mitochondrial DNA sequences into nuclear DNA sequences; Sorensen and Quinn 1998). We followed precautions to eliminate or identify mitochondrial DNA inclusions within nuclear DNA (Sorensen and Quinn 1998): multiple individuals for most species and subspecies were used (Table 2); chromatograms were checked for double peaks at nucleotide residues; sequences were examined for insertions or deletions; translated sequences were checked for stop codons; and overlapping sequences were examined for ambiguities. No evidence of nuclear copies was detected.

Data Sets

Sequence data were obtained from replicate individuals for most species and subspecies to check for intraspecific variation and to verify the authenticity of sample identification. Two nucleotide data sets were derived from the cyt *b* sequence data: the long data set (1101 base pairs; bp) and the short data set (596 bp). The long data set corresponds to the chicken mitochondrial DNA at base pair numbers 14968 to 16068; the short data set corresponds to numbers 14968 to 15563 (Desjardins and Morais 1990). The short data set was included in this study to add extra individuals and several species for which poorly preserved feather samples resulted in the amplification of short nucleotide fragments. Because the shorter DNA sequences increased our taxonomic representation (see Graybeal 1998, Hillis 1998), we chose to include them in our analyses.

An inferred amino acid data set (366 amino acid residues), including the same species from the long data set, was also generated. The long and amino acid data sets include 47 operational taxonomic units (OTUs) consisting of 17 species of *Amazona*, four subspecies of *A. leucocephala*, two subspecies of *A. ochrocephala*, and three outgroup species (see below). Sequences were obtained from at least two individuals for 11 of the 17 species of *Amazona*. The short data set includes 72 OTUs with 20 species of *Amazona*. The three new species added to this data set are *A. auropalliata*, *A. viridigenalis*, and *A. amazonica*. Two of the six species represented by one individual from the long and amino acid data sets are replicated in the short data set. In all of the data sets, *A. dufresniana*, *A. versicolor*, *A. finschi*, and *A. farinosa* are represented by single samples. *Amazona auropalliata* and *A. amazonica* are represented by single samples in the short data set.

Analysis

To understand and examine reconstructed topologies under a variety of assumptions, we employed neighbor-joining, parsimony, and maximum likelihood analyses (as reviewed in Swofford *et al.* 1996). Analyses were done using the PAUP* (version 4.0b4a) software package (Swofford 1998). Unless otherwise stated, phylogenetic analyses used the default settings for a given analysis. The traditional, or non-parametric, bootstrap method (Felsenstein 1985, Hillis and Bull 1993) was used to evaluate support for branching patterns in the reconstructed phylogenetic trees. Parsimony and neighbor-joining bootstrap scores were based on 1000 iterations, and 100 were employed to assess maximum likelihood estimates. Three data sets were examined: a long data set, a short data set, and an amino acid data set (Table 4).

Preliminary trees were reconstructed to determine the most appropriate outgroups. *Pionus menstruus*, *Ara ararauna* (GenBank #U70761), *Aratinga aurea* (#U70762), *Deroptyus accipitrinus*, and *Poicephalus gulielmi* were considered. Three outgroups were selected for final analyses. *Pionus menstruus* was the closest outgroup to *Amazona*. Previous molecular studies have indicated that *Pionus* is more closely related to *Amazona* (Birt *et al*. 1992) than *Amazona* is to either *Ara* or *Aratinga* (Miyaki *et al*. 1998). *Pionus* and *Amazona* share cytogenic similarities (Valentine 1990), a loss of the uropygial gland (Collar 1997), and similar orbital ring structures (Thompson 1899). *Deroptyus accipitrinus* (South America; Williams 1998) and *Poicephalus gulielmi* (Africa) were also used as more distant outgroups relative to *Pionus*.

A LogDet/Paralinear model (Lake 1994, Lockhart *et al*. 1994) was used in the neighbor-joining analysis of the DNA sequence data. For the amino acid data set, the neighbor-joining search used mean character difference. Parsimony analyses assumed equal character weighting. To determine the most appropriate model of nucleotide evolution for the maximum likelihood analyses, we examined (with and without a gamma correction): the Jukes-Cantor one-parameter correction, the Kimura two-parameter correction, the Hasegawa-Kishino-Yano correction, the Tamura-Nei, and the general time-reversible models (assumptions are explained in Swofford *et al*. 1996). These models of nucleotide substitution were evaluated to determine the best fit to the data using a likelihood ratios approach, similar to that of MODELTEST (Posada and Crandall 1998; although their specific script and program were not employed). The general time-reversible model (i.e., with rate matrix and gamma estimated) was used in comparison of all the neighbor-joining trees produced with different models. The likelihood scores under this most general model of these neighbor-joining topologies were evaluated using a Kishino-Hasegawa two-tailed t-test (Kishino and Hasegawa 1989). Three models (Kimura two-parameter, Hasegawa-Kishino-Yano, Tamura-Nei) without a gamma correction had significantly worse scores than all other models tested. No significant differences were found between likelihood scores for the other seven models. The Hasegawa-Kishino-Yano model with empirically derived settings for nucleotide frequency, and estimations of the Ti/Tv ratio (i.e., kappa) and the gamma shape parameter was chosen for likelihood analyses because this model allows considerable savings on computation time without employing an overly simplistic model (e.g., Jukes-Cantor). Databases and results can be obtained from TREEBASE (http://www.treebase.org/treebase).

