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Rapid and recent diversification of curassows, guans, and chachalacas (Galliformes: Cracidae) out of Mesoamerica: Phylogeny inferred from mitochondrial, intron, and ultraconserved element sequences

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ABSTRACT

The Cracidae (curassows, guans, and chachalacas) include some of the most spectacular and endangered Neotropical bird species. They lack a comprehensive phylogenetic hypothesis, hence their geographic origin and the history of their diversification remain unclear. We present a species-level phylogeny of Cracidae inferred from a matrix of 430 ultraconserved elements (UCEs; at least one species sampled per genus) and eight more variable loci (introns and mtDNA; all available species). We use this phylogeny along with probabilistic biogeographic modeling to test whether Gondwanan vicariance, ancient dispersal to South America, ancient dispersal from South America, or massive global cooling isolated cracids in the Neotropics. Contrary to previous estimates that extant cracids diversified in the Cretaceous, our fossil-calibrated divergence time estimates instead support that crown Cracidae originated in the late Miocene. Species-rich genera *Crax*, *Penelope*, and *Ortalis* began diversifying as recently as 3 Mya. Biogeographic reconstructions indicate that modern cracids originated in Mesoamerica and were isolated from a widespread Laurasian ancestor, consistent with the massive global cooling hypothesis. Current South American diversity is the result of multiple colonization events following uplift of the Panamanian Isthmus, coupled with rapid diversification and evolution of secondary sympatry. Of the four major cracid lineages (curassows, chachalacas, typical guans, horned guan), the only lineage that has failed to colonize and diversify South America is the unique horned guan (*Oreophasis derbianus*), which is sister to curassows and chachalacas rather than typical guans.

1. Introduction

A major focus in avian biogeography is determining the history and origins of the worlds most diverse avifauna, that of the Neotropics (Cracraft, 1985; Haffer, 2008; Mayr, 1969). The Neotropics comprises three major sub regions: Mesoamerica, South America, and the Caribbean. Each contains distinct endemic elements presumably related to their differing geologic histories. Much of the debate over Neotropical bird origins has revolved around the general time frame of avian diversification, and differentiating between proposed geologic and environmental mechanisms influencing its avifaunal assembly requires robust time-calibrated estimates of phylogeny (Claramunt and Cracraft, 2015; Smith et al., 2014).

The geologically oldest hypothesis relevant to Neotropical avian diversification is the Gondwanan vicariance model (Cracraft, 1973, 2001; Ericson et al., 2002; Haddrath and Baker, 2012; McGlone, 2005). Under Gondwanan vicariance, continental drift isolated South American lineages from their relatives, where they diversified in 'splendid isolation' over the past 90–100 million years (Cracraft, 1973; Simpson, 1980). The Gondwanan vicariance model requires early Cretaceous diversification of modern birds, and implies a South American origin of Neotropical groups (Cracraft, 2001, 1973). Some time-calibrated molecular phylogenies have supported an early Cretaceous timeframe for the modern bird radiation (Haddrath and Baker, 2012; Stein et al., 2015), but recent assessments based on genome-scale molecular data and improved fossil calibrations suggest that modern bird diversification was extremely limited in the Cretaceous. Rather, the modern avian radiation occurred in the early Cenozoic (Claramunt and Cracraft, 2015; Jarvis et al., 2014; Prum et al., 2015). This more recent timeframe for diversification is also congruent with the paucity of modern bird fossils from the Cretaceous (Clarke et al., 2005;

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Cracraft et al., 2015; Feduccia, 2003). Rejection of the Gondwanan vicariance model in birds, a long-held paradigm in avian biogeography (McGlone, 2005), raises the question: without the aid of ancient connections between continents, how did various tropical bird lineages achieve their widespread, present-day distributions?

