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A molecular phylogenetic analysis of the genera of fruit doves and their allies using dense taxonomic sampling

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Abstract

Fruit doves and their allies are a diverse group within the pigeon and dove family (Aves: Columbidae). Progress toward subfamilial classification of Columbidae relies on identifying major groups and the phylogenetic relationships within these groups. One such recently proposed group is the Raphinae, based on previous evidence that the extinct dodo is potentially within what was formerly recognized as the Treroninae (fruit doves and allies). Although several studies have explored the phylogenetic relationships within Columbidae, most have focused either on broad-scale, familial-level relationships or finer-scale, species-level relationships. Here we use mitochondrial and nuclear gene sequences from a diverse taxonomic sample to identify relationships among the genera and species of fruit doves and their allies. In particular, our goal is to identify which of these genera should be included within Raphinae (the name that has taxonomic priority over Treroninae), focusing on an inclusive, well-supported, monophyletic group. We also use dense taxon sampling to explore relationships among genera and species in this group, expanding on previous studies. In addition, we use resulting phylogenetic hypotheses to reconstruct the ancestral evolutionary history of foraging mode and biogeographic patterns of dispersal within the group. We use two data sets for phylogenetic analysis: the first consisting of novel sequences generated for this project and the second of additional, previously published sequences from the fruit-dove genus (*Ptilinopus*). Our analyses found support for the monophyly of a clade that contains a large fraction of the genera currently classified within Raphinae and also found several well-supported clades within this group of pigeons and doves. Character reconstruction methods based on the resulting phylogeny recover multiple transitions from a terrestrial to an arboreal foraging mode and evidence for multiple dispersal events from Asia to Africa throughout the history of the clade.

Introduction

Pigeons and doves (Aves: Columbidae) are a highly successful and diverse group of birds that are globally distributed and inhabit a variety of habitats (Goodwin 1983; Gibbs et al. 2001). However, despite publication of several studies on phylogenetic relationships of Columbiformes, there are still many uncertainties about the diversification patterns within the order (Johnson and Clayton 2000a and 2000b; Johnson et al. 2001; Pereira et al. 2007; Gibb and Penny 2010; Johnson et al. 2010; Johnson and Weckstein 2011; Cibois et al. 2014; Sweet and Johnson 2015). One group that remains ambiguous is the fruit pigeons and doves ("fruit doves" hereafter) and allied genera (*Ptilinopus*, *Ducula*, *Gymnophaps*, *Lopholaimus*, *Hemiphaga*, *Phapitreron*, *Goura*, *Caloenas*, *Otidiphaps*, *Trugon*, *Turtur*, *Oena*, *Chalcophaps*, and *Treron*), which had previously been considered to be members of a subfamily, the Treroninae (del Hoyo et al. 1997). However, a more recent classification (del Hoyo et al. 2014) places all of these genera within an expanded group, the Raphinae, upon the discovery that the extinct dodo (*Raphus cucullatus*) is phylogenetically embedded within Treroninae (Shapiro et al. 2002; Pereira et al. 2007), and with Raphinae being the oldest available name for this group, as discussed by Cracraft in Dickinson and Remsen (2013). Pereira et al. (2007) identified the monophyly and composition of this group, but the result was somewhat unstable across analyses and included only limited taxon sampling.

In addition to the more typical and large genera of fruit doves (*Ptilinopus*, *Ducula*, and *Treron*), several less diverse genera are associated with the fruit doves and allies. Del Hoyo et al. (1997) defined Treroninae as including the green pigeons (*Treron*), long-tailed pigeons (*Gymnophaps, Cryptophaps, Lopholaimus,* and *Hemiphaga*), fruit doves (*Ducula*, *Alectroenas*, *Drepanoptila*, and *Ptilinopus*), and brown pigeons (*Phapitreron*). The molecular phylogeny of Pereira et al. (2007) also included wood doves (*Turtur*, *Oena*, and *Chalcophaps*), ground pigeons (*Otidiphaps*, *Trugon*, *Didunculus*, *Microgoura*, *Goura,* and *Caloenas*), cloven-feathered doves (*Drepanoptila*), and blue pigeons (*Alectroenas*) in a clade with the Treroninae genera of del Hoyo et al. (1997). However, Gibbs et al. (2001) considered the wood doves (*Chalcophaps*, in particular) to be more closely related to bronzewings (*Henicophaps*) in the phabine clade (*Phaps*, *Geophaps*, *Ocyphaps*, *Petrophassa*, *Geopelia*, and *Leucosarcia*). Goodwin (1983) likewise considered *Chalcophaps*, along with *Oena* and *Turtur*, to be closely related to the phabines. He also included green pigeons, long-tailed pigeons, fruit doves, blue pigeons, and the cloven-feathered doves as a clade. Recently, del Hoyo et al. (2014) removed Treroninae from their classification and instead included all proposed Treroninae genera in an expanded subfamily Raphinae. This classification corresponds to "Clade C" from Pereira et al. (2007) and is expanded to include the phabine genera and allies. However, the inclusion of the phabines in this group was quite unstable. Shapiro et al. (2002) first recovered *Drepanoptila* and *Alectroenas* nested within *Ptilinopus*, a relationship that has remained consistent in more recent studies (Cibois et al. 2014). This study had an extensive representation of the diverse *Ptilinopus* genus but did not focus on other related genera. Given the recent instability in these classification schemes, it is important to sample genera and species more densely to identify stable phylogenetic patterns.

The phylogenetic and taxonomic statuses of these lineages has important implications for the evolution of Columbiformes, because this group could encompass a geographically and ecologically diverse subset of taxa (Goodwin 1983; Gibbs et al. 2001; del Hoyo et al. 2014). The most species-rich genus within this group, *Ptilinopus*, is found primarily in forest canopies of Southeast Asia and Oceania. Species in *Ptilinopus* vary in size but are all primarily frugivorous. Species from two other diverse genera, *Ducula* and *Treron*, are also primarily found in forest canopies and forage on fruit. However, *Treron* has a broad geographic range, with representatives in Asia and Africa. Additional arboreal and frugivorous groups with phylogenetic affinities likely include the long-tailed pigeons from Australasia (*Gymnophaps*, *Lophalamius,* and *Hemiphaga*), *Phapitreron* from the Philippines, *Drepanoptila* and *Cryptophaps* from Oceania, and *Alectroenas* from islands in the western Indian Ocean. Other allied genera are terrestrial and primarily granivorous. The large ground pigeons are terrestrial and found in rainforest habitats in Oceania. Shapiro et al. (2002) place the terrestrial *Caloenas nicobarica* (Nicobar pigeon) as the closest living relative to the extinct dodo (*Raphus cucullatus*). The small-bodied wood doves also forage on the ground and are distributed in Africa and Australasia. Thus, understanding the transitions between terrestrial and arboreal foraging requires more-detailed understanding of the phylogenetic relationships among these genera.

