Origin and diversification of the genera Aratinga, Eupsittula and Psittacara (Aves: Psittacidae)

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Abstract

The arrival of psittacines in North America is well known but undefined. It is widely accepted that the origin of these birds occurred in South America, and it has been suggested that different factors have promoted the biodiversity of birds in Mexico. However, in general, for North American psittacines there are no proposed divergence times and the possible influence of different geological events on these processes is unknown. In this study, phylogenetic relationships, divergence times and the ancestral areas of the genera *Aratinga*, *Eupsittula* and *Psittacara* and related genera were estimated to propose hypotheses of origin, diversification, and dispersal of groups under a Bayesian inference framework, based on mitochondrial molecular markers. We found that of the seven monophyletic clades within the Arini tribe, four coincided with the genera *Psittacara*, *Eupsittula*, *Rhynchopsitta*, and *Pyrrhura*, and three clades were integrated by different genera. The genera *Aratinga* and *Eupsittula* originated during the Miocene, and the genus *Psittacara* originated at the Miocene-Pliocene boundary. *Aratinga* is the oldest, followed by *Eupsittula* and the youngest is *Psittacara.* Biogeographic reconstruction suggests that the most likely origin of these genera is the Amazonian or Chaco regions. The diversification of these groups is related to geo-climatic events associated with the uplift of the central and northern portions of the Andes and the closure of the Isthmus of Panama. We propose dispersion routes from south to north in the Neotropics and the use of the Greater and Lesser Antilles as a northward path.

Introduction

Psittaciformes are one of the most representative avian orders, since their coloration, cognitive capacity, and the ability to imitate human words distinguish them from other birds. Unfortunately, this group is also notable for being among the most endangered birds globally. In the Neotropical region, the main threats they face and that have caused their populations to decrease are human activities, such as agriculture, logging, and capture for the pet trade, among others (Berkunsky et al., 2017; Cantú-Guzmán et al., 2007). Consequently, all neotropical psittaciform species are listed in the CITES protected species appendices (CITES, 2022).

In the Neotropics parrots are exceptionally rich in species, and there are approximately 158 species distributed from northern Mexico to southern South America (Clements et al., 2021; Forshaw, 1989). South America in particular shows considerable radiative speciation, and in North America, only 21 currently living species have reached the northernmost distribution in Mexico and the USA (Collar, 1997; Darlington, 1957; Forshaw, 1989; Joseph et al., 2012; Schweizer et al., 2011). The records for the northernmost distribution of psittacines in America are for *Rhynchopsitta pachyrhyncha*, which was recorded from the mountains of southern Arizona, and the extinct *Conuropsis carolinensis*, which inhabited large areas throughout the eastern United States (Forshaw, 1989; Wetmore, 1935).

Through phylogeographic analyses and phylogenetic reconstructions with molecular data of some species of parrots in South America, it has been established that the triggers of speciation were geotectonic events such as the uplift of the Andes, marine incursions, fluvial dynamics, and the influence of the Pleistocene glacial cycles (Eberhard and Bermingham, 2005; Eberhard et al., 2004; Ribas et al., 2005, 2006; Ribas and Miyaki, 2004; Tavares et al., 2006). However, analyses of this type for parrots in their northernmost distribution (Mexico) are scarce and it is unknown how and when the psittacines arrived in North America.

It has previously been suggested that factors such as climatic oscillations, Pleistocene roosts, topographic complexity, and geographic position promote bird biodiversity in Mexico (Escalante-Pliego et al., 1993). In this sense, Weir et al. (2009) recognized the role of events such as the Great American Biota Exchange in promoting the exchange of bird species between North and South America. Furthermore, they propose that the direction of bird traffic across the land bridge was primarily from south to north (Weir et al., 2009). In this exchange, the arrival of psittacines from the south to the north is intuited; however, for North American parrots there are no publications on the influence of events such as the great exchange of American biota or proposals on the time of divergence.

The tools developed for phylogeographic analysis and the gradual increase in information available for reviewing taxonomic relationships, particularly those based on DNA sequences, have allowed the generation of hypotheses that explain the origin and diversification of natural groups. In this sense, the genera *Aratinga*, *Eupsittula* and *Psittacara* have information that can be analyzed together, which to date has not been considered under this approach. In addition, these genera are widely distributed with species present in northern Mexico, Central America, and the Caribbean islands and South America (Forshaw, 1989, 2010; Howell and Webb, 1995). Therefore, they are a good example to infer ancestral areas, patterns of diversification and divergence times of psittacines from south to north in the Neotropical region.

Some changes have been proposed for the classification and nomenclature of the species of the genus *Aratinga* based on morphological data (Peters, 1937; Salvadori, 1891; Vigors, 1825), and for more than eighty years this genus was considered a monophyletic group (Peters, 1937; Remsen et al., 2013) (Table 1). However, based on evidence demonstrated by phylogenetic reconstructions from molecular data, some species were reclassified and recognized in the genera *Aratinga*, *Eupsittula, Thectocercus*, and *Psittacara* (BLI, 2015; Chesser et al., 2014; Clements et al., 2021; del Hoyo et al., 2014; Remsen et al., 2013) (Table 1). Currently, according to different authors, six or seven species are recognized in the genus *Aratinga*, five or six in the genus *Eupsittul*a, and twelve species have been recognized in the genus *Psittacara* (BLI, 2015; Chesser et al., 2014; Clements et al., 2021; del Hoyo et al., 2014; Remsen et al., 2013) (Table 1). Although there are independent studies where relationships have been established between some species of these genera, there is no consensus on the relationships between them and with other related ones, mainly because these relationships have been established independently and with a limited number of species. To show the scope of the proposals made on relationships between genera, according to different authors the related genera are *Diopsittaca*, *Guaruba*, *Pyrrhura*, *Anodorhynchus*, *Nandayus*, *Cyanopsitta*, *Primolius*, *Ara*, *Orthopsittaca*, and *Leptosittaca* (Kirchman et al., 2012; Ribas and Miyaki, 2004; Tavares et al., 2006, 2004).

Table 1
Contrasting classifications of the genera *Aratinga, Eupsittula* and *Psittacara*

Salvadori (1891)		Peters (1937)		Remsen et al. (2013); Clements et al. (2021)		Chesser et al. (2014)		del Hoyo et al. (2014); (2015)	
Conurus	*acuticaudatus*	*Aratinga*	*acuticaudata*	*Aratinga*	*auricapillus*	*Aratinga*	*auricapillus*	*Aratinga*	*auricapi*
	aztec		*astec*		*jandaya*		*jandaya*		*C. caroli*
	aureus		*aurea*		*maculata*		*maculata*		*jandaya*
	auricapillus		*auricapillus*		*nenday*		*nenday*		*maculat*
	cactorum		*cactorum*		*solstitialis*		*solstitialis*		*nenday*
	canicularis		*canicularis*		*weddellii*		*weddellii*		*solstitia*
	chloropterus		*chloroptera*						*weddelli*
	rubrolarvatus		*erythrogenys*	*Eupsittula*	*aurea*	*Eupsittula*	*astec*		
	euops		*euops*		*cactorum*		*aurea*	*Eupsittula*	*astec*
	finschi		*finschi*		*canicularis*		*cactorum*		*aurea*
	guarouba		*guarouba*		*nana*		*canicularis*		*cactoru*
	holochlorus		*holochlora*		*pertinax*		*nana*		*canicula*
	jendaya		*jandaya*				*pertinax*		*nana*
	leucophthalmus		*leucophthalmus*	*Thectocercus*	*acuticaudatus*				*pertinax*
	mitratus		*mitrata*			*Psittacara*	*acuticaudatus*		
	nanus		*nana*	*Psittacara*	*brevipes***		*chloropterus*	*Psittacara*	*acuticau*
	pertinax		*pertinax*		*chloropterus*		*erythrogenys*		*chloropt*
	solstitialis		*solstitialis*		*erythrogenys*		*euops*		*erythrog*
	wagleri		*strenua*		*euops*		*finschi*		*euops*
	weddellii		*wagleri*		*finschi*		*frontatus*		*finschi*
	nenday		*weddellii*		*holochlorus*		*holochlorus*		*frontatu*
	brevipes				*labati***		*leucophthalmus*		*holochlo*
	frontatus	*Nandayus*	*nenday*		*leucophthalmus*		*mitratus*		*labati**
					*maugei***		*rubritorquis*		*leucoph*
					mitratus		*strenuus*		*mitratus*
					strenuus		*wagleri*		*rubritorq*
					wagleri				*wagleri*

*Only considered by BLI (2015)

** Only considered by Clements et al. (2021)

In this study we present a phylogenetic hypothesis on the relationships between the genera *Aratinga*, *Eupsittula* and *Psittacara* using molecular data from the mitochondrial genes for cytochrome oxidase subunit I (COI) and NADH dehydrogenase subunit 2 (ND2). We also make a proposal about the time of divergence, probable ancestral areas, and possible dispersal routes of these groups, with emphasis on their arrival at the extreme north of their distribution. This study increases knowledge about the presence of parrots in Mexico and helps build a broader view of the processes that could influence the presence and diversity of neotropical birds in their northernmost distribution.

Material And Methods

Sequence samples

Sequences used in the analyses were obtained from the National Center for Biotechnology Information (NCBI) GenBank database. To establish the relationships of the *Aratinga*, *Eupsittula* and *Psittacara* genera, we analyzed the Arini tribe, including 17 of the 18 genera that compose it. The out-group comprises species representing the tribes Incertae sedis (8 of 10 genera), Androglossini (*Amazona ochrocephala*), Melopsittacini (*Melopsittacus undulatus*), and Cacatuini (*Cacatua sulphurea*), and the species *Coracopsis vasa*, *Nestor notabilis*, *Falco peregrinus*, and *Columba livia*. The taxa included in these analyses were chosen according to results previously reported by Ribas and Miyaki (2004), Tavares et al. (2006, 2004), and Kirchman et al. (2012), and the proposed Arini tribe of Joseph et al. (2012). In detail, a total of 76 terminal taxa were included in the analyses, of which 54 belong to the Arini tribe. According

to the classification of Remsen et al. (2013) and Clements et al. (2021), we included all species of the genera *Aratinga* (6 species) and *Eupsittula* (5 species). Additionally, according to the classification by Clements et al. (2021), we included 9 of 10 living species of *Psittacara* (and the subspecies *P. h. rubritorquis*), 7 of 9 species from *Forpus*, all the species of the genera *Primolius* (3 species), *Pionites* (2 species), and *Rhynchopsitta* (2 species). We also included the genera *Deroptyus*, *Cyanoliseus*, *Conuropsis*, *Cyanopsitta*, *Orthopsittaca*, *Leptosittaca*, *Guaruba*, *Thectocercus*, and *Diopsittaca*. Finally, according to Clements et al. (2021), other genera and the proportion of species also included are described below: *Ara* (7 of 8 living species), *Enicognathus* (1 of 2 species), *Anodorhynchus* (2 of 3 species), and *Pyrrhura* (8 of 23 species) (Table 2). We analyzed the sequences of two molecular markers of mitochondrial DNA (mtDNA): cytochrome c oxidase subunit I (COI) and NADH dehydrogenase subunit 2 (ND2) (Table 2).