To trace the evolution of a feather character, the speculum, we mapped its presence or absence on our molecular phylogeny with the computer program MacClade (Version 3.04; Maddison and Maddison 1992). The speculum is a patch of contrasting color found at the base of three to five outer secondary wing feathers (i.e., secondary wing patch; Smith 1975, Forshaw 1989, Collar 1997). Feather patterns of the Greater Antillean *Amazona* and their close Central American relatives were examined in a previous study using 369 museum skins (Snyder *et al*. 1987). We traced several of these plumage characters onto the branches of our inferred molecular phylogeny.

RESULTS AND DISCUSSION

This molecular genealogy provides a hypothesis of the evolutionary relationships of West Indian *Amazona*. We address two issues: 1) the phylogeographic structure of the genus *Amazona* in the West Indies relative to the mainland, and 2) estimation of colonizations of the West Indies by *Amazona*.

We obtained cyt *b* sequences from 20 extant species of *Amazona*. These included nine species and four of the five *A. leucocephala* subspecies (*A. l. hesterna* was not sampled) from the West Indies and 11 species from Central and South America (Figs. 1 and 2). Neighbor-joining, parsimony, and maximum likelihood analyses were used to compare these DNA sequences. For illustrative purposes, we chose the parsimony trees from the long and short data sets (Figs. 3 and 4) to best represent the evolutionary history of West Indian *Amazona*. Branching patterns of tree topologies among all analyses were consistent with these parsimony trees except where discussed below.

Biogeography of Amazona

The emergence of the genus *Amazona* occurred after the separation of the short-tailed from the long-tailed New World parrots, which has been placed in the Eocene (Miyaki *et al*. 1998). Because of continued controversy over the reliability of a molecular clock, we interpret divergences of *Amazona* in geologic time as approximate estimates. Our estimates of *Amazona* divergence from the short-tailed *Pionus* are based on previous calibrations of avian mitochondrial DNA evolution (2% per million years; Shields and Wilson 1987, Tarr and