Some studies have indicated that increased taxon sampling can help resolve phylogenetic relationships (Pollock et al. 2002; Hedtek et al. 2006; Prum et al. 2015), so here we include dense sampling to improve the ability to resolve the phylogenetic relationships within the fruit doves and their allies, focusing in particular on species from many of the genera mentioned. The taxa included in such a clade would provide insight into the taxonomic composition and phylogenetic structure to help

guide future subfamilial classifications. To address this question, we use multiple mitochondrial and nuclear genes for phylogenetic reconstruction. In addition to novel-sequence data, we also perform analyses combining newly collected sequence data with previously published data to provide a more comprehensive phylogeny of this group. Because these lineages of pigeons and doves are ecologically diverse, we use the resulting phylogenies to provide insight into diversification patterns through ancestral state reconstruction of feeding mode and biogeographic areas.

Methods

Samples

We sampled representatives from 14 genera (of 17 extant genera) and 45 species (of 155 extant species) of fruit doves and allies (Table 1). We also sampled 15 outgroup species from the three major clades of Columbiformes identified by Pereira et al. (2007), including multiple representatives from each clade. We rooted the tree on Clade A (*Columba*, *Streptopelia*, *Patagioenas*, *Macropygia*, *Turacoena*, *Geotrygon*, and *Leptotila*) identified by Pereira et al. (2007), because this group is consistently separated from members of Raphinae and/or Treroninae across all studies and classification schemes. These Clade A genera are part of the subfamily Columbinae, according to del Hoyo et al. (2014).

DNA extraction, amplification, and sequencing

We extracted DNA from feather and tissue samples of wild or captive birds using a Qiagen Blood and Tissue Kit (Qiagen, Valencia, California, USA). Using polymerase chain reaction (PCR), we amplified three mitochondrial loci: cytochrome oxidase subunit 1 (COI), cytochrome *b* (Cytb), and NADH dehydrogenase subunit 2 (ND2), and two nuclear loci: beta-fibrinogen introns 7 (FIB7) and 5 (FIB5). We used primers L6625 and H7005 to amplify COI (Hafner et al. 1994), primers L14841 and H4a (Kocher et al. 1989) to amplify Cytb, primers L5215 and H6313 (Johnson and Sorenson 1998) to amplify ND2, primers FIBB17U and FIBB17L (Prychitko and Moore 1997) to amplify FIB7, and primers FIB5L and FIB6H (Marini and Hackett, 2002) to amplify FIB5. For sequencing we used the primers from the amplifications; for larger genes we also used the following internal sequencing primers: L15517 and H15299 for Cytb (Harshman 1996), L5758s and H5766s for ND2 (Price et al. 2004), FIBDOVEF and FIBDOVER for FIB7 (Johnson and Clayton 2000a), and FIB-P4H and FIB-P3L for FIB5 (Cibois et al. 2014).

We amplified selected loci with PCR according to previously used protocols for each locus (Johnson 2004; Pereira et al. 2007; Marini and Hackett 2002). We purified resulting PCR products using a Qiagen PCR Purification kit (Valencia, California, USA), and sequenced them using ABI Prism BigDye Terminators and Sanger DNA sequencing on an ABI 3730xl DNA Analyzer (University of Illinois Roy J. Carver Biotechnology Center, Champaign, Illinois, USA). We resolved resulting complementary chromatograms and trimmed primer sequences using Sequencher v. 5.0.1 (Gene Codes, Ann Arbor, Michigan, USA), and deposited all sequences in GenBank. We obtained additional sequences from GenBank to provide a more comprehensive data matrix with respect to taxon sampling, although fewer genes were available from published studies (see methods below).

Phylogenetic analysis of complete five-gene data set

For each of the five loci, we aligned all available sequences using MUSCLE (Edgar 2004) and visually reviewed alignments in Seaview v. 4.2 (Gouy et al. 2010). To check for major discordances among gene trees, we constructed neighbor-joining and majority-rule maximum parsimony trees (100 random sampling replicates, Tree Bisection and Reconnection (TBR) branch swapping, 100 bootstrap replicates) for each gene separately using PAUP* v. 4.0b10 (Swofford 2003). With no major conflicts among gene trees, we proceeded to concatenate all loci using Seaview.

Using the concatenated data set partitioned by locus, we used Bayesian and Maximum Likelihood (ML) mixed model analysis. We estimated appropriate models for each locus using jModelTest2 (Akaike 1974; Darriba et al. 2012) based on the Akaike Information Criterion (AIC) values testing 88 different models. Model testing indicated that GTR+I+G models were best for mitochondrial loci (COI, Cytb, ND2) and GTR+G models were best for nuclear loci (FIB7 and FIB5).

We ran ML analysis on our concatenated data set using Garli v. 2.0 (Zwickl 2006) with the aforementioned gene-partition models and 500 bootstrap replicates, treating the mitochondrial genes as a single locus and the nuclear genes as two separate loci. We obtained a 50% majority-rule consensus tree from the bootstrap replicates using SumTrees (Sukumaran and Holder 2008). For Bayesian analysis, we used MrBayes v. 3.2 (Ronquist and Huelsenbeck 2003) on the CIPRES portal (Miller et al. 2010) with a mixed model analysis similar to our ML analysis and default priors. We ran 4 runs with 4 chains for 20 million generations under MCMC sampling every 1,000 trees and viewed resulting trace files in Tracer v. 1.4 (Rambaut and Drummond 2007) to ensure chain mixture and stationarity (ESS>200). We

TABLE 1 Pigeon and dove samples used for a phylogenetic analysis of fruit doves and their allies.