Table 2
List of the species (and/or subspecies) used in this study, including locality, identification and GenBank accession numbers

Specie	Locality	Museum/ collection (identification)	GenBank Access	
			COI	ND2
Amazona ochrocephala	Unknown	Unknown	NC_027840	NC_027840
Anodorhynchus hyacinthinus	Captive, locality unknown	LSU(B100020/B-13478)	GU826173.1	HQ270480.1
Anodorhynchus leari	Brazil, Raso da Catarina	LGEMA(0410)	AF370736	AY669446
Ara ambiguus	Ecuador, Guayas: Bosque Protector Cerro Blanco	AamPB3(stri-x-172)	KP411032	KP411041
Ara ararauna	Captive, locality unknown	Unknown	NC_029319	NC_029319
Ara chloropterus	Unknown	GWM-HARI	KR017982	—
Ara glaucogularis	Unknown	Unknown	NC_026029.1	NC_026029.1
Ara macao	Captive, USA, Iowa, Blank Park Zoo	Unknown	CM002021.1	CM002021.1
Ara militaris	Unknown	Unknown	NC_027839	NC_027839
Ara severus	Unknown	Unknown	KF946546	KF946546
Aratinga auricapillus	Captive, USA, Texas, Clarence Killian Aviary	LSU(B-29884)	GU826176.1	HQ270483.1
Aratinga jandaya	Unknown	Unknown	—	JX645194.1
Aratinga maculata	Monte Alegre PA (Naturaleza)	LGEMA(9158)	—	KJ142296.1
Aratinga nenday	Captive, Spain, Canary Islands, Tenerife, Loro Parque	LPF(LP07-23)	EU621632	EU327636
Aratinga solstitialis	Captive, locality unknown	NMNH(B06816)	GU826185.1	HQ270491.1
Aratinga weddellii	Brazil, Acre	LGEMA(2085)	—	AY669445.1
Bolborhynchus lineola	Costa Rica, San Jose Province	LSU(B-16252)	GU826187	HQ270493
Cacatua sulphurea	Captive, USA, Florida, Miami Zoo	Unknown	EU621602.1	EU327605.1
Columba livia	China, Wuhu, Anhui Province	Unknown	NC_013978	NC_013978
Conuropsis carolinensis	USA, Florida, Manatee County	NYSM(9421)	GU826189	HQ270495
Coracopsis vasa	Unknown	Unknown	NC_027841	NC_027841
Cyanoliseus patagonus	Argentina, Neuquen, Departmento Anelo, Sierra Auca Mahuida	AMNH (DOT 10384)	EU327613	EU621609
Cyanopsitta spixii	Captive, Spain, Canary Islands, Tenerife, Loro Parque	LPF(Cyspi01)	EU621610.1	EU327614.1
Deroptyus accipitrinus	Unknown	Unknown	KM611476	KM611476
Diopsittaca nobilis	Guyana, Karaudanawa	NMNH B12392	EU621614.1	EU327618.1
Enicognathus leptorhynchus	Captive, Spain, Canary Islands, Tenerife, Loro Parque	LPF07-34(UV)	EU621616	EU327620
Eupsittula aurea	Brazil, Para, Altamira	NMNH(b07010)	GU826175.1	HQ270482.1
Eupsittula cactorum	Brazil, Tocantins	LGEMA(0992)	AF370750.1	—
Eupsittula canicularis	Captive, locality unknown	AMNH(DOT9252)	HQ629753.1	HQ629718.1
Eupsittula canicularis	Mexico, Michoacan, Palos Marías	CMEB(AceMpm53)	KJ612381	KJ612390
Eupsittula canicularis	Mexico, Sinaloa, Badirahuato	CMEB(AccSb14)	KJ612385	KJ612394
Eupsittula nana	Panamá, Bocas del Toro, San Cristobal I, Bocatorito	NMNH(B00465)	GU826184.1	HQ270490.1
Eupsittula pertinax	Venezuela, Caracas, Phelps Ornithological Collection	POC(ML683)	NC_015197.1	NC_015197.1
Falco peregrinus	Unknown	Unknown	NC_000878	NC_000878
Forpus coelestis	Ecuador, Loja	16697	–	JX877366

Abbreviations for collections: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences, Philadelphia; CMEB, Centro Multidisciplinario de Estudios en Biotecnología, Universidad Michoacana de San Nicolás de Hidalgo; LGEMA, Laboratorio de Genetica e Evolucao Molecular Universidade de Sao Paul, Brazil; LPF, Loro Parque Fundación Tenerife, Spain; LSU, Louisiana State University Museum of Natural Science; LSUMNS, Louisiana State University Museum of Natural Science; NMNH, Smithsonian National Museum of Natural History; NRM, Swedish Museum of Natural History; NYSM, New York State Museum; POC, Phelps Ornithological Collection

Specie	Locality	Museum/ collection (identification)	GenBank Access	
			COI	ND2
Forpus conspicillatus	Captive, locality unknown	Foconpsic	—	JX877387
Forpus cyanopygius	México, Nayarit	ITM127	—	JX877382
Forpus modestus	Unknown	Unknown	HM755882	HM755882
Forpus passerinus	Unknown	Unknown	NC_027843	NC_027843
Forpus xanthops	Peru, Amazonas	395954	–	JX877378
Forpus xanthopterygius	Ecuador, Morona-Santiago	16620	—	JX877363
Guaruba guarouba	Captive, locality unknown	NMNH(B-06578)	EU621624.1	EU327628
Hapalopsittaca melanotis	Bolivia, La Paz Department	LSU(B-1229)	GU826192	HQ270498
Leptosittaca branickii	Ecuador, Jimbura: E Slope Cord. Lagunillas	ANSP(4966)	EU621626.1	EU327630.1
Melopsittacus undulatus	Unknown	Unknown	NC_009134	NC_009134
Myopsitta monachus	Unknown	Unknown	NC_027844	NC_027844
Nestor notabilis	Unknown	Unknown	NC_027845	NC_027845
Orthopsittaca manilatus	Captive, locality unknown	Unknown	KJ579139.1	KJ579139.1
Pionites leucogaster	Unknown	Unknown	KM611479	KM611479
Pionites melanocephalus	Guyana, North West, Baramita	NMNH(B09553)	EU621644	EU327648
Primolius auricollis	Brazil, Mato Grosso	LGEMA(1742)	AF370753	DQ143302
Primolius couloni	Captive, locality unknown	Unknown	NC_025742.1	NC_025742.1
Primolius maracana	Captive, locality unknown	Unknown	KJ562357	KJ562357
Psilopsiagon aymara	Unknown	LSUMNS B-1201	HQ629774	HQ629738
Psittacara brevipes	Captive, Mexico, Puebla, African Safari Parque	Unknown	NC_021764.1	NC_021764.1
Psittacara chloropterus	Captive, Spain, Canary Islands, Tenerife, Loro Parque	LPF(LP07-26)	GU826178	HQ270484
Psittacara erythrogenys	Captive, Rio Zoo R. J.	LGEMA(9166)	—	KJ142291.1
Psittacara euops	Captive, Spain, Canary Islands, Tenerife, Loro Parque	LPF(LP07-25)	GU826179	HQ270485
Psittacara finschi	Panamá, Bocas del Toro, San Cristobal I, Bocatorito	NMNH(B00402)	GU826180.1	HQ270486.1
Psittacara holochlorus	Captive, USA, Texas	LSU(B-23651)	GU826181.1	HQ270487.1
Psittacara h. rubritorquis	Captive, Spain, Canary Islands, Tenerife, Loro Parque	Unknown	JX524614.1	JX524614.1
Psittacara leucophthalmus	Argentina, Corrientes, 45 km S, Manuel Derqui	NMNH(B05906)	GU826182.1	HQ270488.1
Psittacara mitratus	Captive, Spain, Canary Islands, Tenerife, Loro Parque	LPF(LP07-12)	GU826183.1	HQ270489.1
Psittacara wagleri	Captive, Spain, Canary Islands, Tenerife, Loro Parque	LPF(LP07-14)	GU826186.1	HQ270492.1
Pyrrhura albipectus	Unknown	LSUMNS B-5958	HQ629779	HQ629743
Pyrrhura frontalis	Unknown	NRM 966989	—	JN614685
Pyrrhura hoffmanni	Unknown	NMNH(B05272)	HQ629780	HQ629744
Pyrrhura leucotis	Captive, locality unknown	LGEMA3921	–	DQ143307
Pyrrhura molinae	Unknown	CJV-LAMI	KR017992	–
Pyrrhura perlata	Brazil, Para, Altamira, Bank Rio Xingu	NMNH (B07007)	GU826196	HQ270502
Pyrrhura picta	Brazil, Para, Altamira, Bank Rio Xingu	NMNH(B06897)	EU621660	EU327664
Pyrrhura rupicola	Unknown	Unknown	NC_028404	NC_028404

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Specie	Locality	Museum/ collection (identification)	GenBank Access	
			COI	ND2
Rhynchopsitta pachyrhyncha	Captive, locality unknown	NMNH(B08714)	EU621661.1	EU327665.1
Rhynchopsitta terrisi	Captive, Mexico, Puebla, African Safari Parque	Unknown	NC_021771	NC_021771
Thectocercus acuticaudatus	Captive, locality unknown	Unknown	NC_020325	NC_020325
Touit purpuratus	Unknown	NMNH (B09558)	HQ629781	HQ629745

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Phylogenetic Analysis

Sequence editing, alignments, and the construction of the data matrices were carried out with Sequencher v.4.1 (Gene Codes Corporation, 2015) and PhyDE (Müller et al., 2005). To estimate genetic distances (uncorrected *p* distance) among closely related species we used MEGA 5.05 software (Tamura et al., 2011). Separate analyses were run for each genetic marker where the sequences with “N” were excluded, and used the Kimura 2-Parameter model with gamma distribution of rates among sites. Molecular evolution models were obtained with jModelTest 2.1.1 (Posada, 2008) and selected using the corrected Akaike Information Criterion (cAIC) (Alfaro and Huelsenbeck, 2006). The best model obtained using this criterion for COI was HKY + G + I (Hasegawa, Kishino and Yano + Gamma distribution of rates among sites + Invariant sites - Hasegawa et al., 1985), for ND2, GTR + G + I (General Time Reversible + Gamma distribution of rates among sites + Invariant sites - Tavaré, 1986), and GTR + G + I for all the sequence data after concatenation (COI + ND2).