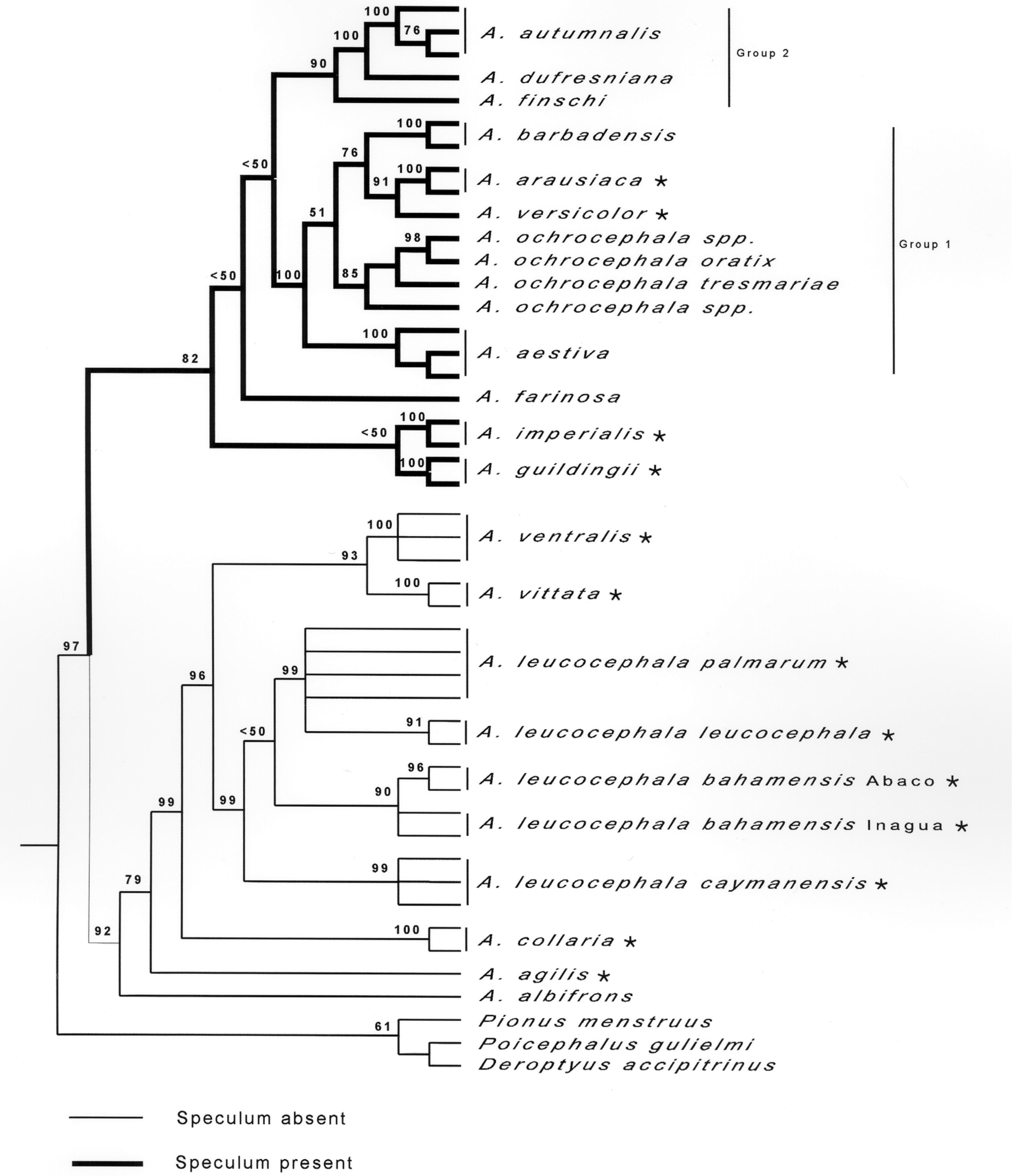

Fig 3. Parsimony analysis (PAUP*, version 4.0b4a; Swofford 1998) of the long data set as represented by the consensus tree of 48 best trees. The bold lines indicate the presence of a feather character, the speculum, as traced with MacClade (version 3.04; Maddison and Maddison 1992). Bootstrap evaluations were done with 1000 iterations and their values are shown above the branches. Specific indices from these trees include a tree length of 832, a consistency index (CI) of 0.5493, a homoplasy index (HI) of 0.4507, CI excluding uninformative characters of 0.4628, HI excluding uninformative characters of 0.5372, and a retention index of 0.8212. (* = *Amazona* of the West Indies).

Fig. 4. Single most parsimonious tree obtained in a heuristic search (PAUP*, version 4.0b4a; Swofford 1998) using the short data set. Bootstrap evaluations were done with 1000 iterations and their values are shown above the branches. Specific indices from this tree include a tree length of 419, a consistency index (CI) of 0.5251, a homoplasy index (HI) of 0.4749, CI excluding uninformative characters of 0.4707, HI excluding uninformative characters of 0.5293, and a retention index of 0.8820. Sequence data for two feather samples were obtained for *A. ochrocephala oratix* (*i.e.*, F#1 is feather 1 and F#2 is feather 2). (* = *Amazona* of the West Indies).

Fleischer 1993; see reviews in Mindell and Thacker 1996, Klicka and Zink 1997, Avise and Walker 1998). Our uncorrected nucleotide divergence values (p-distances) of approximately 0.10 put their divergence to be around 5 mybp, perhaps placing the origins of *Amazona* on the mainland during times of intermittent changes in climate and sea level in the Pliocene (4–2.5 mybp; dates reviewed in Haq *et al.* 1987, Donnelly 1988, Webb and Bartlein 1992, Bermingham and Lessios 1993, Emslie and Morgan 1994).

Biogeography of Amazona *in the West Indies*

The deepest nodes in our molecular phylogeny show a distinct bifurcation within the genus *Amazona* (Figs. 3 and 4). The West Indian *Amazona* fall into two assemblages of species: the Greater Antillean and main assemblages of *Amazona*. The Greater Antillean assemblage includes the five species found in the Greater Antilles, Bahamas, and Cayman Islands: *A. collaria* and *A. agilis* (Jamaica); *A. leucocephala* (Cuba, the Bahamas, and the Cayman Islands); *A. vittata* (Puerto Rico); and *A. ventralis* (Hispaniola). At the base of this Greater Antillean assemblage is the close relative, *A. albifrons* from Central America. The main assemblage of *Amazona* includes the four species of the Lesser Antilles (i.e., two species of Dominica, *A. arausiaca* and *A. imperialis*; *A. versicolor* of St. Lucia; and *A. guildingii* of St. Vincent) and the remainder of the South and Central American species included in our study (see Fig. 2).