GENUS	SPECIES	TISSUE SOURCE[1]	COLLECTION LOCALITY	CYTB	COI	ND2	FIB7	FIB5
INGROUP								
Caloenas	*nicobarica*	KUMNH B1580	captive	AF483336	EF373363	KT023402	KT023460	KT029857
Chalcophaps	*indica*	FMNH 357415	Philippines: Mindanao	AY443672	KT023314	—	—	—
Chalcophaps	*indica*	ANWC 43702	Australia: Queensland	KT023365	KT023315	KT023403	KT023461	KT029857
Chalcophaps	*indica*	T. Pratt 2003-035	Papua New Guinea: Normanby Is.	KT023364	KT023313	KT023404	KT023462	KT029858
Chalcophaps	*stephani*	NMNH B4013	captive	AY443673	EF373365	KT023405	AY443695	—
Chalcophaps	*stephani*	T. Pratt 2003-026	Papua New Guinea: Normanby Is.	KT023366	KT023316	—	—	KT029860
Ducula	*bakeri*	LSU B45409	Vanuatu: Espiritu Santo	KT023369	KT023319	KT023408	KT023465	KT029864
Ducula	*bicolor*	LSUMNS B19217	captive	AF182705	KT023321	KT023409	AF182672	KT029865
Ducula	*bicolor*	ANWC 29697	Australia: Queensland	KT023370	KT023319	KT023410	KT023466	KT029866
Ducula	*pacifica*	LSU B45431	Vanuatu: Espiritu Santo	KT023371	KT023322	KT023411	KT023467	KT029867
Ducula	*pacifica*	MKL3	Solomon Is.: Rennell	KT023372	—	—	AY443689	—
Ducula	*pinon*	Smithsonian–NSP	Papua New Guinea: Normanby Is.	KT023373	KT023323	KT023412	KT023468	—
Ducula	*pistrinaria*	UWBM 60203	Solomon Is.: Kiaba Is.	AY443669	KT023324	KT023413	AY443691	KT029868
Ducula	*rubicera*	AMNH MKL 66	Solomon Is.: Isabel	AY443668	KT023325	—	AY443690	KT029869
Ducula	*rufigaster*	KUMNH 7408	Papua New Guinea: Wabo	KT023374	KT023326	KT023414	KT023469	KT029870
Goura	*cristata*	KUMNH B1588	captive	AF182709	KT023327	KT023415	AF182676	KT029871
Goura	*victoria*	KUMNH 6880	Papua New Guinea: Oro Prov.	AF483320	KT023328	KT023416	KT023470	KT029872
Gymnophaps	*albertisii*	LSUMNS B28856	captive	AY443665	KT023329	KT023417	AY443687	KT029873
Hemiphaga	*novaseelandiae*	feather	New Zealand	AY443666	KT023330	KT023418	AY443688	KT029874
Lopholaimus	*antarcticus*	ANWC 43527	Australia	EF373282	KT023331	KT023419	EF373485	KT029877
Oena	*capensis*	LSUMNS B34207	South Africa	AF182707	EF373383	EF373345	AF182674	—
Oena	*capensis*	FMNH 352791	Madagascar	KT023376	KT023333	KT023421	KT023472	KT029881
Otidiphaps	*nobilis*	LSUMNS B16808	captive	AF483352	KT023334	KT023422	EF373487	KT029882
Otidiphaps	*nobilis*	SEA398	Papua New Guinea: Herowana	KT023377	KT023335	KT023423	KT023473	KT029883
Phapitreron	*amethystina*	FMNH ATP92-109	Philippines	AF182706	AF279738	KT023424	AF182673	KT029884
Phapitreron	*amethystina*	FMNH 392232	Philippines: Mindanao	KT023378	EF373387	—	AF182673	—
Phapitreron	*cinereiceps*	FMNH 357410	Philippines	KT023379	KT023338	KT023425	KT023474	KT029885
Phapitreron	*leucotis*	FMNH 392228	Philippines: Mindanao	AF279712	AF279739	—	AF279722	—
Ptilinopus	*cinctus*	LSU B16767	captive	KT023380	KT023338	KT023427	KT023476	KT029887

Ptilinopus	*coronulatus*	KUMNH 5214	Papua New Guinea: Gulf	—	KT023339	KT023428	KT023477	KT029888
Ptilinopus	*greyii*	LSU B45811	Vanuatu: Espiritu Santo	KT023381	KT023340	KT023429	KT023478	KT029889
Ptilinopus	*iozonus*	LSU B19412	captive	—	—	—	KT023479	KT029890
Ptilinopus	*leclancheri*	FMNH 358259	Philippines: Sibuyan	AF182708	KT023341	KT023431	AF182675	—
Ptilinopus	*magnificus*	BWB637	Papua New Guinea: Oro Prov.	KT023383	KT023342	KT023432	KT023481	KT029891
Ptilinopus	*melanospila*	KUMNH B1581	captive	KT023384	—	—	—	KT029892
Ptilinopus	*melanospila*	LSUMZ B16811	captive	KT023385	KT023343	KT023433	KT023482	KT029893
Ptilinopus	*occipitalis*	FMNH 392238	Philippines: Mindanao	AF279713	AF279740	KT023434	AF279723	—
Ptilinopus	*perousii*	UWBM 42842	Tonga	KT023386	KT023344	KT023435	KT023483	KT029894
Ptilinopus	*porphyreus*	LSU B14209	captive	KT023387	KT023345	KT023436	KT023484	KT029896
Ptilinopus	*porphyreus*	FMNH 431135	captive	KT023388	KT023346	KT023437	KT023485	KT029895
Ptilinopus	*pulchellus*	KUMNH 6870	Papua New Guinea: Oro Prov.	EF373285	EF373389	KT023438	KT023486	KT029897
Ptilinopus	*rarotongensis*	UWBM 42545	Cook Is.: Atiu	AY443663	KT023347	KT023439	AY443685	KT029898
Ptilinopus	*regina*	ANWC 29878	Australia: Queensland	KT023389	KT023348	KT023440	KT023487	KT029899
Ptilinopus	*rivoli*	KUMNH 7412	Papua New Guinea: Herowana	KT023395	KT023354	KT023446	KT023493	KT029904
Ptilinopus	*rivoli*	T. Pratt 2003-100	Papua New Guinea: Fergusson Is.	KT023390	KT023349	KT023441	KT023488	KT029900
Ptilinopus	*rivoli*	KUMNH 4745	Papua New Guinea	KT023391	KT023350	KT023442	KT023489	KT029901
Ptilinopus	*rivoli*	KUMNH 4771	Papua New Guinea	KT023392	KT023351	KT023443	KT023490	KT029902
Ptilinopus	*rivoli*	KUMNH 4788	Papua New Guinea	KT023393	KT023352	KT023444	KT023491	—
Ptilinopus	*rivoli*	KUMNH 4805	Papua New Guinea	KT023394	KT023353	KT023445	KT023492	KT029903
Ptilinopus	*superbus*	BWB638	Papua New Guinea: Oro Prov.	—	KT023355	KT023447	KT023494	KT029905
Treron	*calva*	LSU B45256	Ghana	KT023396	EF373392	KT023448	KT023495	KT029907
Treron	*calva*	AMNH ALP 80	Central African Republic	AY443674	KT023356	KT023449	AY443696	—
Treron	*sieboldii*	LSU B16978	Japan: Osaka Prefecture	KT023397	KT023357	KT023450	—	KT029908
Treron	*vernans*	LSUMZ B20696	captive	AF483321	KT023358	KT023452	AF182677	KT029910
Treron	*waalia*	FMNH 396406	Ghana	AF483350	KT023359	KT023453	—	KT029911
Trugon	*terrestris*	KUMNH B5100	Papua New Guinea: Gulf	—	—	KT023451	KT023496	KT029909
Turtur	*abyssinicus*	LSUMZ B45034	Ghana: Northern Region	KT023398	KT023360	KT023454	KT023497	KT029912
Turtur	*abyssinicus*	feather	Cameroon	KT023399	KT023361	KT023455	—	—
Turtur	*afer*	AMNH RWD23761	Central African Republic	KT023400	KT023362	KT023456	—	—
Turtur	*brehmeri*	AMNH PRS 2048	Central African Republic	AY151005	AY151008	KT023457	AY151006	—
Turtur	*chalcospilos*	LSUMZ B34263	South Africa	AY443671	EF373395	EF373357	AY443693	—
Turtur	*tympanistria*	FMNH 355252	Uganda	KT023401	—	KT023459	KT023498	—

(*continued*)

TABLE 1 Pigeon and dove samples used for a phylogenetic analysis of fruit doves and their allies (*continued*).