Phylogenetic reconstructions were generated with concatenated sequences using maximum likelihood (ML) and Bayesian inference (BI) frameworks. The ML and BI reconstructions were performed using Genetic Algorithm for Rapid Likelihood Inference (GARLI) (Zwickl, 2006) and MrBayes v3.2 (Ronquist and Huelsenbeck, 2003) software, respectively. The branch support values were estimated by the BP of 500 replicates and by PP. MrBayes runs were performed using the following parameters: four independent runs of four chains each (one cold chain and three hot chains) for 10 million generations with sampling one tree every 1000 generations. Trees and parameters were summarized after discarding 25% of the data (burn-in). The remaining trees were summarized as a majority consensus tree and visualized using FigTree v1.4.0 (Rambaut, 2012).

Inference Of Divergence Time

To estimate divergence times, we considered data from previous calibrations performed by Jarvis et al. (2014), who proposed estimates made under Bayesian inference with genomic sequences from 45 bird species. Based on nineteen fossil age calibrations, they proposed that the most basal divergences within Neoaves (Columbea-Passerea) occurred before the Cretaceous-Paleogene transition (67 to 69 million years ago -Mya-). They also reported that Falconiformes and Psittaciformes share an ancestor of approximately 60 Mya.

In this analysis, divergence times with concatenated sequences (COI + ND2) were estimated under Bayesian inference using BEAST v1.7.4 (Drummond and Rambaut, 2007). To establish the divergence age we used one calibration point using a normal distribution for the root of the tree (*Columba livia*, average = 69.5 Mya, SD = 1.0). The following specifications were used: an uncorrelated lognormal relaxed clock model was selected with a GTR + G + I selection model. We used a Yule-type speciation model because it is appropriate for the analysis of sequences obtained from different species (Aldous, 2001; Yule, 1924). Markov Chain Monte Carlo (MCMC) analyses were run for 10 million generations with sampling one tree every 1000 generations. To assess convergence, effective sample size (ESS) values were observed with MCMC Trace Analysis Tool v1.5.0 (Drummond and Rambaut, 2007). The results were summarized using TreeAnnotator v1.7.4 (Drummond and Rambaut, 2007). After 10% of the trees were discarded, the remaining trees were summarized as a maximum clade credibility tree, including the average divergence times and their associated 95% high posterior densities (HPDs). Trees were visualized using FigTree v1.4.0 (Rambaut, 2012).

Reconstruction Of Ancestral Areas

Reconstruction of ancestral areas was performed using 10,001 trees generated by BEAST (Drummond and Rambaut, 2007). Dispersal-vicariance analysis was performed using the S-DIVA tool in RASP v 3.0 (Yu et al., 2014). S-DIVA analyses are advantageous because they provide statistical support for ancestral area reconstructions (Yu et al., 2010). To run S-DIVA, we follow the recommendations of the authors of the program (Yu et al., 2014), taking into account binary trees = 10,001, discard trees = 1000, and random trees = 100. In this analysis, six geographic zones were considered: A) Central/North American, B) Northwestern/South American, C) Amazonian, D) Chaco, E) Parana and F) South American transition (Fig. 2A). The Central North American region (A) comprises central and southern Mexico, Belize, Guatemala, El Salvador Honduras, and the Antilles. The northwestern South American region (B) consinst of Costa Rica, Panama, northwestern South America, Ecuador, Colombia, Venezuela, and Trinidad and Tobago. The Amazonian region (C) is the largest in the Neotropical region and extends through most of Brazil and the Guyanas and parts of Venezuela, Colombia, Ecuador, Peru, Bolivia, Paraguay, and Argentina. The Chaco region (D) encompasses northern and central Argentina, southern Bolivia, western and central Paraguay, Uruguay and central and northwestern Brazil. The Parana region (E) includes northwestern Argentina, the eastern region of Paraguay and the areas of extreme south and east Brazil. The South

American transition region (F) comprises the Highlands of the Andes between western Venezuela and northern Chile and central western Argentina (Fig. 2A). The distributions of the genera were established in geographic maps according to records produced by different authors and summarized in del Hoyo et al. (2014) (Table 3).

Table 3
Species distribution according to del Hoyo et al. (2014) and codes assigned to the distribution areas

Specie	Distribution	Area code
Amazona ochrocephala	Panama, Colombia, Venezuela, Guianas, Brazil, Ecuador, Peru, Bolivia	BCD
Anodorhynchus hyacinthinus	Brazil, Bolivia, Paraguay	CD
Anodorhynchus leari	Brazil	D
Ara ambiguus	Honduras, Nicaragua, Costa Rica, Panama, Colombia Ecuador	AB
Ara ararauna	Panama, Colombia, Venezuela, Guianas, Ecuador, Peru, Bolivia Brazil, Paraguay, Argentina, Ecuador	BCDE
Ara chloropterus	Panama, Colombia, Venezuela, Guianas, Brazil, Paraguay, Ecuador, Peru, Bolivia, Argentina.	BCDE
Ara glaucogularis	Bolivia	C
Ara macao	Mexico, Central America, Colombia, Venezuela, Guianas, Brazil, Ecuador, Peru, Bolivia	ABCD
Ara militaris	Mexico, Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina	ABCD
Ara severus	Panama, Colombia, Ecuador, Venezuela, Guianas, Peru, Bolivia, Brazil	BCD
Aratinga auricapillus	Brazil	DE
Aratinga jandaya	Brazil	CDE
Aratinga maculata	Brazil	C
Aratinga nenday	Bolivia, Brazil, Paraguay, Argentina	CD
Aratinga solstitialis	Brazil, Guiana	C
Aratinga weddellii	Colombia, Ecuador, Peru, Brazil, Bolivia	CD
Bolborhynchus lineola	Mexico, Panama, Venezuela, Colombia, Bolivia	ABC
Cacatua sulphurea	-	G
Columba livia	-	G
Conuropsis carolinensis	USA	A
Coracopsis vasa	-	G
Cyanoliseus patagonus	Argentina, Uruguay, Chile	DF
Cyanopsitta spixii	Brazil	D
Deroptyus accipitrinus	Colombia, Ecuador, Peru, Venezuela, Guianas, Brazil, Bolivia	C
Diopsittaca nobilis	Venezuela, Guianas, Brazil	BC
Enicognathus leptorhynchus	Chile	F
Eupsittula aurea	Suriname, Brazil, Peru, Bolivia, Paraguay, Argentina	CDE
Eupsittula cactorum	Brazil	CDE
Eupsittula canicularis	Mexico, Costa Rica	AB
Eupsittula canicularis	Mexico, Costa Rica	AB
Eupsittula canicularis	Mexico, Costa Rica	AB
Eupsittula nana	Mexico, Jamaica	A
Eupsittula pertinax	Panama, Colombia, Venezuela, Antilles, Guiana, Brazil	BC
Falco peregrinus	-	G
Forpus coelestis	Ecuador, Peru, Colombia	BF
Forpus conspicillatus	Panama, Colombia, Venezuela	B
Forpus cyanopygius	Mexico	A
Forpus modestus	Colombia, Venezuela, Brazil, Ecuador, Peru, Bolivia	C
Forpus passerinus	Colombia, Venezuela, Trinidad, Guianas, Brazil	BC
Forpus xanthops	Peru	C
Forpus xanthopterygius	Colombia, Ecuador, Peru, Brazil, Bolivia, Paraguay, Argentina	CDE

Specie	Distribution	Area code
Guaruba guarouba	Brazil	C
Hapalopsittaca melanotis	Peru, Bolivia	C
Leptosittaca branickii	Colombia, Ecuador, Peru	BF
Melopsittacus undulatus	-	G
Myopsitta monachus	Bolivia, Paraguay, Brazil, Argentina, Uruguay	CDEF
Nestor notabilis	-	G
Orthopsittaca manilatus	Colombia, Ecuador, Peru, Bolivia, Venezuela, Trinidad, Guianas, Brazil	BCDE
Pionites leucogaster	Brazil	CD
Pionites melanocephalus	Colombia, Venezuela, Guianas, Brazil, Ecuador, Peru	C
Primolius auricollis	Bolivia, Brazil, Paraguay, Argentina	CD
Primolius couloni	Peru, Brazil, Bolivia	C
Primolius maracana	Brazil, Parana, Paraguay, Argentina	CDE
Psilopsiagon aymara	Bolivia, Argentina	CDF
Psittacara brevipes	Mexico	A
Psittacara chloropterus	Hispaniola Island	A
Psittacara erythrogenys	Ecuador, Peru	B
Psittacara euops	Cuba	A
Psittacara finschi	Nicaragua, Costa Rica, Panama	AB
Psittacara holochlorus	Mexico, Nicaragua	A
Psittacara h. rubritorquis	Guatemala, El Salvador, Honduras, Nicaragua	A
Psittacara leucophthalmus	Colombia, Ecuador, Peru, Brazil, Guianas, Venezuela, Bolivia, Paraguay, Argentina, Uruguay	BCDE
Psittacara mitratus	Peru, Bolivia, Argentina	CD
Psittacara wagleri	Colombia, Venezuela	B
Pyrrhura albipectus	Ecuador, Peru	C
Pyrrhura frontalis	Brazil, Paraguay, Argentina, Uruguay	DE
Pyrrhura hoffmanni	Costa Rica, Panama	B
Pyrrhura leucotis	Brazil	E
Pyrrhura molinae	Bolivia, Brazil, Paraguay, Argentina	CD
Pyrrhura perlata	Brazil, Bolivia	CD
Pyrrhura picta	Venezuela, Brazil	C
Pyrrhura rupicola	Peru, Brazil, Bolivia	C
Rhynchopsitta pachyrhyncha	Mexico	A
Rhynchopsitta terrisi	Mexico	A
Thectocercus acuticaudatus	Colombia, Venezuela, Brazil, Bolivia, Paraguay, Argentina	BCD
Touit purpuratus	Venezuela, Brazil, Colombia, Ecuador, Peru	C

Table 4
Pairwise genetic distance between *Psittacara* species, estimated under K2P model using ND2 (above diagonal) and COI (below diagonal)