High bootstrap values (82–92%) consistently supported both the Greater Antillean and main assemblages of *Amazona* in the parsimony trees using the long and amino acid data sets. These clades were also supported by high bootstrap values of 86–97% in the neighbor-joining LogDet paralinear analyses for these data sets. As is typical for maximum likelihood analysis (as reviewed in Hasegawa and Kishino 1994), lower bootstrap values were found in the long data set than in the same data set for the neighbor-joining or parsimony analyses: <50% for the main assemblage of *Amazona* and 74% for the Greater Antillean assemblage. In the short data set (neighbor-joining, parsimony, maximum likelihood analyses), nodes at the base of the main and Greater Antillean assemblages of *Amazona* show less than 50% bootstrap support. The DNA fragment size is perhaps too short to resolve deep nodes for such a large number of taxa.

Plumage and body sizes of West Indian species within the Greater Antillean and main assemblages of *Amazona* are distinctly different. Those species belonging to the Greater Antillean assemblage are generally smaller than those of the main assemblage of *Amazona*. The plumages of the Greater Antillean assemblage are mostly green with color variation in the head, wings, tail, and lower ventral regions of the body (Snyder *et al.* 1987, Wiley 1991). Most species from South and Central America within the main assemblage of *Amazona* share an overall plumage that is primarily green, but patches of other vivid colors are present on different parts of the body (Forshaw 1989, Collar 1997). The four large-bodied species found in the Lesser Antilles possess dramatic and colorful plumages (Forshaw 1989, Collar 1997). The larger size of these species may reflect behavioral and physiological characters that have been hypothesized to enhance survival on islands (Gotelli and Graves 1990).

The mainland species included in the main assemblage of *Amazona* and those species in the Lesser Antilles possess a speculum (Fig. 3; Smith 1975, Forshaw 1989, Collar 1997). Mainland species have specula with predominately red to yellow-orange colors. The speculum of the Lesser Antilles species *A. versicolor* is red, and *A. arausiaca* has a red to yellow speculum. *Amazona imperialis* has a deep maroon speculum, whereas *A. guildingii* has a smaller speculum that is orange and yellow. The species of *Amazona* in the Greater Antilles assemblage do not have a speculum. Thus the distribution of this plumage character in *Amazona* corroborates the basal bifurcation in our molecular hypothesis.

Colonization of the West Indies by Amazona

Our analysis suggests that *Amazona* colonized the Greater and Lesser Antilles during the Pliocene. This estimate is based upon nucleotide divergences within the main and Greater Antillean assemblages of *Amazona*. Divergences (p-distance) of 0.06 to 0.08 (3-4 mybp) were observed between the basal species of the main assemblage of *Amazona* (*A. imperialis*, *A. guildingii*, and *A. farinosa*) and the more derived species (*A. autumnalis*, *A. dufresniana*, *A. barbadensis*, *A. versicolor*, *A. auropalliata*, *A. ochrocephala*, and *A. aestiva*). Similar values for divergences within the Greater Antillean assemblage (*A. albifrons* compared to *A. ventralis*, *A. vittata*, and *A. leucocephala*) are estimated at approximately 0.06. Therefore, our data indicate that colonization of the West Indies probably occurred by overwater dispersals (as proposed by Bond 1963, 1979; Darlington 1957) and not by any Late Cretaceous to early Tertiary vicariant event in the Caribbean basin (Rosen 1976), or over proposed land corridors between either northwestern South America and Greater Antilles (Iturralde-Vinent and MacPhee 1999) or the emergent Nicaraguan Rise and western Jamaica (Donnelly 1988, and as reviewed in Portell *et al.* 2001). Both of these corridors were submerged by the Pliocene. As a result of early Tertiary ocean volume changes, Jamaica was also intermittently below sea level until the early Miocene (Buskirk 1985). Colonization of West Indian *Amazona* would have occurred after these events.

Colonization of the Greater Antilles by Amazona

Amazona albifrons from Central America at the base of the Greater Antillean assemblage (Figs. 3 and 4) is supported by all analyses with the exception of the neighbor-joining LogDet paralinear model for the short data set. In this case *A. agilis*, one of two species found on Jamaica, is more basal than *A. albifrons*. Bootstrap support is less than 50% for this branching pattern. *Amazona collaria*, also found on Jamaica, appears as an independent basal branch, well differentiated from *A. agilis* (p-distance = 0.056). The placement of *A. collaria* is strongly supported by high bootstrap values (greater than 97%) in parsimony and distance analyses of all data sets; maximum likelihood analyses show lower bootstrap values (70% and above) for this node. These analyses indicate that there may have been two dispersal events by ancestral *Amazona* to Jamaica.

Recent studies also suggested substantial differences between these two sympatric species *A. agilis* and *A. collaria* in their behavior and ecological needs (Koenig 2001). Lack (1976) also wrote that island-niches are usually occupied by different founder species. He hypothesized that beak size differences between *A. agilis* and *A. collaria* resulted from segregation of feeding strategies of populations of *A. albifron*s, and that they originated from two separate invasions into the Greater Antilles through Jamaica (*Amazona agilis*) and Cuba (*A. leucocephala*), the latter giving rise to *A. collaria*. Similar movements into Jamaica and Cuba were also proposed by Snyder *et al.* (1987; see full description below), Wiley (1991), and Lanterman (1997).