GENUS	SPECIES	TISSUE SOURCE[1]	COLLECTION LOCALITY	CYTB	COI	ND2	FIB7	FIB5
OUTGROUPS								
Claravis	*mondetoura*	LSU B16221	Costa Rica	KJ639093	KJ630878	KJ645736	KJ668686	KT029861
Columba	*iriditorques*	FMNH 486842	Malawi	KT023367	KT023317	KT023406	KT023463	—
Columba	*rupestris*	UWBM 59755	Russia	AF353410	AF353482	AF353434	AF353461	KT029863
Columbina	*passerina*	KUMNH B1755	USA: Missouri	KJ639102	KJ630887	KJ645745	KJ668695	—
Geotrygon	*costaricensis*	NMNH 01544	Panama	AY443660	HQ993529	HQ993549	AY443682	—
Leptotila	*jamaicensis*	KMNH 2135	Mexico	AF279706	AF279726	HQ993543	AF279716	KT029875
Leucosarcia	*melanoleuca*	ANWC 49717	Australia	—	EF373379	EF373341	KT023471	KT029876
Macropygia	*mackinlayi*	AMNH MKL-82	Solomons Is.	AF353415	AF353490	AF353444	AF353466	KT029878
Macropygia	*phasianella*	292119	Australia	KT023375	KT023332	KT023420	AF182660	KT029879
Metriopelia	*melanoptera*	KGM443	Argentina	KJ639092	KJ630877	KJ645735	KJ668692	KT029880
Patagioenas	*picazuro*	LSU 16159	captive	KT023368	KT023318	KT023407	KT023464	KT029862
Phaps	*elegans*	ANWC 4287	Australia	—	KT023337	KT023426	KT023475	KT029886
Streptopelia	*orientalis*	UWBM 47282	Russia	AF353405	AF353476	AF353426	AF353456	KT029906
Turacoena	*manadensis*	16959	captive	EF373287	KT023363	KT023458	—	KT029913
Uropelia	*campestris*	LSU CCW925	Bolivia	KJ639098	KJ630883	KJ645741	KJ668691	KT029914

Note: Accession numbers for sequences generated from this study begin with KT. GenBank accession numbers indicate successful sequences.

1. Museum or collection voucher number.

also assessed topological convergence between runs using AWTY (Wilgenbusch et al. 2004). Based on the trace files, ESS values, and AWTY results, we discarded the first 2,000 trees (10%) as a burn-in. We edited the resulting consensus trees in Figtree v. 1.4 (Rambaut 2012).

Phylogenetic analysis with additional taxon sampling

In addition to our own data, we obtained GenBank sequences for loci ND2 and FIB5 (GenBank accession numbers KF446677- through KF446871) from some *Ptilinopus*, *Alectroenas*, *Drepanoptila*, *Ducula*, *Treron*, and *Caloenas* from a previously published study (Cibois et al. 2014) and combined them with our data to form a more taxonomically comprehensive data set (referred to throughout as the "combined data set"). Several sequences deposited in GenBank by Cibois et al. (2014) were generated from the same museum tissue samples that we used to generate our own data set. Thus, we did not include these GenBank sequences in our combined data set. Sequences for the other three genes for these additional taxa were not available, so we coded them as missing data. For this combined data set we carried out phylogenetic inference using the same methods as with our five-gene data set, aligning each locus with MUSCLE and checking each alignment by eye. We used both Bayesian and ML analyses on the combined concatenated data set. We once again tested for appropriate models at each locus using jModelTest2 and found AIC results identical to our smaller data set. We implemented ML and Bayesian analyses as with our complete five-gene data set, using Garli v. 2.0 and MrBayes v. 3.2, respectively.

Ancestral state reconstruction

Since we are interested in both biogeographic and ecological (foraging mode) patterns of evolution in this group of doves, we used both ancestral state–reconstruction and ancestral range–reconstruction methods. To reconstruct the ancestral state of foraging-mode transitions within this group, we inferred an ultrametric tree and used several ancestral state–reconstruction methods. We were interested in testing how many transitions in foraging mode occurred in this group. To infer an ultrametric tree, we used BEAST v. 1.8.1 (Drummond et al. 2012) on the CIPRES portal. We partitioned the data by locus, using the same models as those used in the Bayesian and ML analyses, a Yule tree prior, and strict branch-length priors with uniform distributions for each gene partition. We ran a single MCMC of 20 million generations, sampling every 1,000 trees and discarding the first 2,000 trees as burn-in. We confirmed that the run reached stationarity in Tracer by ensuring that the Effective Sample Size (ESS) values were >200, and we summarized the posterior distribution of post-burn-in trees with a maximum clade credibility tree generated in TreeAnnotator v. 1.8.1. We then coded each tip as either an arboreal or terrestrial forager according to Gibbs et al. (2001) and Goodwin (1983) and mapped the character state reconstruction onto the ultrametric tree using both parsimony and likelihood reconstruction methods in Mesquite v. 2.75 (Maddison and Maddison 2015). We used the MK1 model in the likelihood reconstruction. We also used a Bayesian reconstruction method—Bayesian binary MCMC (BBM)—as implemented in Reconstruct Ancestral State in Phylogenies (RASP) v. 3.0 (Yu et al. 2014). Although this method is primarily intended to reconstruct biogeographic scenarios, it is also appropriate for use in character reconstruction of binary characters. Allowing for one maximum state at each node (BBM allows for the possibility of multiple state probabilities at each ancestral node), we ran the MCMC analysis for 10 chains of 5 million generations, sampling every 1,000 generations and discarding the first 500 samples as a burn-in. For each of the three analyses (parsimony, likelihood, and BBM), we used data sets with and without the outgroup taxa included to test for biases in results due to outgroup character states.

For ancestral range reconstruction, we used BBM implemented in RASP. Because RASP can use multiple trees to account for phylogenetic uncertainty, we input the post-burn-in posterior distribution of BEAST trees and removed outgroup and duplicate (conspecific) taxa. We then coded each taxon as having an Asian or African range distribution. We randomly sampled 1,000 BEAST trees using the RASP interface and ran BBM allowing for two maximum states at each node. We set the MCMC analysis parameters to run 10 chains of 5,000,000 cycles, sampling every 100 samples and discarding the first 100 samples as a burn-in.