	P. leucophthalmus	*P. wagleri*	*P. mitratus*	*P. euops*	*P. chloropterus*	*P. erythrogenys*	*P. h. rubritorquis*	*P. holochlorus*	*P. finschi*	*P. brevipes*
P. leucophthalmus		0.051	0.061	0.060	0.066	0.067	0.071	0.070	0.070	0.063
P. wagleri	0.053		0.030	0.044	0.045	0.039	0.043	0.047	0.041	0.045
P. mitratus	0.043	0.026		0.029	0.028	0.027	0.032	0.040	0.029	0.034
P. euops	0.053	0.033	0.029		0.022	0.025	0.033	0.041	0.025	0.029
P. chloropterus	0.058	0.036	0.031	0.015		0.027	0.034	0.042	0.027	0.030
P. erythrogenys	-	-	-	-	-		0.018	0.025	0.015	0.020
P. h. rubritorquis	0.063	0.041	0.036	0.019	0.022	-		0.016	0.013	0.019
P. holochlorus	0.066	0.043	0.038	0.022	0.024	-	0.006		0.021	0.024
P. finschi	0.064	0.041	0.036	0.019	0.022	-	0.013	0.011		0.011
P. brevipes	0.061	0.038	0.029	0.017	0.020	-	0.011	0.008	0.006	

(-) No available Data

Table 5
Divergence times of the genera *Aratinga*, *Eupsittula* and *Psittacara*

Node	Mean	HPD 95%	Origin	Probability of area
1	11.69	8.96–14.71	Indeterminate (most probable C)	0.37
1a	7.66	5.76–9.82	Amazonian (C)	1
2	13.15	10.25–16.24	Most probable D / or CD	0.52 / 0.47
2a	10.98	8.23–14.02	Most probable D / or C	0.52 / 0.47
2b	9.24	6.43–12.32	Most probable AD / or AC	0.53 / 0.46
2c	1.2	0.74–1.78	Indeterminate (most probable CD)	0.35
3	14.5	11.46–17.86	Indeterminate (most probable F)	0.18
3a	4.77	3.13–6.72	Amazonian (C)	1
3b	3.45	2.03–5.28	Chaco (D)	1
4	5.38	3.76–7.36	Amazonian (C)	1
4a	1.92	1.36–2.58	North American (A)	1
5	7.88	5.59–10.85	Amazonian (C)	1
5a	0.66	0.34–1.11	Most probable A / B	0.51 /0.49
6	5.09	3.5–7.01	Amazonian (C)	1
6a	0.82	0.33–1.48	Indeterminate (CE)	1
6b	0.2	0.0-0.84	Amazonian (C)	1
7	17.8	14.28–21.75	Indeterminate (most probable AC/ACD)	0.63/0.37
8	14.21	11.32–17.41	Indeterminate (most probable CD)	0.38
9	15.08	11.66–18.87	Amazonian (C)	1
10	15.95	12.81–19.39	Indeterminate (most probable D)	0.22
11	20.41	16.25–24.86	Amazonian (C)	1
12	13.4	9.47–17.82	Amazonian (C)	1
13	29.93	24.45–35.81	Amazonian (C)	1
14	35.65	29.21–42.52	Indeterminate (CG)	1

The values Mean and HPD 95% are in millions of years. The nodes correspond to the chronogram in Fig. 2; HPD (high posterior densities) indicate 95% confidence intervals for the estimation of node age

Results

Phylogenetic analyses

To the best of our knowledge, our study is the most complete presented to date on the Arini tribe; 94.4% of the genera recognized in the Arini tribe were covered. In particular, for the genus *Psittacara*, 90% of the recognized species were considered, and for the *Aratinga* and *Eupsittula* genera, 100% of the species within each genus were included (Table 2). The alignments contained 1610 bp corresponding to the concatenated sequences of COI and ND2 (570 + 1040 bp) of 76 taxa. In the alignment of COI, 338 invariable (monomorphic) characters, 198 parsimony informative sites, 14 singleton variable sites, and 212 variable (polymorphic) characters were identified. In the alignment of ND2, 357 invariable (monomorphic) characters, 542 parsimony informative sites, 83 singleton variable sites, and 625 variable (polymorphic) characters were identified.

Bayesian inference (BI) and maximum likelihood (ML) analyses produced trees with similar topologies. Overall, the posterior probability (PP) and bootstrap probability (BP) values provided sufficient support for the phylogenetic relationships established within each group (Fig. 1). We found that of the seven monophyletic clades within the Arini tribe, four coincide with the genera *Psittacara*, *Eupsittula*, *Rhynchopsitta*, and *Pyrrhura*, and three clades consisted of different genera as follows: Clade 1 (C1) is formed by the genera *Ara*, *Primolius* and *Orthopsittaca*, which was retrieved as the basal genus in the clade; Clade 2 (C2) is formed by the genera *Aratinga*, *Conuropsis* and *Cyanopsitta*; and Clade 3 (C3) is formed by the genera *Thectocercus*, *Diopsittaca*, *Guaruba*, *Leptosittaca*, *Enicognathus*, *Anodorhynchus*, and *Cyanoliseus* (Fig. 1).

Regarding the genera (*Aratinga*, *Eupsittula* and *Psittacara*) that were the main objective of this work, our results show that clade C2 containing the genus *Aratinga* is sister to clade C1 and that the genus *Eupsittula* is a sister clade to the *Psittacara* clade. Clade C2 contains eight taxa, including six species from the genera *Aratinga*, the extinct *Conuropsis carolinensis* and *Cyanopsitta spixii*. In this clade, the position of *Cyanopsitta spixii* as a basal genus is weakly supported; therefore, more analyses are recommended. Additionally, in a well-supported node, *A. weddellii* is the ancestor of *C. carolinensis* and the rest of the *Aratinga* species. Within the *Eupsittula* clade, *E. aurea* and *E. nana* form a sister clade to *E. canicularis*; and *E. cactorum* and *E. pertinax* form a polytomy together with the rest of the group.

Within the *Psittacara* clade is subclade 1 (Sc1), which includes to *P. finschi*, *P. brevipes*, *P. holochlorus*, *P. h. rubritorquis*, and *P. erythrogenys*, (Fig. 1). The topologies of the BI and ML trees shows to *P. holochlorus* and *P. h. rubritorquis* (*P. rubritorquis* in the tree) as sister taxa, which also has a low genetic distance (Table 4). *P. brevipes* was found closely related to *P. finschi*. The genetic distance between *P. holochlorus* and *P. brevipes* was greater than that between *P. brevipes* and *P. finschi* (Table 4). We found *P. chloropterus* and *P. euops* to be sister species closely related to Sc1 (Fig. 1). In addition, *P. leucophthalmus*, *P. wagleri* and *P. mitratus* indicate an early divergence within the *Psittacara* clade; where *P. leucophthalmus* can be observed as a basal species. The greatest genetic distance between the closely related species in this genus was 0.071 (with ND2) between *P. leucophthalmus* and *P. h. rubritorquis*, and the shortest distance was 0.006 (with COI) between *P. brevipes* and *P. finschi* (Table 4).

Inference Of Divergence Times And Reconstruction Of Ancestral Areas

The estimated age of the nodes and the biogeographic reconstruction are shown in Table 5 and Fig. 2. In convergence testing for Bayesian analyses (Kass et al., 1998), the effective sample size values (ESS) for different statistics were acceptable (all higher than 200). In general, the results show that most of the analyzed genera of interest began their diversification during the Miocene epoch, then during the Pliocene the diversification among species continued, within each genus.

Clades C1 and C2 shared a common ancestor that also originated during the Miocene, which may have inhabited the Amazonian or Chaco regions (node 8, Table 5, Fig. 2), and their split was estimated to have ocurred around 11.32–17.41 millions years ago (Mya). In clade C1, the split of *Orthopsittaca manilatus* as an ancestral lineage was estimated to have occurred approximately 8.96–14.71 Mya, with the most likely ancestral area being the Amazonian region (region C) (node 1, Table 5, Fig. 2). Here, the genus *Ara* diverges during the Miocene, approximately 5.76–9.82 Mya, in the Amazonian region (node 1a, Table 5, Fig. 2).

The estimated age for the divergence of C2, with *C. spixii* as the basal lineage, is approximately 10.25–16.24 Mya, with a common ancestor that probably lived in the Chaco region (D) (node 2, Table 5, Fig. 2). Within C2, the subsequent diversification of the genus *Aratinga* (including *C. carolinensis*) occurred approximately 8.23–14.02 Mya; the biogeographic reconstruction obtained with S-DIVA shows this clade with an origin in the Amazonian or Chaco regions (regions C or D) (node 2a, Table 5, Figs. 2 and 3). It should be noted that the divergence time between the species *C. carolinensis* and the rest of the group was estimated at approximately 6.43–12.32 Mya (node 2b, Table 5, Figs. 2 and 3); *A. jandaya*, *A. auricapillus*, *A. maculata*, and *A. solstitialis* are the youngest group with a time of the most recent common ancestor (TMRCA) estimated to be approximately 0.74–1.78 Mya (node 2c, Table 5, Figs. 2 and 3). In this group, the Dispersal-vicariance analysis (S-DIVA) suggested three dispersal events and two vicariance events.

The divergence of the clade C3 lineages began at approximately 11.46–17.86 Mya, although the ancestral area of C3 could not be determined (node 3, Table 5, Fig. 2). However, it is clear that most of the genera that make up this clade diversified during the Miocene, with the following notable aspects: the TMRCA of *Thectocercus* and *Diopsittaca* was estimated to have originated approximately 3.13–6.72 Mya, and it was assigned to the Amazonian region (region C) (node 3a, Table 5, Fig. 2). Furthermore, TMRCA estimates for *Anodorhynchus* species indicate that the splits occurred approximately 2.03–5.28 Mya, and the ancestral area was possible in the Chaco region (region D) (node 3b, Table 5, Fig. 2).

According to the results, the sister genera *Psittacara* and *Eupsittula* are proposed to diverge around the Langhian stage, and TMRCA was estimated to have occurred at approximately 11.66–18.87 Mya. The origins of these genera can be assigned to the Amazonian region (region C) (node 9, Table 5, Fig. 2). The genus *Eupsittula* was estimated to have originated 5.59–10.85 Mya (node 5, Table 5, Figs. 2 and 4). In this group, *E. canicularis* is the youngest species with

an origin of approximately 0.34–1.11 Mya in the central and North American or in the northwestern regions of South America (regions A or B) (node 5a, Figs. 2 and 4). In this clade, the S-DIVA results suggested five dispersal events and one vicariance event.