Our molecular data generally agree with these authors: *Amazona albifrons* from Central America is basal to the Jamaican species *A. agilis* and *A. collaria*, and *A. leucocephala* and *A. collaria* are derived from a common, most-recent ancestor. Differences in our data suggest, however, that movement of this ancestral species was directly to Jamaica, and not via Cuba.

Bond (1963) and Lantermann (1997) considered *A. collaria*, *A. leucocephala*, and *A. ventralis* (Hispaniola) as superspecies, and suggested that a close relationship exists between *A. agilis* and *A. vittata* (Puerto Rico). Snyder *et al.* (1987) agreed with their assessments, and placed these species into three groups (Fig. 5) as based on comparison of plumage characteristics. The first group consists of the two Central American sibling species, *A. albifrons* and *A. xantholora* (not included in this study), which are similar with a white forehead, red primary coverts, and mostly green throat and belly. *Amazona xantholora* has a dark ear patch, yellow lores, and darker scalloping on contour feathers, all of which are lacking in *A. albifrons*. The second group includes Bond's superspecies (see above), all of which share a white forehead, blue primary coverts, a dark ear patch, differing amounts of pink or maroon on the throat, and traces of a maroon belly-patch. The third group, *A. agilis* and *A. vittata*, share the characteristics of a red-forehead patch (most significant characteristic), green throat with varying amounts of maroon feathers, and a green belly. Given these three groups, the following hypothesis of colonization of the West Indies was proposed by Snyder and coworkers (Snyder *et al.* 1987): members of the second group (*A. leucocephala*, *A. collaria*, *A. ventralis*) are descendants of the two Central American species, and their initial colonization occurred independently of *A. agilis* of Jamaica; *Amazona vittata* was derived directly from *A. agilis*.

This proposed relationship of *A. agilis* and *A. vittata* implies a direct colonization from Jamaica to Puerto Rico (Snyder *et al.* 1987, Lantermann 1997). Alternately, a stepping-stone model would suggest that taxa with a red forehead-patch went extinct on intermediate islands (Cuba and Hispaniola). The red-forehead patch shared between *A. vittata* and *A. agilis* may, however, be the result of convergent evolution (Snyder *et al.* 1987).

There are differences between these species; most individuals of *A. agilis*, but not *A. vittata*, have a reduced dark ear-patch, darker color of the eye-ring and bill, and variable presence of red primary coverts. Even though the primary coverts on *A. agilis* are mostly red, some specimens have varying amounts of blue and the females have mostly green primary coverts. Blue primary coverts are characteristic of *A. collaria*, *A. leucocephala*, *A. ventralis*, and *A. vittata*, and may be a derived plumage char-