If the avian radiation post-dated Gondwanan rift, then diversity and endemism in South America could be a product of ancient long distance dispersal from other continents (Mitchell et al., 2014; Poux et al., 2006). Some birds, such as migratory species and those dependent on freshwater and marine habitats, are highly vagile and clearly capable of colonization via long distance dispersal (Billerman et al., 2011; Moralez-Silva and Nassif Del Lama, 2014). The limited distance between South America and Africa early in the Cenozoic, in concert with the likely existence of islands spanning the South Atlantic (Selvatti et al., 2015), could have facilitated colonization of South America from Africa during this period (Poux et al., 2006). However, there are a number of bird lineages with limited capacity to disperse, such as those that inhabit dense tropical forests (Burney and Brumfield, 2009; Moore et al., 2008). This raises a major question about the basis for disjunct pantropical distributions on multiple isolated continents featured by non-vagile bird groups (Moyle et al., 2005, 2006; Moyle, 2004).

Separate geological and environmental factors influenced Mesoamerican avifaunas. Throughout most of the time relevant to modern bird diversification, Eurasia and North America (Laurasia) were linked by both the North Atlantic route (until ca. 55 Mya; Brikiatis, 2014) and the Beringian land bridge (until the late Miocene, and then intermittently during Pleistocene climate oscillations; Hopkins, 1967; Marincovich and Gladenkov, 1999; Simpson, 1947). Also throughout much of the Cenozoic, global temperatures were much warmer than present day, especially in polar regions. During the Eocene optimum, and to a lesser extent the mid-Miocene, temperatures were high enough that temperate and subtropical lineages could persist into the arctic circle (Zachos, 2001). Declining temperatures would have restricted widespread Laurasian lineages to Mesoamerica and the Paleotropics, creating disjunct pan-tropical distributions (Hosner et al., 2016).

Most recently, (Claramunt and Cracraft, 2015) hypothesized that modern birds originated in the Neotropics, and that world bird diversity evolved from repeated dispersal events out of then-isolated South America. This model requires no colonization of the Neotropics by modern birds, but it does imply South American origins for most major tropical bird groups. Exceptions include the oscine passerines (true songbirds), which diversified after colonizing Australia, and the Coraciornithia/Afroaves, (a diverse assemblage comprising taxa ranging from hawks and owls to woodpeckers and rollers) which diversified after colonizing Laurasia.

At more recent timescales, uplift and closure of the Panamanian Isthmus in the late Miocene/Pliocene had a profound influence on the Neotropical avifauna (Bacon et al., 2015; Barker, 2007; Dacosta and Klicka, 2008; Webb, 1976; Weir et al., 2009). Following isthmus uplift, Mesoamerican and South American avifaunas that evolved in isolation then rapidly dispersed across the isthmus, creating conglomerate communities including species of both Mesoamerican and South American ancestries. This event is referred to as the Great American Biotic Interchange (GABI; Mayr, 1946; Webb, 1976; Weir et al., 2009). There is uncertainty around the precise timing of Panamanian Isthmus closure. The fossil record demonstrates that there was free exchange of non-vagile organisms from 3.5 Mya until present (Coates et al., 2004; Weir et al., 2009), but geologic and other biological evidence suggests isthmus closure could have been as early as 8–10 Mya (Bacon et al., 2015; Montes et al., 2015). Regardless of the exact timing of isthmus closure, the phylogenetic expectations of the GABI are clear: non vagile groups of Mesoamerican origin could disperse to South America only after the late Miocene/Pliocene, and vice versa.

The Cracidae (guans, chachalacas, and curassows) are a unique and charismatic yet highly threatened bird group endemic to the Neotropical realm (Del Hoyo, 1994; Delacour and Amadon, 2004). Cracids are one of the major lineages of galliform birds (e.g. chickens, grouse, quail, pheasants, guineafowl, megapodes). Because Galliformes are one of the four oldest modern bird lineages (Claramunt and Cracraft, 2015; Jarvis et al., 2014; Prum et al., 2015), deciphering galliform origins is key to deciphering bird origins as a whole. Cracids are most diverse in western Amazonia where as many as six species can be found in proximity, but two monotypic genera are restricted to montane forests of Mesoamerica. Multiple lines of evidence imply that Cracids have limited dispersal ability. They are non-migratory, absent from oceanic islands, and their distributions often coincide with geographic barriers such as large Amazonian rivers or deep dry river valleys. However, vagility may be plesiomorphic in Galliformes. The deepest branching lineage within Galliformes is the megapodes (Hosner et al., 2016; Kimball and Braun, 2014), a vagile group that has colonized oceanic islands in the Australo-Pacific region (Harris et al., 2014). If indeed vagility is plesiomorphic in Galliformes, a dispersive cracid ancestor could have colonized South America over water before evolving more sedentary behavior and morphology.