The estimated age of divergence for the genus *Psittacara* is in the boundary of the Miocene-Pliocene epochs and constitutes one of the most diversified genera. This clade began its diversification with the separation of *P. leucophthalmus* approximately 3.76–7.36 Mya, and the Amazonian region was estimated as the ancestral area (region C) (node 4, Table 5, Figs. 2 and 5). Within this group, the species *P. finschi*, *P. brevipes*, *P. rubritorquis*, *P. holochlorus*, *P. erythrogenys*, *P. euops*, and *P. chloropterus* shared an ancestor dating to approximately 1.36–2.58 Mya and diversified in the Central-North American region (region A) (node 4a, Table 5, Figs. 2 and 5). In this clade, the S-DIVA suggested three dispersal events and three vicariance events.

On the other hand, the genus *Pyrrhura* diverges during the Pliocene epoch, originating at approximately 3.5–7.01 Mya in the Amazonian region (region C) (node 6, Table 5, Fig. 2). In this clade, the sister species *P. rupicola* and *P. molinae* (node 6b, Table 5, Fig. 2), and *P. picta* and *P. leucotis* (node 6a, Table 5, Fig. 2) are the most recent species.

Another interesting observation is the divergence of the genus *Rhynchopsitta* in the Langhian to Aquitanian stages. For the genus *Rhynchopsitta*, with an origin of approximately 14.28–21.75 Mya, the region of origin was not determinate, but the results suggested a possible origin in the Amazonian region (region C) (node 7, Table 5, Fig. 2). The TMRCA between *R. pachyrhyncha* and *R. terrisi* was estimated to have occurred approximately 0.04–0.42 Mya. S-DIVA results showed no dispersal or vicariance events in *Rhynchopsitta*.

Discussion

Phylogenetic analyses

In the present study we analyzed the mitochondrial sequences of taxa of the genera *Aratinga*, *Eupsittula*, and *Psittacara* to establish phylogenetic relationships as a first step required to estimate their divergence time and origin. The topology of the BI and ML trees revealed the Arini tribe as monophyletic and *Pionites-Deroptyus* as the sister group (Fig. 1). Clade C2 consisted of the genera *Aratinga*, *Conuropsis* and *Cyanopsitta* and is sister to clade C1 comprising the genera *Ara*, *Primolius* and *Orthopsittaca*, a relationship previously observed by Kirchman et al. (2012). However, the relationship of *Cyanopsitta* is questionable; here, it is retrieved as the basal genus of *Aratinga*, and in Kirchman et al. (2012), their inference shows *Cyanopsitta* as basal to clade C1, although in both studies, the relationships are recovered with low support values. In previous studies, the extinct *C. carolinensis* is located as a sister genus of *Aratinga* (del Hoyo et al., 2017; Kirchman et al., 2012); however, in our results, *C. carolinensis* is integrated into clade C2 with the genus *Aratinga*.

Regarding the genus *Eupsittula*, our analysis recovered the relationship of *E. aurea* and *E. nana* as sister species, as observed by Kirchman et al. (2012) (Fig. 1). Our results also corroborate those of Remsen et al. (2013), who placed *E. aurea* and *E. cactorum* in this genus. However, our results contrast those of Kirchman et al. (2012) who proposed *R. pachyrhyncha* as a sister group to *Eupsittula*.

Some uncertainties remain within the *Psittacara* genus; for some authors, *P. finschi* and *P. chloropterus* are conspecific with *P. leucophthalmus*, and it has been suggested that *P. rubritorquis* is conspecific with *P. holochlorus* (Collar et al., 2016; Collar and Sharpe, 2016). However, in our results, the phylogenetic trees and genetic distance demonstrate that *P. leucophthalmus* is basal and distant from *P. finschi* and *P. chloropterus* (Fig. 1). Similar to what was observed by Kirchman et al. (2012), in this study, *P. euops* and *P. chloropterus* are sister species. Additionally, *P. holochlorus* is conspecific with *P. rubritorquis* (Fig. 1, Table 4). We found that *P. brevipes* (restricted to the Revillagigedo Islands of Mexico) clearly is not a subspecies of *P. holochlorus* (distributed from the east and south of Mexico to the north of Nicaragua), as has traditionally been considered (BLI, 2015; del Hoyo et al., 2014). The genetic distance of *P. brevipes* is greater with *P. holochlorus* than with *P. finschi* (distributed in Nicaragua, Costa Rica, and Panama) (Table 4). In trees, *P. finschi* and *P. brevipes* are placed in an unresolved subclade. However, the inclusion of another taxon and character could resolve this uncertainty.

Divergence Times And Reconstruction Of Ancestral Areas

Overall, our results show that most of the taxa of the Arini tribe originated and diversified during the Miocene and Pliocene epochs, and only a few taxa diverged more recently in the Pleistocene epoch (Fig. 2). This coincides with what was previously reported where it is established that the diversification in Neotropical birds and other taxa was continuous throughout the Miocene and up to the Pleistocene under the complex multifactorial conditions described for South America (Antonelli et al., 2009; Barker, 2007; Brumfield and Edwards, 2007; Brumfield et al., 2007; Burns and Naoki, 2004; Cheviron et al., 2005; Cortés-Ortiz et al., 2003; García-Moreno and Fjeldså, 2000; Lim, 2007; Lovette, 2004; Miller et al., 2008; Santos et al., 2009).

In Central America, the closure of the Isthmus of Panama facilitated the phenomenon known as “The Great American Biotic Interchange,” which allowed the dispersion of taxa from north to south and from south to north, with the subsequent diversification of some taxa in new areas (Leigh et al., 2013; O’Dea et al., 2016; Woodburne, 2010). For different bird species, it has been established that the closure of the Isthmus of Panama promoted the dispersion and invasion of South American lineages toward North America (Weir et al., 2009).

Our results on the genera *Aratinga*, *Eupsittula* and *Psittacara* show that among the three, genus *Aratinga* is the oldest, followed by *Eupsittula* and the youngest is *Psittacara* (Fig. 2B). These genera originated in South America, most likely in the Amazon region (Fig. 2A). For the genus *Aratinga* (8.23–14.02 Mya) with *A. weddellii* as their ancestor, the center of origin was the Amazonian or Chaco regions, from which a first dispersal event occurred, suggesting that it took place to the southeast, west and east of the Amazonian region and to the north (Fig. 3). The northernmost species of all American parrots, *C. carolinensis* (6.43–12.32 Mya), would have originated through a vicariance event during the Miocene. However, given its ancient origin and distribution, we propose that the initial vicariance event was followed by dispersal events where it may have used the Greater and Lesser Antilles as part of its northward route (Fig. 3).

For *Eupsittula* (5.59–10.85 Mya), the most likely ancestral area was the Amazonian region, and dispersal events were the main promoters of diversification within the genus (Fig. 4). Range expansion occurred mainly to southeastern and northeastern South America and westward North America. Currently, species of the genus *Eupsittula* are found in the south of the Amazonian region (*E. aurea*, *E. cactorum* and *E. pertinax*), in North America *(E. canicularis* and *E. nana*) and in the Chaco and Parana regions (*E. aurea* and *E. cactorum*) (Fig. 4). In South America, this group may have benefited from the biotic and abiotic changes that caused the disappearance of Lake Pebas and the establishment of the Acre system conditions (Hoorn et al., 2010). The only mainland species in the group with a North American distribution is *E. canicularis*. Based on the estimated divergence time (0.34–1.11 Mya) and ancestral area (Central/North America) for this species, it is suggested that it crossed into North America until the Isthmus of Panama was well established (last closed 3.5 Mya (Leigh et al., 2013), with range expansion and subsequent speciation *in situ* (Fig. 4). We propose that populations from northern Mexico expanded their range northwestward, perhaps following the tropical dry forest (Pacific slope) with which it is strongly associated (Forshaw, 1989).

Age estimates for species of the genus *Psittacara* are presented here for the first time. According to our results, *Psittacara* is a recent genus whose divergence begins at the Miocene-Pliocene limits (Fig. 5). The genus *Psittacara* is widely distributed in the neotropics, with species inhabiting areas from North America to South America. Furthermore, it is one of the largest and has experienced the fastest diversification within the Arini tribe (TMRCA 3.76–7.36 Mya). According to our results, the events that promoted within-group diversification are dispersion and vicariance, suggesting a complex evolutionary history. The diversification of the first split in *Psittacara* occurs in the Amazonian region coinciding with the disappearance of the Acre system and the establishment of modern drainage in the Amazon basin (Hoorn et al., 2010). Additionally, it has been proposed that the Andes are an important geographic barrier that has promoted diversification in various bird species (Burns and Naoki, 2004; Cheviron et al., 2005; Weir, 2009). Considering the geographic range of *P. leucophthalmus* and *P. wagleri* and our results, we propose that the northern Andes (Venezuela and Colombia) are the geographic barrier that promoted diversification (Fig. 5). The uplift of the Andes of Colombia and Venezuela occurred approximately 5 – 3 Mya (Audemard, 2003; Dhont et al., 2005; Gregory-Wodzicki, 2000), which coincides with the origin of *P. wagleri* at approximately 3.48 Mya. *P. mitratus* also diverges by vicariance, but when observing the distribution of the species, there is no current geographical barrier related to its origin by vicariance. However, the most likely region of origin is the Amazon (2.69 Mya), where rivers or changes in vegetation could promote their separation (Fig. 5). For the species distributed in Central and North America and in the Antilles, we propose that the diversification most likely occurred in Central America, where 85.71% of its species are found (Fig. 5). Diversification of this subgroup occurred after the establishment of the Isthmus of Panama 3.5 Mya (Leigh et al., 2013), suggesting range expansion and subsequent *in situ* speciation, particularly for *P. finschi*, *P. rubritorquis* and *P. holochlorus*, which reached northwestern and eastern Mexico (del Hoyo et al., 2014; Howell and Webb, 1995).

Other notable observations are that with respect to the genus *Rhynchopsitta* currently inhabiting North America, its area of origin in South America indicates a possible single event of ancestral arrival before the closure of the Isthmus of Panama. It is possible that the ancestor used the Neogene volcanic arc of Central America to reach North America, as has been reported for other taxa (Coates et al., 2004; Fritz et al., 2012; Parada et al., 2013; Prothero et al., 2014; Weir et al., 2008). Subsequently, the genus recently diversified (TMRCA = 0.04–0.42 Mya) in Mexico during the Pleistocene epoch.