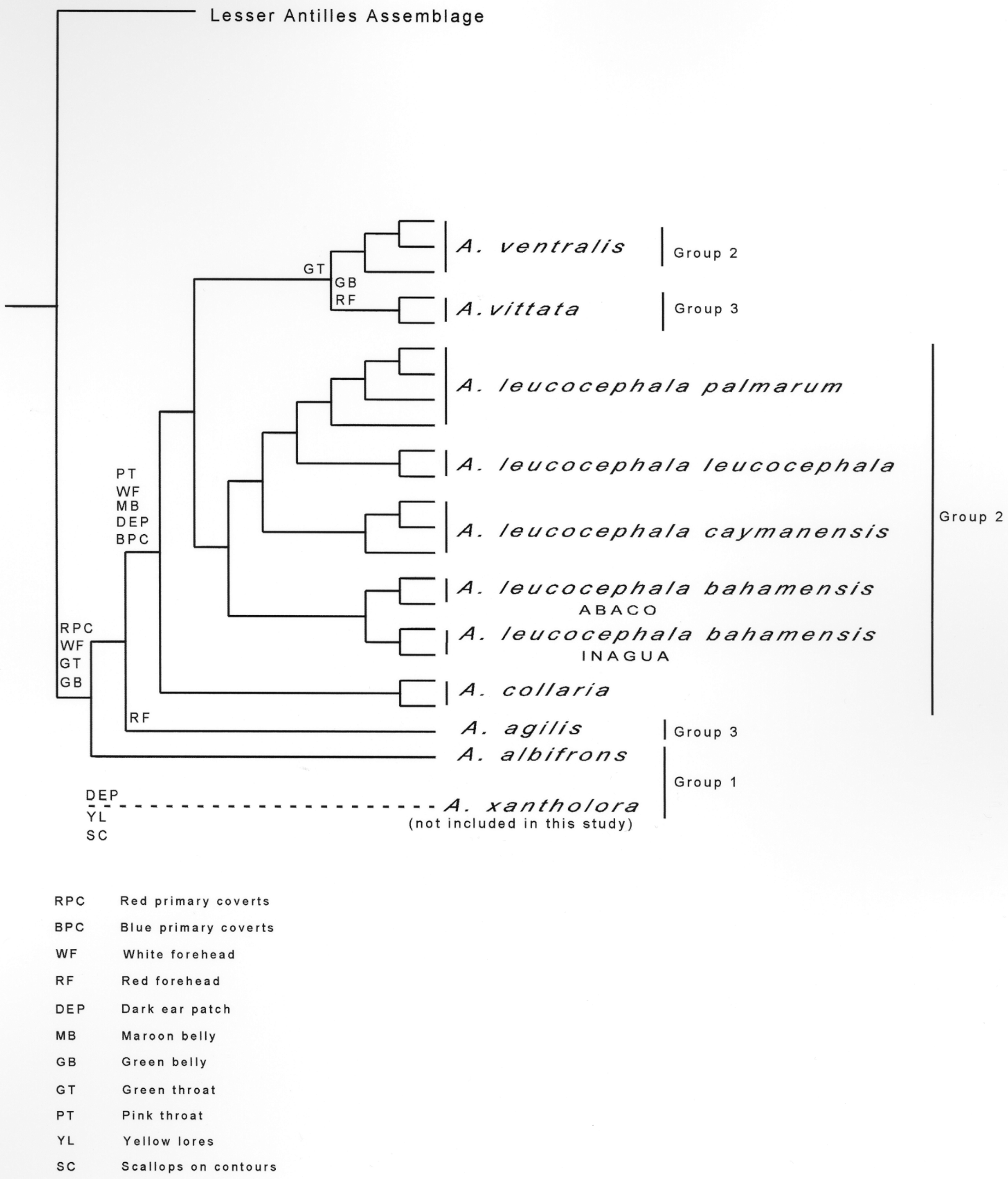

Fig. 5. Phylogenetic distribution of feather characters in West Indian and Central American *Amazona*. Greater Antillean *Amazona* and the Central American, *A. albifrons* and *A. xantholora* are placed into three groups (Snyder *et al*. 1987) as determined by similar feather characters. The feather characters are placed on branches of the Neighbor-joining LogDet paralinear tree (long data set). Branch lengths are not proportional to distances.

acteristic in the Greater Antillean *Amazona*. If this hypothesis is correct, then the presence of red primary coverts on *A. agilis* might suggest that this species evolved early in the history of *Amazona* and that there is not a close relationship with *A. vittata*. Red primary coverts are also found in several mainland species: *Amazona pretrei* and *A. tucumana* from South America, and the two sibling species *A. albifrons* and *A. xantholora* from Central America (see a complete description in Snyder *et al*. 1987).

A close relationship of *A. vittata* to *A. ventralis*, and not *A. agilis*, is more attractive geographically. This relationship implies rapid evolution of plumage characters from *A. ventralis* to *A. vittata*, including transformation of the white forehead-patch into a red one; a loss of distinct dark ear-patches and blue feathers on the lores, throat and cheeks; and partial losses of the maroon belly-patch and blue crown color. Several plumage similarities link *A. vittata* to *A. ventralis*; e.g., some specimens of *A. vittata* have scattered maroon belly-feathers and they both share yellow bills, white eye-rings, and blue primary coverts (see a complete description in Snyder *et al*. 1987). Indeed, our data do not support *A. agilis* and *A. vittata* as sister lineages. They support Lack's (1976) view that *A. ventralis* and *A. vittata* are sister lineages that share a common ancestry with *A. leucocephala*. A common most-recent ancestor gave rise to two lineages that resulted in *A. collaria* and the clade formed by *A. leucocephala*, *A. ventralis*, and *A. vittata*. *Amazona agilis* is basal to these Greater Antillean species.

Our molecular data show the four subspecies of *A. leucocephala* as distinct lineages that reflect their current geographic distributions. *Amazona l. bahamensis* and *A. l. caymanensis* probably diverged nearly simultaneously in geologic time. The branching order of these two subspecies varies among analyses: e.g., the 48 best trees found in parsimony analysis of the long data set (Fig. 3) showed 50% of trees with *A. l. bahamensis* as the most basal subspecies and 50% with *A. l. caymanensis* as most basal. Cuba's *A. l. leucocephala* and *A. l. palmarum* are weakly differentiated in the short data set (Fig. 4) and only segregate in the analysis of the long data set (Fig. 3), which has more resolving power; they appear to be the last populations to become genetically independent.