Results

Phylogenetic analysis

The final concatenated data set collected by us was 4,277 aligned base pairs from a total of 77 different individual samples (Table 1). We obtained sequence data for each of the 5 loci for the majority of the ingroup and outgroup samples, with an 88% complete matrix (obtained sequence data/possible sequence data). Both the ML and Bayesian analyses generated similar trees (Figure 1), and a large percentage of ingroup nodes from both the ML tree (~75%) and the Bayesian tree (~79%) received high support values (≥90% maximum likelihood bootstrap replicates [ML]/≥0.95 posterior probability

[PP]). The Bayesian analysis provided strong support (1.0 PP) for monophyly of the group containing all of the previously recognized genera allied with the fruit doves, exclusive of the phabines, and the ML analysis provided modest support (68 ML) for this relationship. We suggest this is the clade that should designate the Raphinae, because it is relatively well supported, containing genera previously placed within either Treroninae or Raphinae. In addition, further expansion of this clade lacks support.

In addition to defining a major clade of fruit doves and allied genera, there is high support from both analyses for several subclades within the ingroup. The genera *Ptilinopus* and *Ducula* form reciprocally monophyletic groups (100 ML/1.0 PP for both *Ptilinopus* and *Ducula*). However, the relationship between the two clades is unclear, with low support of a sister relationship in both analyses (52 ML/0.85 PP). *Lopholaimus*, *Gymnophaps*, and *Hemiphaga* also form a well-supported clade (100 ML/1.0 PP), and together with *Ptilinopus* and *Ducula* form a clade (95 ML/1.0 PP). Other well-supported monophyletic genera (not including genera with a single representative species) are *Phapitreron*, *Goura*, *Otidiphaps*, *Turtur*, *Chalcophaps*, and *Treron*. Among these genera, *Goura* has support as being sister to the monotypic genus *Caloenas,* whereas *Trugon* and *Otidiphaps* have moderate support as being sister taxa (72 ML/1.0 PP). *Turtur* is supported as sister to the monotypic genus *Oena* (100 ML/1.0 PP), and together with *Chalcophaps* form a clade (100 ML/1.0 PP). Species of the genus *Treron* have support as being sister to the rest of the ingroup in the Bayesian analysis (1.0 PP) but not in the ML (<50 ML) analysis. Given our limited within-species sampling, we recovered all species as monophyletic with the exception of *Treron calva*. *Treron waalia* is nested within *T. calva* (93 ML/1.0 PP).

The combined data set, including our data and data from Cibois et al. (2014), resulted in a total of 204 samples. As with the previous complete five-gene data set, a high fraction of nodes were strongly supported (≥90% ML/≥0.95 PP) by both the ML (~55%) and Bayesian (~85%) analyses (Supplementary Figure S1). The combined data analysis is generally consistent with the results of analysis on our five-gene data set. With this expanded taxon sampling, the species *Ptilinopus purpuratus*, *P. porphyraceus*, *P. mericierii*, and *P. viridis* (in addition to *Treron calva*) are not monophyletic. *Ptilinopus* and the embedded genera *Alectroenas* and *Drepanoptila* have strong support as a monophyletic group (100 ML/1.0 PP). We recover *Ducula* as being monophyletic (100 ML/1.0 PP), but its relationship as sister to the *Ptilinopus* clade is not well supported.

Ancestral character state reconstruction and biogeographic analysis

The parsimony, likelihood, and Bayesian ancestral character reconstruction methods of foraging mode all produced very similar results (Figure 2). In the analysis that included outgroups, all three methods recovered a terrestrial foraging ancestral state for the fruit-doves-and-allies clade, with two independent transitions to an arboreal foraging state. We estimated that these transitions occurred along the branch leading to the *Treron* clade and again along the branch leading to the *Ptilinopus* + *Ducula* + *Lopholaimus* + *Gymnophaps* + *Hemiphaga* clade. Using all three ancestral character state–reconstruction methods, our character state–reconstruction analysis without outgroups also indicated multiple transitions in foraging mode, although we were unable to confidently determine directionality of these transitions (Supplementary Figure S2).

The Bayesian ancestral range reconstruction method (BBM) recovered an Asian ancestral range for this group (1.0 probability). The analysis also recovered two independent dispersal events from Asia to Africa (Figure 2). One dispersal event was recovered at the ancestral node of *Chalcophaps* (an Asian genus) and *Turtur* and *Oena* (both African genera). The second dispersal event was recovered at the ancestral node of *Treron vernans* (an Asian species) and *Treron calva*, and *Treron waalia* (both African species).

Discussion

Identification of a monophyletic clade among the fruit doves and allies

Phylogenetic relationships of fruit doves and their allies based on five molecular loci are generally well supported. They largely agree with previous, less exhaustive phylogenetic analyses (Johnson et al. 2001; Pereira et al. 2007; Gibb and Penny 2010; Cibois et al. 2014), although important distinctions exist. Perhaps most notable, we recovered a clade of fruit doves and allies as monophyletic with high support in most of our analyses, which includes most, but not all, of the genera currently classified in the Raphinae by del Hoyo et al. (2014). This major clade was poorly resolved in previous studies, in particular because of weakly supported deeper-level relationships within Columbiformes. Pereira et al. (2007) placed the Australian phabine clade (represented in our data set by *Phaps* and *Leucosarcia*) as sister to a poorly supported fruit-doves-and-allies clade. Gibb and Penny (2010) do not recover a monophyletic fruit-doves-and-allies clade, placing small New World ground doves (subfamily Claravinae) within the clade. However, our analysis places the small New World ground doves clearly