Conclusions

To the best of our knowledge, this report includes analyses of the largest number of species of the Arini tribe. We identified seven well supported clades, some of which coincided with recognized genera (*Rhynchopsitta*, *Psittacara*, *Eupsittula*, and *Pyrrura*). Some relationships between the clades are not widely supported, but they are constant under different analyses. Our analyses show a complex evolutionary history within the tribe, with most of the analyzed genera originating during the Miocene (*Ara*, *Orthopsittaca*, *Aratinga*, *Cyanopsitta*, *Guaruba*, *Leptosittaca*, *Enicognathus*, *Cyanoleus, Eupsittula*, and *Rhynchopsitta*) and some around the Miocene-Pliocene (*Psittacara* and *Pyrrhura*). We propose that the genera *Rynchopsitta* and *C. carolinensis* reached North America before the closure of the Isthmus of Panama by independent events. Additionally, the lineages that arrived in North America after the closure of the Isthmus of Panama are *P. finschi*, *P. brevipes*, *P. holochlorus*, and *E. canicularis*. Because the Arini tribe includes a great diversity of species with a wide distribution in the Neotropics, this study supports the needs for further analyses for each of the seven identified clades. Additionally, it is recommended to consider species and subspecies within each group and expand the number of characters to refine the proposed results.

Declarations

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Author´s contribution

MGZP, GPJ, TCMR, and HCC conceived and designed the study. GPJ carried out the experiments. GPJ and MGZP carried out the bioinformatics analyses. GPJ, MGZP, TCMR, and HCC drafted the manuscript. All authors read and approved the final manuscript.

Data availability

The datasets supporting the conclusions of this article are available in the GenBank repository [https://www.ncbi.nml.gov/] under the accession numbers listed in Table 2.

Conflict of interest

The authors declare that they have no conflict of interest.

References

1. Aldous, D. J. (2001). Stochastic models and descriptive statistics for phylogenetic trees, from yule to today. *Statistical Science*, *16*(1), 23–34.
2. Alfaro, M. E., & Huelsenbeck, J. P. (2006). Comparative performance of bayesian and aic-based measures of phylogenetic model uncertainty. *Systematic biology*, *55*(1), 89–96.
3. Antonelli, A., Nylander, J. A., Persson, C., & Sanmartín, I. (2009). Tracing the impact of the Andean uplift on Neotropical plant evolution. *Proceedings of the National Academy of Sciences, 106*(24), 9749 – 9754.
4. Audemard, M., F (2003). Geomorphic and geologic evidence of ongoing uplift and deformation in the Mérida Andes, Venezuela. *Quaternary International*, *101*, 43–65.
5. Barker, F. K. (2007). Avifaunal interchange across the Panamanian isthmus: Insights from *Campylorhynchus* wrens. *Biological Journal of the Linnean Society*, *90*(4), 687–702.
6. Berkunsky, I., Quillfeldt, P., Brightsmith, D. J., Abbud, M., Aguilar, J., Alemán-Zelaya, U., et al. (2017). Current threats faced by Neotropical parrot populations. *Biological Conservation*, *214*, 278–287.
7. Brumfield, R. T., & Edwards, S. V. (2007). Evolution into and out of the Andes: A bayesian analysis of historical diversification in T*hamnophilus* antshrikes. *Evolution*, *61*(2), 346–367.
8. Brumfield, R. T., Tello, J. G., Cheviron, Z., Carling, M. D., Crochet, N., & Rosenberg, K. V. (2007). Phylogenetic conservatism and antiquity of a tropical specialization: Army-ant-following in the typical antbirds (*Thamnophilidae*). *Molecular Phylogenetics and Evolution*, *45*(1), 1–13.
9. Burns, K. J., & Naoki, K. (2004). Molecular phylogenetics and biogeography of Neotropical tanagers in the genus *Tangara*. *Molecular Phylogenetics and Evolution*, *32*(3), 838–854.
10. Cantú-Guzmán, J. C., Sánchez-Saldaña, M., Grosselet, M., & Silva-Gámez, J. (2007). *Tráfico ilegal de pericos en México: Una evaluación detallada*. Defenders of Wildlife.
11. Chesser, R. T., Banks, R. C., Cicero, C., Dunn, J. L., Kratter, A. W., Lovette, I. J., et al. (2014). Fifty-fifth Supplement to the American Ornithologists' UnionCheck-list of North American birds. *The Auk*, *131*(4), CSi–CSxv.
12. Cheviron, Z., Hackett, S. J., & Capparella, A. P. (2005). Complex evolutionary history of a Neotropical lowland forest bird (*Lepidothrix coronata*) and its implications for historical hypotheses of the origin of Neotropical avian diversity. *Molecular Phylogenetics and Evolution*, *36*(2), 338–357.
13. Clements, J., Schulenberg, T. S., Iliff, M. J., Billerman, S. M., Fredericks, T. A., Gerbracht, J. A. (2021). The eBird/Clements checklist of birds of the world: v2021. Retrieved June 2022, from https://www.birds.cornell.edu/clementschecklist/download/
14. Coates, A. G., Collins, L. S., Aubry, M. P., & Berggren, W. A. (2004). The geology of the Darien, Panama, and the late Miocene-Pliocene collision of the Panama arc with northwestern South America.Geological Society of America Bulletin, *116*(11–12), 1327 – 1344.
15. Collar, N. J. (1997). Family Psittacidae (parrots). In J. del Hoyo, A. Elliott, & J. Sargatal (Eds.), *Handbook of the birds of the world* (Vol. 4). Lynx Edicions.
16. Collar, N. J., Boesman, P., & Sharpe, C. J. (2016). White-eyed Parakeet (Psittacara leucophthalmus). In del J. Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & de E. Juana (Eds.), *Handbook of the Birds of the World Alive*. Lynx Edicions.
17. Collar, N. J., & Sharpe, C. J. (2016). Red-throated Parakeet (Psittacara rubritorquis). In del J. Hoyo, A. Elliott, J. Sargatal, D. A. Christie, & de E. Juana (Eds.), *Handbook of the Birds of the World Alive*. Lynx Edicions.
18. Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (2022). The cites appendices. Retrieved June 2022, from https://cites.org/eng/app/appendices.php
19. Cortés-Ortiz, L., Bermingham, E., Rico, C., Rodrıguez-Luna, E., Sampaio, I., & Ruiz-Garcıa, M. (2003). Molecular systematics and biogeography of the Neotropical monkey genus, *Alouatta*. *Molecular Phylogenetics and Evolution*, *26*(1), 64–81.
20. Darlington, P. J. Jr. (1957). *Zoogeography: The geographical distribution of animals*. John Wiley & Sons.
21. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., & de Juana, E. (2017). *Handbook of the birds of the world alive*. Lynx Edicions.
22. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., & de Juana, E. (2014). *Handbook of the birds of the world alive*. Lynx Edicions.
23. Dhont, D., Backé, G., & Hervouët, Y. (2005). Plio-Quaternary extension in the Venezuelan Andes: Mapping from SAR JERS imagery. *Tectonophysics*, *399*(1), 293–312.
24. Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, *7*, 214.
25. Eberhard, J. R., & Bermingham, E. (2005). Phylogeny and comparative biogeography of *Pionopsitta* parrots and *Pteroglossus* toucans. *Molecular Phylogenetics and Evolution*, *36*(2), 288–304.
26. Eberhard, J. R., Bermingham, E., & Zink, R. (2004). Phylogeny and biogeography of the *Amazona ochrocephala* (Aves: Psittacidae) complex. *The Auk*, *121*(2), 318–332.
27. Escalante-Pliego, P., Navarro, A., & Peterson, A. T. (1993). A geographic, ecological and historical analysis of land bird diversity in Mexico. In T. P. Ramamoorthy, R. Bye, A. Lot, & J. Fa (Eds.), *Biological diversity of Mexico: Origins and distribution*. Oxford University Press.
28. Forshaw, J. (1989). *Parrots of the world*. Lansdowne Editions.
29. Forshaw, J. (2010). *Parrots of the world*. Princeton University Press.
30. Fritz, U., Stuckas, H., Vargas-Ramírez, M., Hundsdörfer, A. K., Maran, J., & Päckert, M. (2012). Molecular phylogeny of Central and South American slider turtles: Implications for biogeography and systematics (Testudines: Emydidae: *Trachemys*). *Journal of Zoological Systematics and Evolutionary Research*, *50*(2), 125–136.