Fluctuating sea levels throughout the last three million years, from the late Pliocene throughout the Pleistocene, affected mammalian distribution patterns in Cuba, the Cayman Islands, and the Bahamas (Morgan 1989). Although estimates of divergences in geologic times become even less reliable at the subspecies and population levels, we roughly estimate diversification (p-distance of 0.0058 to 0.0094) of *A. leucocephala* to be sometime in the middle to late Pleistocene. A long interglacial period occurred in the middle Pleistocene (approximately 420,000 ybp), raising sea levels by 20 m; it dramatically affected low-island complexes (Hearty *et al*. 1999). The last interglacial event (about 120,000 ybp) increased sea levels 5–9 m higher than present (Slikas *et al*. 2002). The Bahamas (Olson 1977) and most of the small islands between Cuba and Isla de Pinos (Buden and Olson 1989) were likely to have been submerged. Later, though, low sea levels (nearly 120 m lower than present) during the last Wisconian glaciation (approximately 17,000 ybp) probably exposed most of the once submerged lands (as reviewed in Morgan 2001). Exposed land provided new habitat and less formidable overwater barriers for vertebrates to cross between Cuba and the Cayman Islands, and between Cuba and the Bahamas (Steadman and Morgan 1985). Land connections between Cuba and Isla de Pinos persisted as recently as 8000 ybp (Buden and Olson 1989). Initial movements and subsequent isolation of populations of *A. leucocephala* most likely occurred sometime during these eustatic sea level changes.

Amazona l. bahamensis was at one time widely distributed in the Bahamas, as evidenced by historic, fossil, and archeologic findings on Acklins, Crooked, Fortune, Grand Turk, San Salvador, Long, and New Providence islands (Wetmore 1938, Brodkorb 1959, Olson and Hilgartner 1982; as reviewed in Snyder *et al*. 1982, Gnam and Burchsted 1991, Wiley 1991, Williams and Steadman 2001). Reduction in the range of this subspecies, as suggested for other vertebrate species, was probably the result of human disturbances (Olson and Hilgartner 1982, Morgan 1994) and fragmentation of islands caused recently by rising sea levels (Pregill and Olson 1981, Olson and Pregill 1982, Morgan 1994). The remaining two populations of *A. l. bahamensis* in Abaco and Great Inagua appear genetically separated in all our analyses except in the parsimony analysis of the short data set (Fig. 4). The cyt *b* differences (p-distance = 0.009) support behavioral, ecological, and morphological distinctions of these populations as noted by others (Snyder *et al*. 1982; Gnam 1990, 1991; Gnam and Rockwell 1991; Gnam *et al.* 1995).

Colonization of the Lesser Antilles by Amazona

Our data support Bond's (1963) view that the four large *Amazona* currently in the Lesser Antilles reached the islands from South America. There appears to have been a minimum of two, and possibly three, dispersals of *Amazona* into the Lesser Antilles, in agreement with a recent study by Klein and Brown (1994), which found that multiple colonizations of some avian species occurred in these islands.

The three species at the base of the main assemblage of *Amazona* (*A. farinosa*, *A. imperialis*, and *A. guildingii*) are separated by nodes that are unstable in all analyses and not well supported by bootstrap values. These three species are among the largest of the genus. *Amazona farinosa* is widely distributed in South and Central America and has a rather dull, uniform green plumage as compared to the multi-colored plumages of *A. imperialis* (Dominica) and *A. guildingii* (St. Vincent). *Amazona imperialis* has a striking purple-hued plumage and is the largest species of the genus. *Amazona guildingii* has two color morphs with a kaleidoscope of colors ranging from brown and bronze to orange, yellow, and green (Snyder *et al*. 1987). Colonization of St. Vincent by an ancestor of *A. guildingii* may have been a single dispersal event from South America independent from that of the ancestry of *A. imperialis*. Alternatively, there may have been a single dispersal of a common ancestral species of *A. guildingii* and *A. imperialis* from South America with a subsequent linear radiation through the Lesser Antilles.

Several mainland species and the two remaining species from the Lesser Antilles are placed into two groups that are separate from *A. farinosa*, *A. imperialis* and *A. guildingii*. Groups 1 and 2 (Figs. 3 and 4) are supported by high bootstrap values in all analyses (71–100%). Group 1 includes *A. aestiva*, *A. auropalliata* (the short data set only), the *A. ochrocephala* complex, *A. barbadensis*, and the two Lesser Antillean species, *A. arausiaca* (Dominica) and *A. versicolor* (St. Lucia). The majority of analyses show *A. arausiaca* and *A. versicolor* as sister lineages with >80% bootstrap support, and are most closely related to either *A. barbadensis* (e.g., see Fig. 3) found on the northern coast of South America and adjacent islands or *A. aestiva* (e.g., see Fig. 4) from central South America. Alternately, *A. versicolor* is paired with *A. barbadensis* in the neighbor-joining Log/Det paralinear distance analysis of the short and long data sets. The bootstrap support for this arrangement is less than 50%. Even though we do not have >50% bootstrap values, the four remaining neighbor-joining distance trees show *A. arausiaca* and *A. versicolor* as paired lineages. In sum, our data suggest a close sister group relationship, as did Lack (1976), of *A. arausiaca* and *A. versicolor* (p-distance = 0.02). Similar plumage colorations (e.g., blue forehead and facial patches, red neck-patch, and green body plumage) also suggest a close relationship (Snyder *et al.* 1987). Colonization of Dominica and St. Lucia by ancestors of *A. arausiaca* and *A. versicolor* appears as one dispersal event from South America to the Lesser Antilles.