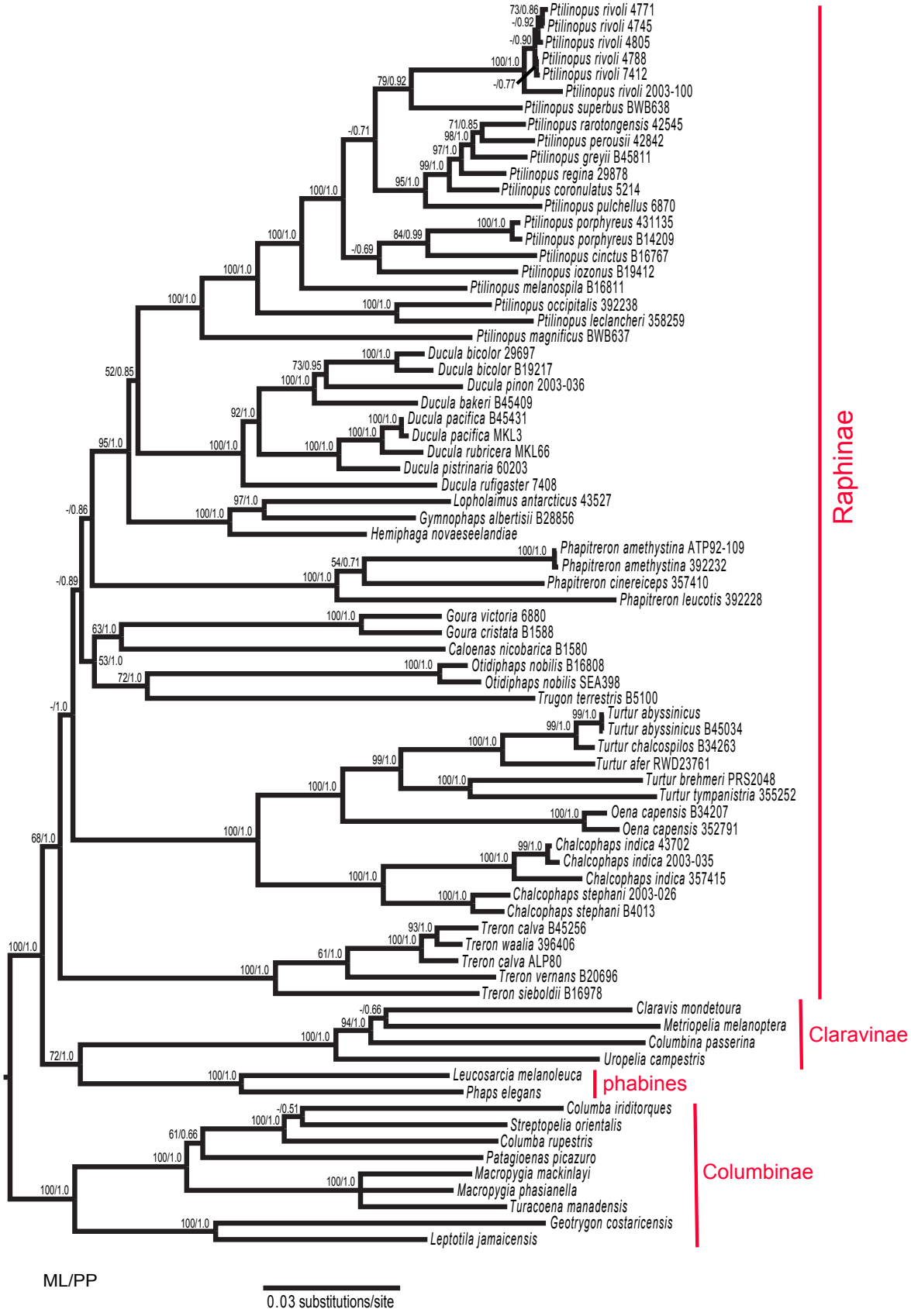

FIGURE 1 Bayesian 50% majority-rule consensus tree of fruit doves and their allies. Numbers at each node indicate the bootstrap and posterior probability values. Dashes indicate bootstrap values <50. Letters and numbers after each taxon name refer to the specific tissue voucher numbers in Table 1. Relevant higher taxonomic groups are indicated to the right of the tip names. The scale bar indicates the rate of nucleotide substitutions per site.

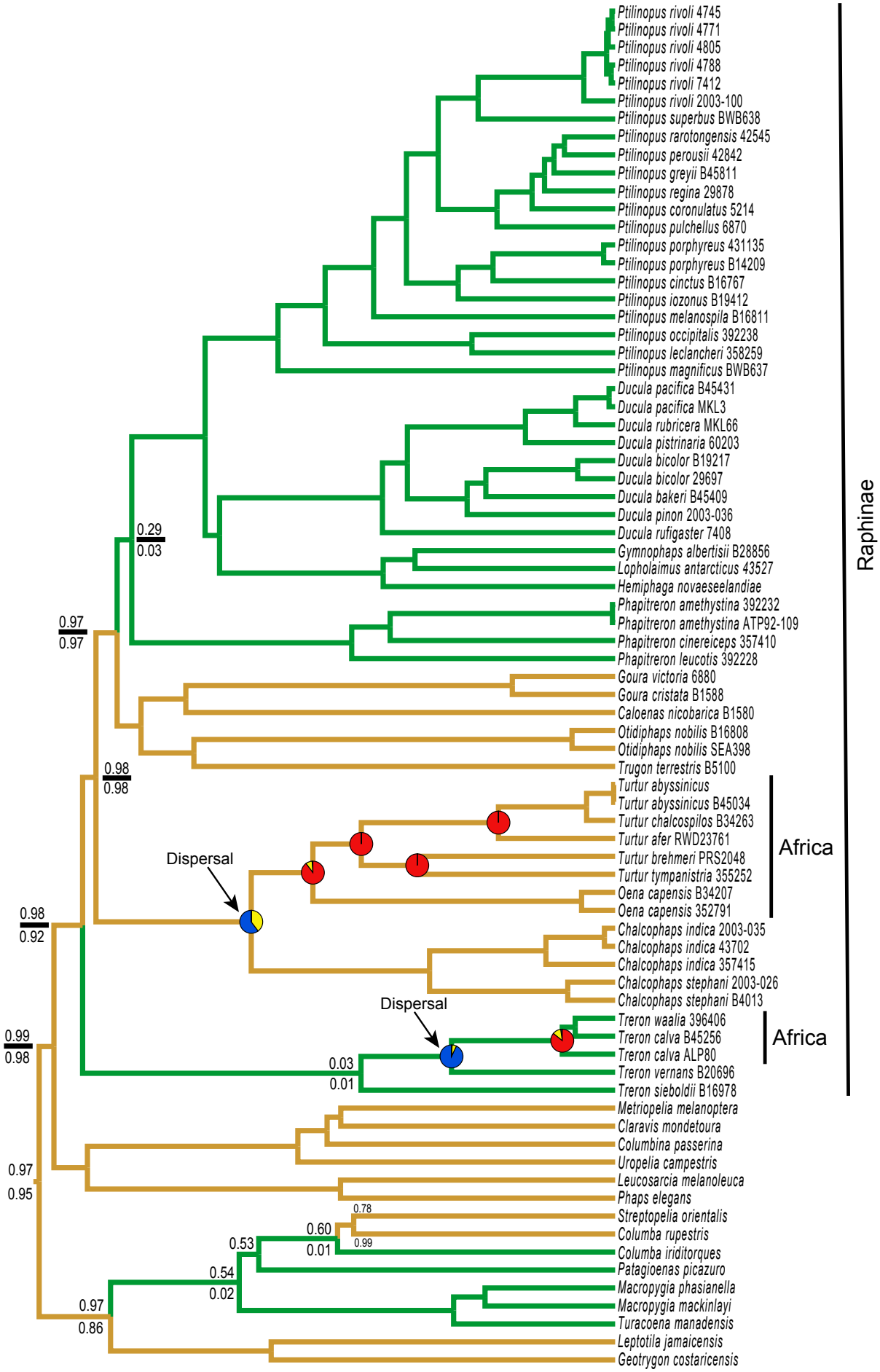
Ptilinopus rivoli 4745
Ptilinopus rivoli 4771
Ptilinopus rivoli 4805
Ptilinopus rivoli 4788
Ptilinopus rivoli 7412
Ptilinopus rivoli 2003-100
Ptilinopus superbus BWB638
Ptilinopus rarotongensis 42545
Ptilinopus perousii 42842
Ptilinopus greyii B45811
Ptilinopus regina 29878
Ptilinopus coronulatus 5214
Ptilinopus pulchellus 6870
Ptilinopus porphyreus 431135
Ptilinopus porphyreus B14209
Ptilinopus cinctus B16767
Ptilinopus iozonus B19412
Ptilinopus melanospila B16811
Ptilinopus occipitalis 392238
Ptilinopus leclancheri 358259
Ptilinopus magnificus BWB637
Ducula pacifica B45431
Ducula pacifica MKL3
Ducula rubricera MKL66
Ducula pistrinaria 60203
Ducula bicolor B19217
Ducula bicolor 29697
Ducula bakeri B45409
Ducula pinon 2003-036
Ducula rufigaster 7408
Gymnophaps albertisii B28856
Lopholaimus antarcticus 43527
Hemiphaga novaeseelandiae
Phapitreron amethystina 392232
Phapitreron amethystina ATP92-109
Phapitreron cinereiceps 357410
Phapitreron leucotis 392228
Goura victoria 6880
Goura cristata B1588
Caloenas nicobarica B1580
Otidiphaps nobilis B16808
Otidiphaps nobilis SEA398
Trugon terrestris B5100
Turtur abyssinicus
Turtur abyssinicus B45034
Turtur chalcospilos B34263
Turtur afer RWD23761
Turtur brehmeri PRS2048
Turtur tympanistria 355252
Oena capensis B34207
Oena capensis 352791
Chalcophaps indica 2003-035
Chalcophaps indica 43702
Chalcophaps indica 357415
Chalcophaps stephani 2003-026
Chalcophaps stephani B4013
Treron waalia 396406
Treron calva B45256
Treron calva ALP80
Treron vernans B20696
Treron sieboldii B16978
Metriopelia melanoptera
Claravis mondetoura
Columbina passerina
Uropelia campestris
Leucosarcia melanoleuca
Phaps elegans
Streptopelia orientalis
Columba rupestris
Columba iriditorques
Patagioenas picazuro
Macropygia phasianella
Macropygia mackinlayi
Turacoena manadensis
Leptotila jamaicensis
Geotrygon costaricensis
Raphinae
Africa
Africa
Dispersal
Dispersal
0.29
0.03
0.97
0.97
0.98
0.98
0.98
0.92
0.99
0.98
0.03
0.01
0.97
0.95
0.78
0.60
0.01
0.99
0.53
0.54
0.02
0.97
0.86