31. García-Moreno, J., & Fjeldså, J. (2000). Chronology and mode of speciation in the Andean avifauna. *Bonner Zoologische Monographien*, *46*, 25–46.
32. Genes Codes-Software Sequencher (2015). Gene Codes Software Sequencer (Version 4.1). Retrieved March 2015, from http://www.genecodes.com/
33. Gregory-Wodzicki, K. M. (2000). Uplift history of the Central and Northern Andes: A review. *Geological Society of America Bulletin*, *112*(7), 1091–1105.
34. Hasegawa, M., Kishino, H., & Yano, T. A. (1985). Dating of the human-ape splitting by a molecular clock of mitochondrial DNA. *Journal of Molecular Evolution*, *22*(2), 160–174.
35. Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., et al. (2010). Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, *330*(6006), 927–931.
36. Howell, S. N., & Webb, S. (1995). *A guide to the birds of Mexico and northern Central America*. Oxford University Press.
37. Jarvis, E. D., Mirarab, S., Aberer, A. J., Li, B., Houde, P., Li, C., et al. (2014). Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science*, *346*(6215), 1320–1331.
38. Joseph, L., Toon, A., Schirtzinger, E. E., Wright, T. F., & Schodde, R. (2012). A revised nomenclature and classification for family-group taxa of parrots (Psittaciformes). *Zootaxa*, *3205*(2), 26–49.
39. Kass, R. E., Carlin, B. P., Gelman, A., & Neal, R. M. (1998). Markov Chain Monte Carlo in practice: A roundtable discussion. *The American Statistician*, *52*(2), 93–100.
40. Kirchman, J. J., Schirtzinger, E. E., & Wright, T. F. (2012). Phylogenetic relationships of the extinct Carolina Parakeet (*Conuropsis carolinensis*) inferred from DNA sequence data. *The Auk*, *129*(2), 197–204.
41. Leigh, E. G., O'Dea, A., & Vermeij, G. J. (2013). Historical biogeography of the Isthmus of Panama. *Biological Reviews of the Cambridge Philosophical Society*, *89*(1), 148–172.
42. Lim, B. K. (2007). Divergence times and origin of neotropical sheath-tailed bats (Tribe Diclidurini) in South America. *Molecular Phylogenetics and Evolution*, *45*(3), 777–791.
43. Lovette, I. J. (2004). Molecular phylogeny and plumage signal evolution in a trans Andean and circum Amazonian avian species complex. *Molecular Phylogenetics and Evolution*, *32*(2), 512–523.
44. Miller, M. J., Bermingham, E., Klicka, J., Escalante, P., do Amaral, F. S. R., Weir, J. T. (2008). Out of Amazonia again and again: Episodic crossing of the Andes promotes diversification in a lowland forest flycatcher. *Proceedings of the Royal Society of London B: Biological Sciences, 275*(1639), 1133 – 1142.
45. Müller, J., Müller, K., Neinhuis, C., & Quandt, D. (2005). Phyde- Phylogenetic data editor. Retrieved March 2015, from http://www.phyde.de/
46. O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L. (2016). Formation of the Isthmus of Panama.Science Advances, 2(8), e1600883.
47. Parada, A., Pardiñas, U. F., Salazar-Bravo, J., D'Elía, G., & Palma, R. E. (2013). Dating an impressive Neotropical radiation: Molecular time estimates for the Sigmodontinae (Rodentia) provide insights into its historical biogeography. *Molecular Phylogenetics and Evolution*, *66*(3), 960–968.
48. Peters, J. L. (1937). *Check-list of birds of the world* (III vol.). Harvard University Press.
49. Posada, D. (2008). JModelTest: Phylogenetic model averaging. *Molecular Biology and Evolution*, *25*(7), 1253–1256.
50. Prothero, D. R., Campbell Jr, K. E., Beatty, B. L., & Frailey, C. D. (2014). New late Miocene dromomerycine artiodactyl from the Amazon Basin: Implications for interchange dynamics. *Journal of Paleontology*, *88*(3), 434–443.
51. Rambaut, A. (2012). FigTree (Version 1.4.0). Retrieved March 2015, from http://tree.bio.ed.ac.uk/software/figtree
52. Remsen, J. J., Schirtzinger, E. E., Ferraroni, A., Silveira, L. F., & Wright, T. F. (2013). DNA-sequence data require revision of the parrot genus *Aratinga* (Aves: Psittacidae). *Zootaxa*, *3641*(3), 296–300.
53. Ribas, C. C., Gaban-Lima, R., Miyaki, C. Y., & Cracraft, J. (2005). Historical biogeography and diversification within the Neotropical parrot genus *Pionopsitta* (Aves: Psittacidae). *Journal of Biogeography*, *32*(8), 1409–1427.
54. Ribas, C. C., Joseph, L., & Miyaki, C. Y. (2006). Molecular systematics and patterns of diversification in *Pyrrhura* (Psittacidae), with special reference to the picta-leucotis complex. *The Auk*, *123*(3), 660–680.
55. Ribas, C. C., & Miyaki, C. Y. (2004). Molecular systematics in *Aratinga* parakeets: Species limits and historical biogeography in the '*solstitialis*' group, and the systematic position of *Nandayus nenday*. *Molecular Phylogenetics and Evolution*, *30*(3), 663–675.
56. Ronquist, F., & Huelsenbeck, J. P. (2003). MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, *19*(12), 1572–1574.
57. Salvadori, T. (1891). *Catalogue of the psittaci, or parrots, in the collection of the british museum* (Vol. XX). Longmans.
58. Santos, J. C., Coloma, L. A., Summers, K., Caldwell, J. P., Ree, R., & Cannatella, D. C. (2009). Amazonian amphibian diversity is primarily derived from late Miocene Andean lineages.PLoS Biol, 7(3), e1000056.
59. Schweizer, M., Seehausen, O., & Hertwig, S. T. (2011). Macroevolutionary patterns in the diversification of parrots: Effects of climate change, geological events and key innovations. *Journal of Biogeography*, *38*(11), 2176–2194.
60. Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M., & Kumar, S. (2011). Mega5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, *28*(10), 2731–2739.
61. Tavaré, S. (1986). Some probabilistic and statistical problems in the analysis of DNA sequences. In R. M. Miura (Ed.), *Lectures on mathematics in the life sciences* (17 vol.). The American Mathematical Society.
62. Tavares, E. S., Baker, A. J., Pereira, S. L., & Miyaki, C. Y. (2006). Phylogenetic relationships and historical biogeography of neotropical parrots (Psittaciformes: Psittacidae: Arini) inferred from mitochondrial and nuclear DNA sequences. *Systematic biology*, *55*(3), 454–470.

63. Tavares, E. S., Yamashita, C., & Miyaki, C. Y. (2004). Phylogenetic relationships among some Neotropical parrot genera (Psittacidae) based on mitochondrial sequences. *The Auk*, *121*(1), 230–242.

64. The BirdLife International (BLI) (2015). The birdlife checklist of the birds of the world (version 8). Retrieved November 2015, from http://www.birdlife.org/datazone/userfiles/file/Species/Taxonomy/BirdLife_Checklist_Version_80.zip

65. Vigors, N. A. (1825). Sketches in ornithology; or observations on the leading affinities of some of the more extensive groups of birds. *The Zoological Journal, II*, 37 – 69.

66. Weir, J. T. (2009). Implications of genetic differentiation in neotropical montane forest birds. *Annals of the Missouri Botanical Garden*, *96*(3), 410–433.

67. Weir, J. T., Bermingham, E., Miller, M. J., Klicka, J., & González, M. A. (2008). Phylogeography of a morphologically diverse Neotropical montane species, the Common Bush-Tanager (*Chlorospingus ophthalmicus*). *Molecular Phylogenetics and Evolution*, *47*(2), 650–664.

68. Weir, J. T., Bermingham, E., & Schluter, D. (2009). The great American biotic interchange in birds. *Proceedings of the National Academy of Sciences, 106*(51), 21737 – 21742.

69. Wetmore, A. (1935). The Thick-Billed Parrot in Southern Arizona. *The Condor*, *37*(1), 18–21.

70. Woodburne, M. O. (2010). The Great American Biotic Interchange: Dispersals, tectonics, climate, sea level and holding pens. *Journal of Mammalian Evolution*, *17*(4), 245–264.

71. Yu, Y., Harris, A., & He, X. (2010). S-DIVA (Statistical Dispersal-Vicariance Analysis): A tool for inferring biogeographic histories. *Molecular Phylogenetics and Evolution*, *56*(2), 848–850.

72. Yu, Y., Harris, A. J., & He, X. J. (2014). Phylogenetics and Evolution Software, RASP (Reconstruct Ancestral State in Phylogenies) (Version 3.0). Retrieved November 2014, from http://mnh.scu.edu.cn/soft/blog/RASP

73. Yule, G. U., & Willis, F. R. S. (1924).Philosophical Transactions of the Royal Society of London Series B, 213,21–87.

74. Zwickl, D. J. (2006). *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion*. University of texas.

Figures

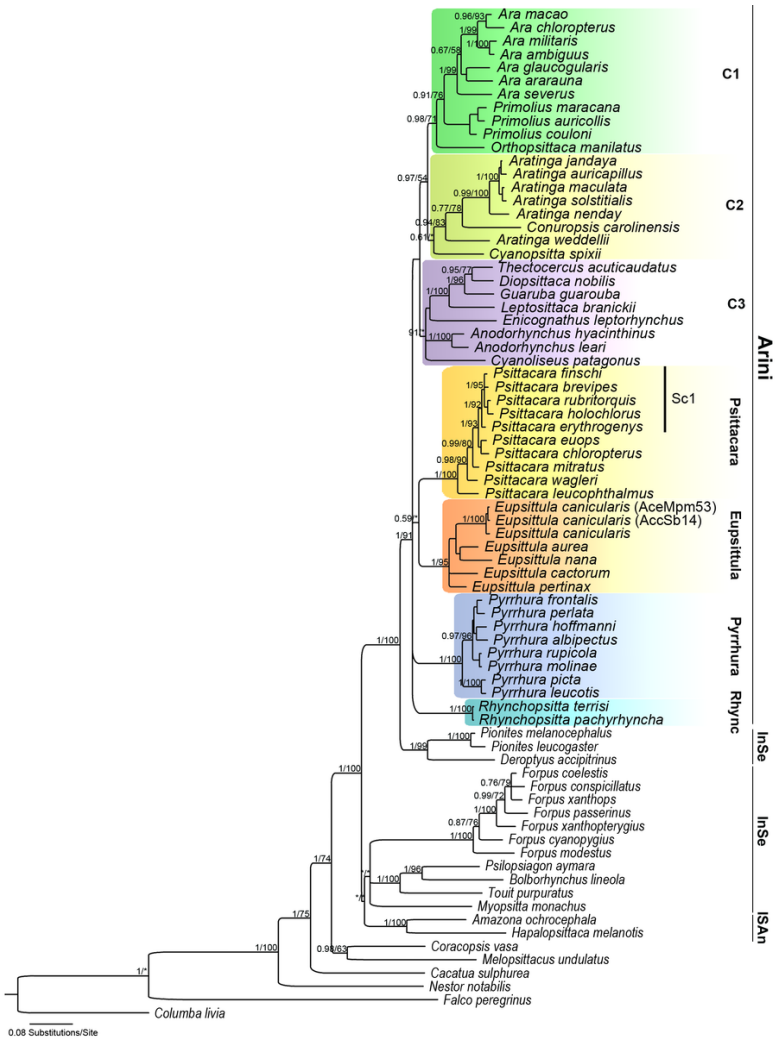

Figure 1

Consensus tree showing the phylogenetic relationships between *Aratinga, Eupsittula* and *Psittacara*and related genera obtained using BI and ML analyses. Estimates were made with 1610 characters corresponding to the concatenated sequences of COI and ND2 (570 +1040 bp) of 76 taxa. Values on the branches represent posterior probabilities and bootstrap values (PP/BP). (*) Value inferior at PP = 0.5 or PB = 50. The scale bar under the tree represents the number of substitutions per site. Abbreviations: C1, C2, C3 = Clade 1, Clade 2, Clade 3; Sc1 = Subclade 1; InSe = Incertae sedis tribe; ISAn = Incertae sedis and Androglossini tribes