Group 2 includes the mainland species *A. autumnalis*, *A. dufresniana*, *A. finschi*, *A. viridigenalis* (short data set only) and *A. amazonica* (short data set only) and is supported with 90% bootstrap values in parsimony, 99% in neighbor-joining, and 69–71% in maximum likelihood analyses of the long and the short data sets. Based on plumage patterns, *A. dufresniana* (northern South America) appears to be closely related to the species of *Amazona* from the Lesser Antilles (Snyder *et al.* 1987, Wege and Collar 1991), but our analysis does not indicate that it is ancestral to the Lesser Antillean species.

The second pair of sympatric species of *Amazona* in the West Indies, *A. arausiaca* and *A. imperialis*, is found on Dominica. Our molecular phylogeny shows that these two species are not sister species and evidently arose from two different dispersals to Dominica at different times in the history of *Amazona*. Even though these two species share highland forest habitats, Lack (1976) hypothesized that they occupy two different ecological niches. He believed that broad niches are occupied first, followed by an adaptation of an incoming species to a more specific unoccupied niche. In our analysis, *A. imperialis* appears to have colonized Dominica before *A. arausiaca*. *Amazona imperialis* does not appear to occupy a broader niche, though, than *A. arausiaca*. *Amazona imperialis* is more sedentary and is most frequently found at higher elevations (600–1300 m). The more nomadic *A. arausiaca* occasionally moves from the highland forests (300–600 m) into open-cultivated areas where it forages on a slightly broader selection of fruits and seeds (as reviewed in Collar 1997).

Biogeographic Junction between the Lesser and Greater Antilles

The late Pleistocene and Holocene fossil records of several vertebrates (iguanas, some birds, and some bats and rodents) provide evidence of extinct species that showed no faunal disjunction between the Greater and Lesser Antilles (Morgan and Woods 1986, Pregill *et al*. 1994, Morgan 2001). Genetic homogeneity of Bananaquit (*Coereba flaveola*) populations from the U. S. Virgin Islands to St. Lucia suggests a continuous gene flow through the Antillean islands chain; i.e., the historic lack of a biogeographic break for that species (Seutin *et al*. 1994). Bond (1963) and Ricklefs and Cox (1972), however, agreed that for many avian groups, a break occurs at the Anegada Passage (Fig. 1). Our molecular data show a distinct genealogical division between extant *Amazona* of the Greater and Lesser Antilles. However, evidence of a small *Amazona*, similar to *A. vittata* (Puerto Rico) and the extinct *A. v. gracilipes* (Isla Culebra, east of Puerto Rico) (Wetmore 1917), was found at archeologic sites on Antigua, at the northern end of the Lesser Antilles (Steadman *et al*. 1984; Pregill *et al*. 1988, 1994). An undated (pre-cultural) rostrum similar to *A. vittata* was also found on Barbuda, and a small species of *Amazona* was discovered on Monsterrat (Williams and Steadman 2001). This archeologic evidence suggests that some limited eastward dispersal of *A. vittata*-like parrots occurred into the Lesser Antilles across the Anegada Passage. An alternate explanation is that *Amazona* from Puerto Rico may have been transported to these northernmost Lesser Antilles by human cultures.

Summary

As Bond (1963, 1979) concluded for other avian species, and Morgan (Morgan and Woods 1986, Morgan 2001) for several mammalian species, our molecular phylogeny suggests that movements of ancestral *Amazona* were from the south to north into the Lesser Antilles and from west to east into the Greater Antilles. Dispersal of *Amazona* from South America throughout the Lesser Antilles involved a minimum of two independent events, perhaps three. *Amazona imperialis* colonized the Lesser Antilles early in the history of *Amazona* and independently of its sympatric species, *A. arausiaca*. *Amazona arausiaca* and *A. versicolor* appear as sister species and are the result of a later colonization of the Lesser Antilles. Colonization of St. Vincent by ancestral *A. guildingii* was also early in the history of *Amazona* and may have been an independent dispersal from the mainland. Our molecular phylogeny, however, does not clearly differentiate the branching pattern among *A. imperialis*, *A. guildingii*, and *A. farinosa* at the base of the main assemblage of *Amazona*. The first island colonized by *Amazona* in the Greater Antilles appears to be Jamaica. *Amazona agilis* and *A. collaria* are clearly differentiated from each other and their colonization of Jamaica may be the result of two separate dispersal events.

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