FIGURE 2 An ultrametric phylogeny for fruit doves and their allies. Taxon names are the same as in Figure 1, with letters and numbers following each name referencing the specific tissue vouchers in Table 1. Branch colors indicate a parsimony reconstruction analysis in Mesquite. Brown branches indicate a terrestrial foraging mode, and green branches indicate an arboreal foraging mode. Values above nodes are the proportional likelihood values from the likelihood reconstruction analysis in Mesquite. Values are from 0 to 1 and indicate the likelihood a particular ancestral node was a terrestrial forager. Nodes without values indicate support for a foraging mode >0.99 and agree with the parsimony results (e.g., a node without associated values that bifurcates into two brown branches has >0.99 support for a terrestrial foraging mode, and vice versa on nodes bifurcating into two black branches). Values listed below the nodes are posterior probability values from a Bayesian MCMC (BBM) reconstruction analysis in RASP. Scale and interpretation are the same as the likelihood results. Pie charts indicate the ancestral range reconstruction from the BBM model. Red indicates the probability of an African ancestral range, blue indicates the probability of an Asian ancestral range, and yellow indicates the probability of an ancestral range in both Africa and Asia. Nodes with probability values >0.95 for an Asian ancestral range are not shown. Arrows indicate probable dispersal events.

outside the group. Our Bayesian analysis recovers a well-supported fruit-doves-and-allies clade (1.0 PP), although bootstrap support by ML analysis is more moderate (68 ML). Both Bayesian and ML analyses of our combined data set also supports the clade (76 ML/1.0 PP). Our overall results are most similar to Pereira et al. (2007), but we had higher support for a fruit-doves-and-allies clade. Although we analyzed fewer loci than Pereira et al. (2007) we had much denser taxonomic sampling, which likely contributed to higher resolution (Pollock et al. 2002; Hedtek et al. 2006). Based on these results and previously published studies, we suggest the Raphinae should be modified from del Hoyo et al. (2014) to include the genera *Trugon*, *Otidiphaps*, *Microgoura* (extinct), *Goura*, *Caloenas*, *Raphus* (extinct), *Pezophaps* (extinct), *Chalcophaps*, *Turtur*, *Oena*, *Phapitreron*, *Treron*, *Ducula*, *Ptilinopus, Alectroenas*, *Drepanoptila*, *Hemiphaga*, *Cryptophaps*, *Gymnophaps*, and *Lopholaimus*. Genera in the phabine clade should not be included in Raphinae.

Phylogenetic relationships within and among genera

All genera except *Ptilinopus* are supported as monophyletic. Inclusion of the data from Cibois et al. (2014) reveals that the genera *Drepanoptila* and *Alectroenas* are embedded within *Ptilinopus*. *Drepanoptila* and *Alectroenas* were not sampled in the five-gene data set, so this result could not be tested using all five genes. However, this result is also consistent with the phylogeny reported by Gibb and Penny (2010). Based on these previous studies, del Hoyo et al. (2014) split *Ptilinopus* into multiple genera, but the other option is to subsume the smaller genera *Drepanoptila* and *Alectroenas* into *Ptilinopus*. With the combined data set, four additional species were recovered as paraphyletic: *Ptilinopus purpuratus*, *P. porphyraceus*, *P. mericierii*, and *P. viridis.* Analysis from Cibois et al. (2014) also recovered *P. purpuratus* and *P. porphyraceus* as paraphyletic. *Ptilinopus viridis* is rendered paraphyletic by the insertion of a closely related sister taxon, *P. eugeniae*, although this relationship is not well supported (<50 ML/0.54 PP). Two specimens of *P. mericierii* are recovered as closer to the sister species *P. dupetithouarsii* than to a third *P. mericierii* specimen, but this is also not well supported (<50 ML/0.68 PP). Cibois et al. (2014) recover *P. mericierii* and *P. dupetithouarsii* as reciprocally monophyletic but with low Bayesian support for the monophyly of *P. mericierii*.