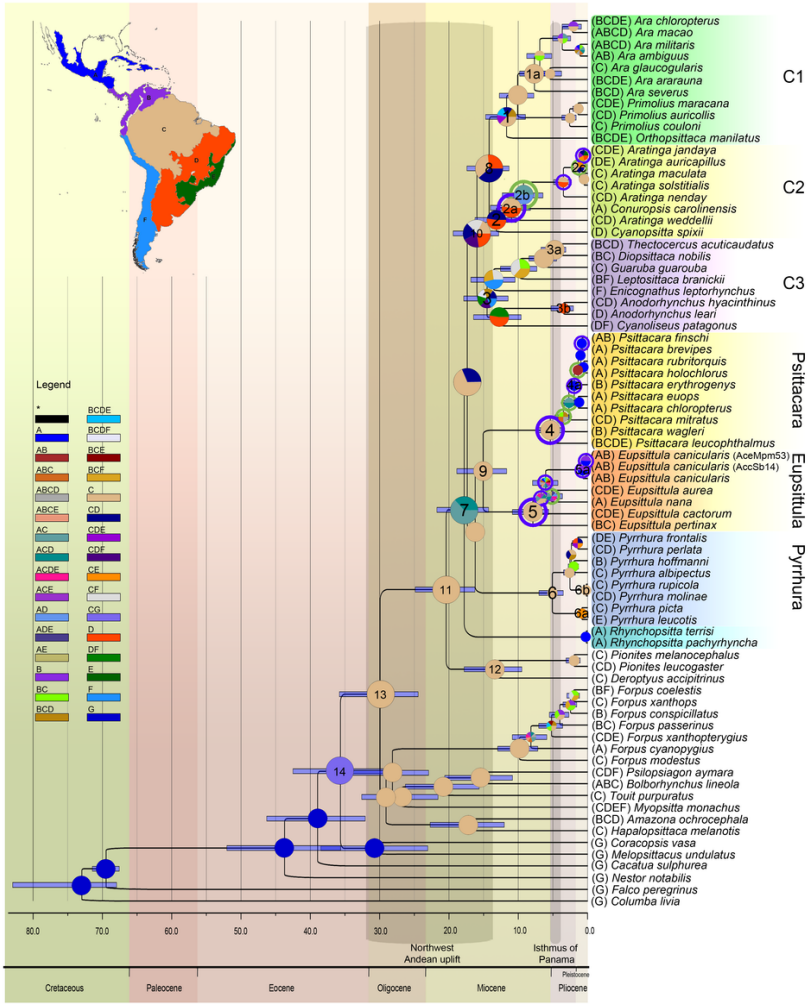

Figure 2

Chronogram with divergence times and ancestral distribution of the genera *Aratinga, Eupsittula* and *Psittacara* and related genera. Bars indicate 95% confidence intervals (high posterior densities, HPD) for node age estimates. The pie charts at the nodes represent the probabilities of the ancestral area at the respective nodes. The legend to the left summarizes the colors and codes that represent geographic zones associated with the labels: A) North American, B) Northwestern South American, C) Amazonian, D) Chaco, E) Parana and F) South American transition. The values of divergence times and ancestral areas can be consulted in Table 5. The green rings represent vicariance events, and the purple rings represent dispersal events

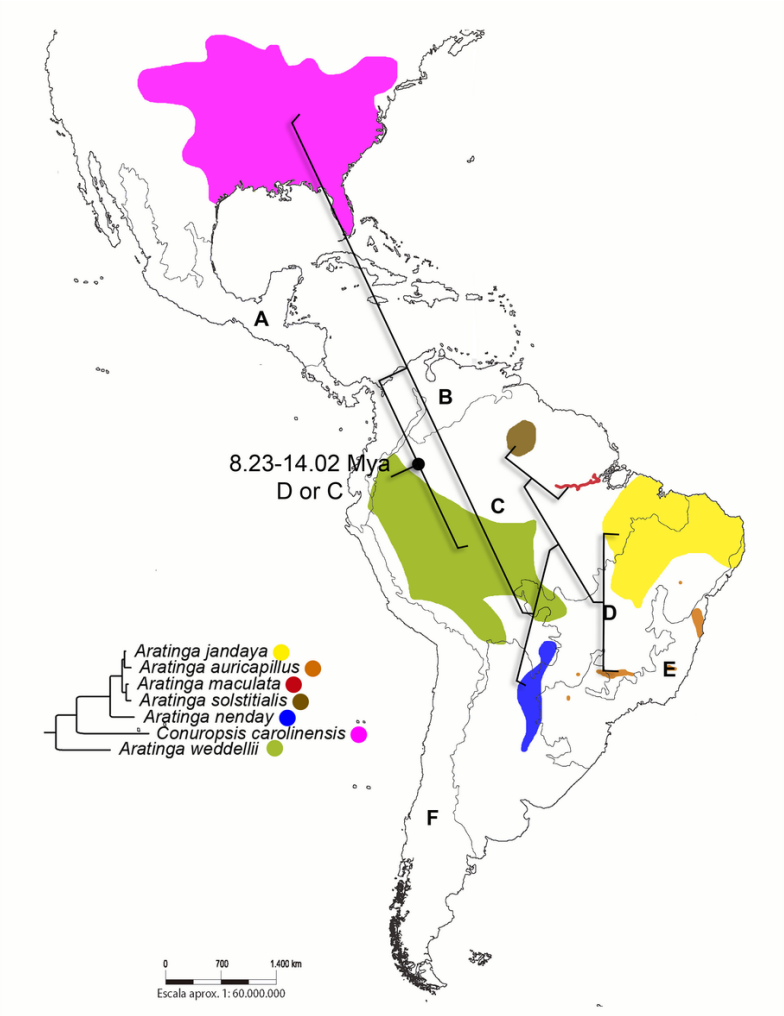

Figure 3

Clade description and map of distribution areas for the genus *Aratinga*. The estimated values of the TMRCA (HPD 95%) and the most likely ancestral area are indicated. The colored distribution areas on the map represent the current distribution of each species of the genus included in this analysis. The letters A, B, C, D, E, and F within the maps represent the six Neotropical regions (details in the text)

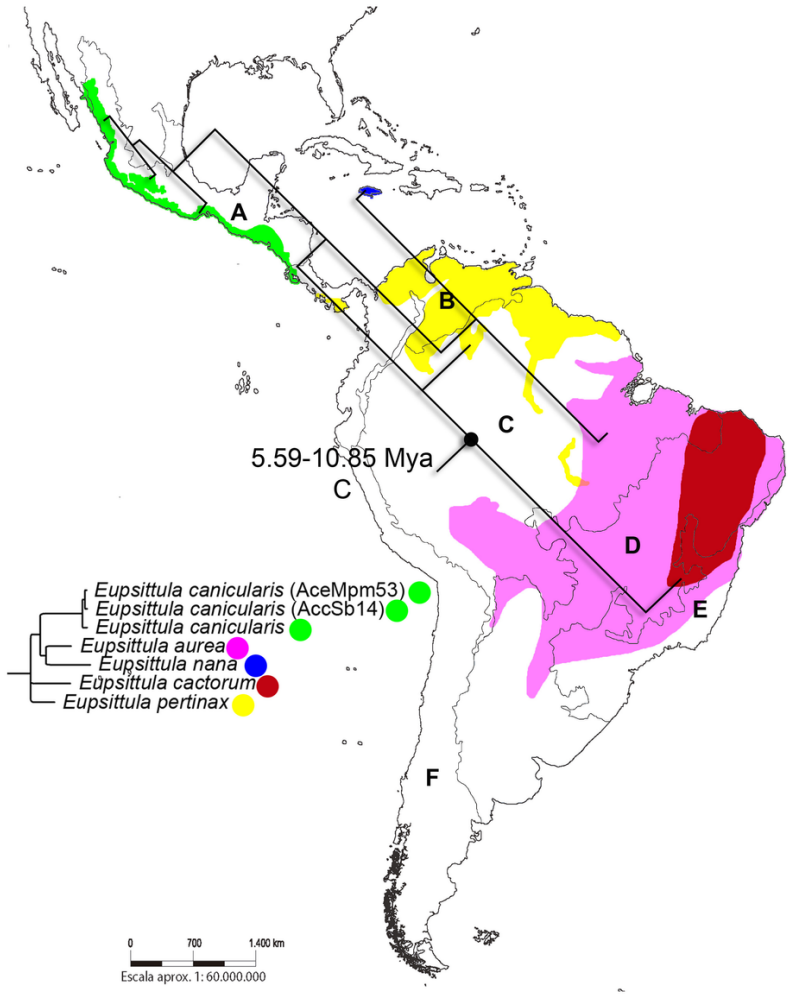

Figure 4

Clade description and map of distribution areas for the genus *Eupsittula*. The estimated values of the TMRCA (HPD 95%) and the most likely ancestral area are indicated. The colored distribution areas in the map represent the current distribution of each species of the genus included in this analysis. The letters A, B, C, D, E, and F within the maps represent the six Neotropical regions (details in the text)

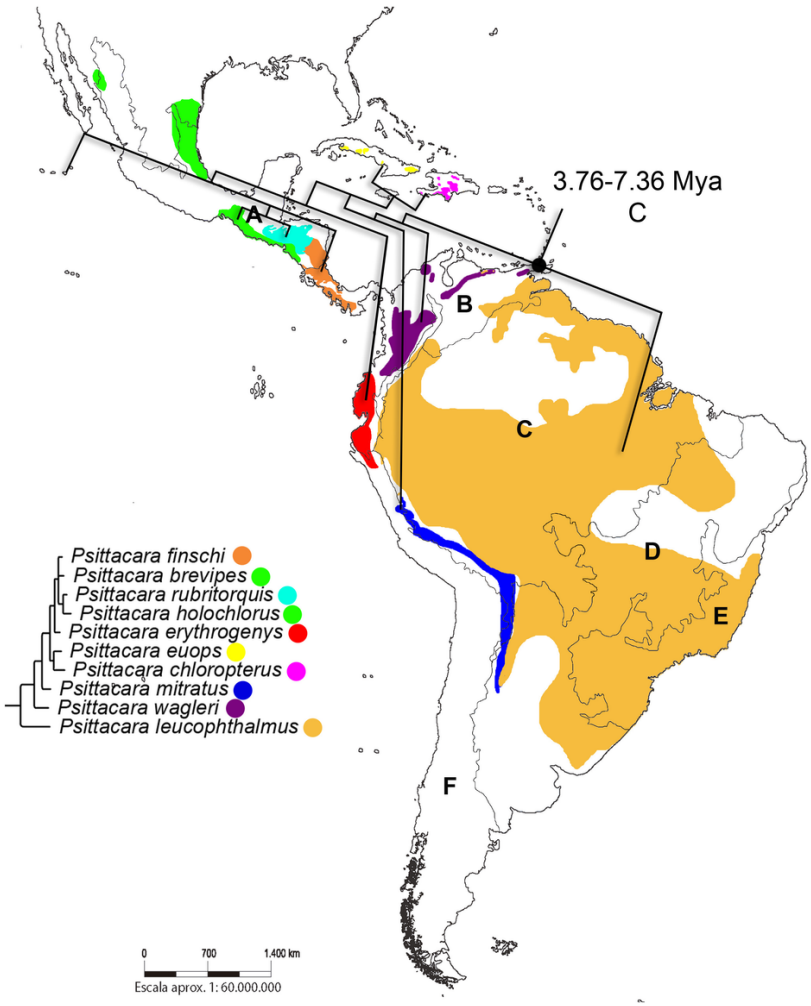

Figure 5

Clade description and map of distribution areas for the genus *Psittacara*. The estimated values of the TMRCA (HPD 95%) and the most likely ancestral area are indicated. The colored distribution areas in the map represent the current distribution of each species of the genus included in this analysis. The letters A, B, C, D, E, and F within the maps represent the six Neotropical regions (details in the text)