Evidence supporting South American or Mesoamerican cracid origin is mixed (Cracraft, 1973). Galliformes have been considered Gondwanan in origin based on their distributions (Cracraft, 2001; Crowe et al., 2006; Darlington, 1957). Previous molecular phylogenetic studies have suggested an early Cretaceous origin supportive of Gondwanan vicariance (Pereira and Baker, 2006; Pereira et al., 2004). However, these studies used fossil calibrations that were later shown to be misplaced, lending to an exaggerated the age of Cracidae (Ksepka, 2009). Even if the origin of cracids was determined to be South American, the Cenozoic divergence-time estimates from phylogenomic studies (Cracraft et al., 2015; Jarvis et al., 2014; Prum et al., 2015) instead suggest trans-oceanic colonization followed by loss of vagility (Mitchell et al., 2014; Poux et al., 2006; Smith et al., 2013; Wang et al., in press) or even a South American origin for all modern birds (Claramunt and Cracraft, 2015).

If cracids are Mesoamerican in origin, separate mechanisms would have influenced their historical biogeography. A Mesoamerican cracid ancestor could have originally colonized North America via Beringia or the North Atlantic route during the warm Eocene or possibly the warm early Miocene without having crossed a marine barrier. They would later become permanently isolated from Old World relatives by global cooling in the late Miocene, and restricted to Mesoamerica with declining temperatures. Diversification in South America would be rapid and recent following uplift of the Panamanian Isthmus (Mayr, 1946). This hypothesis is also consistent with fossils of *Boreortalis*, a small chachalaca-like cracid known from the mid-Miocene of North America (Brodkorb, 1954; Cracraft, 1971; Ducey, 1992).

To evaluate competing hypotheses (Table 1), a more complete, better-resolved, and reliably time-calibrated cracid phylogeny is needed. Existing molecular phylogenies have identified four major lineages of cracids: chachalacas (*Ortalis*), curassows (*Crax*, *Mitu*, *Pauxi*, *Nothocrax*), typical guans (*Penelope*, *Penelopina*, *Chamaepetes*, *Aburria*, *Pipile*), and the endangered, spectacular, and monotypic horned guan (*Oreophasis*; Pereira et al., 2002; Stein et al., 2015). Yet, relationships among these lineages are not resolved with confidence. Similarly, previous studies have not resolved relationships within the typical guans, including placements of *Penelopina* and *Chamaepetes* (Pereira et al., 2002; Stein et al., 2015), and whether *Pipile* is paraphyletic with respect to *Aburria* (Grau et al., 2005).

Table 1
Biogeographic hypotheses proposed to explain initial cracid divergence in the New World, and their chronological and topological expectations.

	Factors	Description	Chronological expectations	Topological expectations
H_1	Gondwanan vicariance	Gondwanan rift isolated lineages on southern Continents	Early Cretaceous cracid divergence	South American cracid origin, recent colonization of Mesoamerica
H_2	Ancient dispersal	Colonization of South America from Africa when Atlantic Ocean was narrow	Early Cenozoic cracid divergence	South American cracid origin, recent colonization of Mesoamerica
H_3	Global cooling	Restriction of Laurasian lineages to central and southern Eurasia and North America driven by massive global cooling events	Oligocene or late Miocene cracid divergence	Mesoamerican cracid origin, recent colonization of South America
H_4	South American origin	Modern birds originated in South America	Cenozoic cracid divergence	South American galliform origin, recent cracid colonization of Mesoamerica