Similar to prior studies, we recover *Ptilinopus*, *Ducula*, and the long-tailed pigeons (*Gymnophaps*, *Lopholaimus*, and *Hemiphaga*) as a clade, although the relationships among these genera are not completely clear. Other studies have placed long-tailed pigeons as sister to *Ptilinopus* (Pereira et al. 2007; Gibb and Penny 2010), but these results were not well supported. In contrast, with relatively weak support we recovered *Ducula* as sister to *Ptilinopus*. Similar to our results, studies by Shapiro et al. (2002) and Cibois et al. (2014) place *Ducula* sister to *Ptilinopus*, although these studies did not have extensive sampling, with only three species of *Ducula* in each study. Future work may require additional nuclear data to elucidate the deeper relationships within this clade. We also recover *Turtur*, *Oena*, and *Chalcophaps* as a well-supported clade. A study by Khan and Arif (2013) found similar results using the mitochondrial locus COI. Our results place *Turtur* sister to *Oena*, with this clade sister to *Chalcophaps*. This agrees with studies by Pereira et al. (2007) and Shapiro et al. (2002). Gibb and Penny (2010) also recovered *Oena* and *Chalcophaps* as sister taxa, although they did not include *Turtur* in their analysis. Our phylogeny also places *Goura* sister to *Caloenas*, and *Otidiphaps* sister to *Trugon*. However, only the Bayesian analysis recovers all four of these genera together as a clade. Gibb and Penny's (2010) phylogeny also places *Goura* sister to *Caloenas*; however, *Trugon* is not included in their analysis. They placed *Goura* and *Caloenas* sister to *Otidiphaps*. Finally, we recover *Treron*—the green pigeons—as sister

to the rest of the fruit-doves-and-allies clade in our Bayesian analysis (1.0 PP). However, this relationship is unresolved in our ML analysis. Analyses of our combined dataset gives similar results, with *Treron* recovered as sister to the remainder of the fruit doves and allies in the Bayesian analysis but as unresolved in the ML analysis. Therefore, we are unable to as confidently resolve the placement of *Treron* with either data set. Although the Bayesian results may be correct in placing the genus as sister to the other ingroup taxa, additional data are needed to confirm this relationship. Additionally, *Treron calva* is the only species recovered as paraphyletic in our analysis, with *T. waalia* nested within the *T. calva* clade. This relationship perhaps indicates recent speciation within the genus *Treron* due to biogeographic dispersal from Asia to Africa.

Multiple foraging transitions

All three of ancestral character reconstruction methods (parsimony, likelihood, and BBM) recover multiple, independent transitions in foraging mode within the fruit doves and allies. We obtain this result in separate sets of analyses with and without the outgroup taxa included. Although we are no longer able to confidently identify the directionality of the foraging transitions (i.e., terrestrial to arboreal, or vice versa) when we remove the outgroup, the reconstructions still retain multiple independent transition combinations (Supplementary Figure S2).

When the outgroup is included, all three of the character reconstruction methods recover terrestrial foraging as the ancestral state for the fruit-doves-and-allies clade (Figure 2). This result is well supported in both the likelihood and Bayesian MCMC analyses. Many species of doves eat seeds and/or fallen fruit from the ground, and these results indicate that at least the common ancestors of the taxa in this analysis were perhaps granivorous terrestrial foragers. These results also suggest that the mostly frugivorous, arboreal foraging habit is a more derived state, thus suggesting that the ancestors of fruit doves and allies may have been primarily terrestrial. Many of the contemporary granivorous, terrestrial foraging doves live in areas dominated by scrubby vegetation and/or grasses (Goodwin 1983; Gibbs et al. 2001). The transitions from terrestrial to arboreal foraging would therefore also indicate a transition in habitat, from scrubby or grassland areas to more heavily forested areas, where fruit would be available in the canopy. Several terrestrial foragers do not live in scrubby or open habitat, however, and in fact prefer heavily forested rainforest habitats. For example, the pheasant pigeon (*Otidiphaps nobilis*) is a terrestrial pigeon from rainforests of New Guinea and nearby islands (Gibbs et al. 2001). Crowned pigeons (in the genus *Goura*) live in similar habitats. These larger ground-foraging pigeons often eat fallen fruits as well as seeds (Pratt et al. 2015). Additionally, some arboreal foragers prefer open habitat. For example, the orange-fronted fruit dove (*Ptilinopus aurantiifrons*) forages on fruit in the canopy but primarily lives in more open areas of New Guinea (Pratt et al. 2015).

Multiple dispersal events into Africa

Our biogeographic analysis recovered two dispersal events from Asia to Africa within the fruit doves and allies clade (Figure 2). Dispersal into Africa likely occurred within the *Chalcophaps*, *Turtur*, and *Oena* clade and the *Treron vernans, Treron clava*, and *Treron waalia* clade. *Turtur* and *Oena* are African genera, whereas species of *Chalcophaps* are distributed in Asia and Australasia. *Chalcophaps* is the sister group to *Turtur* and *Oena*, and the three genera share a relatively deep ancestral node in the phylogeny. This perhaps indicates a more ancient dispersal into Africa. However, dispersal of *Treron* between Asia and Africa likely occurred much later. Most species of *Treron* have ranges in eastern Asia, whereas *T. calva* and *T. waalia* are native to sub-Saharan Africa. The African species of *Treron* from this study are separated from the Asia species by a relatively short branch, suggesting that this was a more recent dispersal event from Asia to Africa. Furthermore, the short branches among *T. calva* and *T. waalia* specimens indicate recent speciation within the African *Treron*. This is perhaps evidence of subsequent radiation once *Treron* dispersed into Africa. It would be interesting to include the other African *Treron* species (*T. delalandii*, *T. griveaudi*, *T. sanctihomae*, *T. pembaensis*, and *T. australis*) in a similar phylogenetic analysis to estimate branch lengths and genetic distances and to assess monophyly among those taxa.

Conclusion

From an extensive sampling of fruit doves and allied genera, we estimated a phylogeny of these taxa from both nuclear and mitochondrial DNA sequences. We found support for seven major clades, as well as identified a clade that we feel could be more confidently defined as the subfamily Raphinae (having priority over Treroninae) within Columbidae. The status of proposed members of this subfamily has been unclear in previously published, family-wide phylogenies of pigeons and doves (e.g., Pereira et al. 2007). These previously published studies provided great insight into many of the phylogenetic relationships within Columbidae. However, they

did not have sufficiently broad taxonomic sampling of the fruit-doves-and-allies clade to represent the taxonomic diversity of this group. Here we used a data set with many representatives from throughout the clade to clarify its status within Columbidae.

Having established many of the phylogenetic patterns among fruit doves and their allies, we were able to address some questions related to the evolutionary history of the group. Since members of the fruit-doves-and-allies clade include both terrestrial and arboreal foragers, we evaluated transitions between these two foraging modes and found evidence for multiple transitions. In our analysis with outgroup taxa, we recovered terrestrial foraging as the ancestral state with two transitions to arboreal foraging. Additionally, we evaluated broad biogeographic patterns in the group. Our ancestral range reconstruction indicated two separate dispersal events from Asia into Africa.

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