Large-scale sequencing approaches are rapidly transforming phylogenetic inference (Faircloth et al., 2012; Jarvis et al., 2014; Lemmon and Lemmon, 2013). One approach with potential is target capture of conserved genomic regions (Faircloth et al., 2012; Hosner et al., 2016; Lemmon et al., 2012; Sun et al., 2014). Combining large numbers of these highly conserved genomic markers with widely used, published legacy markers such as mtDNA and nuclear introns has the potential to improve phylogenetic inference (Persons et al., 2016). Genomic sampling of conserved genomic regions can target nodes unresolved by traditional markers, and traditional markers can provide increased sampling without the cost and computational difficulties associated with large-scale genomic sequencing. However, it is uncertain if combining sequences from these drastically different functional classes will result in negative effects from missing data or model misspecification.

To determine the geographic origin and timing of cracid diversification, we inferred a new phylogeny based on a heterogeneous DNA sequence matrix. We sequenced genome-wide ultraconserved elements and their flanking sequences (Faircloth et al., 2012) to provide a robust backbone phylogeny. We also sequenced mtDNA and nuclear introns with dense taxon sampling, both from newly sequenced samples and from previously published studies. With our new hypothesis of cracid relationships, we fitted biogeographical models to test among historic biogeographical hypotheses (Table 1) regarding the origin of cracids in the Neotropics.

2. Materials and methods

2.1. DNA extraction

We selected available tissues from wild collected specimens or captive individuals from 36 of 55 currently recognized cracid species (Table S1; Gill and Donsker, 2015; Remsen et al., 2014). To supplement sequences from these high-quality fresh tissues, we sampled DNA from toepads of museum skins for two species (Mundy et al., 1997). We extracted genomic DNA using the Gentra Puregene® DNA purification kit (Quigen Inc., Valencia CA), following standard manufacturers protocols.

2.2. Sanger sequencing of mtDNA and nuclear introns

We selected five mitochondrial regions and seven nuclear loci for Sanger sequencing, selected to overlap with previous molecular systematic studies of cracids (Grau et al., 2005; Pereira et al., 2004, 2002) and Galliformes in general (Harris et al., 2014; Hosner et al., 2016, 2015; Kimball and Braun, 2014; Wang et al., 2013). Mitochondrial markers included ATP synthase subunit 6 (ATP6), cytochrome oxidase subunit 1 (COI), cytochrome *b* (CYTB), NADH dehydrogenase subunit 2 (ND2), and NADH dehydrogenase subunit 5 (ND5). Nuclear introns included clathrin heavy chain intron 7 (CLTC), clathrin heavy chain-like intron 7 (CTLCL1), eukaryotic translation elongation factor 2 introns 5 and 6 (EEF2), beta-fibrinogen intron 5 (FGB), rhodopsin intron 1 (RHO), ovalbumin intron 3 (SERPINB14), and transforming growth factor beta 2 intron 5 (TGF*b*2-5). Primers and PCR protocols follow Cox et al. (2007), Kimball et al. (2009), and Wang et al. (2013). PCR products were sequenced at the University of Florida Interdisciplinary Center for Biotechnology Research. We quality controlled and reconciled chromatograms using Geneious 6 (Kearse et al., 2012). Sequences generated for this study are available through GenBank (accession #s KX345855–KX345925, KX356119–KX356312). We supplemented our data matrix with cracid DNA sequences from previous studies, which added an additional nine species (Cox et al., 2007; Frank-Hoeflich et al., 2007; Grau et al., 2005; Kimball and Braun, 2014; Pereira et al., 2004, 2002; Schindel et al., 2011; Wang et al., 2013; Table S1). Final taxon sampling included 47 of 55 currently recognized cracid species (85%; Gill and Donsker, 2015). We included ten species representing all galliform families as outgroups, rooted to an anseriform, the sister group to Galliformes, and aligned sequences for each locus in MAFFT 7 (Katoh and Standley, 2013).

2.3. Illumina sequencing of ultraconserved elements

To supplement Sanger sequences and aid in resolving problematic nodes identified in previous cracid phylogenetic systematic studies, we selected at least one representative of each genus (for *Pipile* we included two species to test monophyly) for target-capture sequencing of ultraconserved elements (Faircloth et al., 2012) by RAPiD Genomics (Gainesville, FL). Illumina TruSeq libraries were prepared using standard manufacturer's protocol (Illumina Inc., San Diego, CA, USA) modified to use primers with custom index tags (Faircloth and Glenn, 2012). Libraries were enriched for 5060 UCE loci targeted using a set of 5472 probes (Mycroarray, Ann Arbor, MI; http://www.mycroarray.com/mybaits/mybaits-UCEs.html) and 150nt paired-end reads were generated using an Illumina HiSeq 2500. Raw reads were demultiplexed, quality controlled with Trimomatic (Peñalba et al., 2014), and assembled using Trinity r20131110 (Grabherr et al., 2011). UCE sequences for *Crax*, *Ortalis,* and outgroups were generated for a previous study (Hosner et al., 2016). We extracted UCE loci from assembled contigs using the PHYLUCE pipeline (Faircloth, 2016), and UCE loci sequenced from all taxa (430 total; a result of reduced yields from captures of toepad extracts). We aligned UCE loci using MAFFT 7 (Katoh and Standley, 2013), trimmed alignments ends when 35% of cells were missing across a 20 bp sliding window, and manually checked alignments for errors. Raw sequence reads are archived at GenBank under BioProject PRJNA324492, and alignments are publically available under the article title at FigShare https://figshare.com/.

2.4. Phylogenetic inference

We analyzed separate alignments of mitochondrial, nuclear intron, and UCE sequence data as well as combined data

alignments. Combined data alignments included all Sanger sequence data (mitochondrial + nuclear intron), total evidence (all mitochondrial, nuclear intron, and UCE sequence data), and pruned total evidence (mitochondrial, nuclear intron, and UCE sequence data, but including only taxa where UCEs were sequenced). We implemented partitionFinder 1.1 (Lanfear et al., 2012) to select an appropriate partition schemes for phylogenetic analyses using the Bayesian Information Criterion (BIC). Each UCE locus, each nuclear intron, and each codon position of each mitochondrial gene were considered data subsets for partitioning. For intron and mitochondrial data, we employed the greedy partitionFinder search with RAxML (Stamatakis, 2014) assuming the GTRGAMMA model. We ran a separate partitionFinder search for UCEs, employing the relaxed clustering algorithm using default settings, also with RAxML assuming the GTRGAMMA model.

For each sequence alignment, we estimated the maximum likelihood (ML) phylogeny with RAxML (Stamatakis, 2014) using the GTRGAMMA model and partitioning schemes identified by partitionFinder. We estimated support with 500 thorough ML bootstrap replicates. As an alternative to ML methods, we also estimated phylogeny for all multilocus alignments with SVDquartets (Chifman and Kubatko, 2014), a method of phylogenetic inference consistent under the multispecies coalescent model. Although this method was developed for single nucleotide polymorphism data, simulations show it performs well on multilocus data (Chifman and Kubatko, 2014). Regardless, our recent analyses of empirical data using SVDquartets and a conceptually similar method (SMRT-ML; DeGiorgio and Degnan, 2010) have shown excellent performance with UCE data comparable to summary coalescent methods (Hosner et al., 2016; Meiklejohn et al., 2016). We computed an SVDquartet optimal tree and 500 bootstrap replicates using PAUP*4a146 (Swofford, 2003; http://people.sc.fsu.edu/~dswofford/paup_test/), reconciling quartets with the QFM algorithm (Reaz et al., 2014) implemented in PAUP*4a146.

To construct a time-calibrated phylogenetic hypothesis, we executed BEAST 2.2 (Bouckaert et al., 2014) on the Sanger sequence matrix using six fossil calibrations from throughout Galliformes (Table 2). For each calibration, we used the estimate of fossil age as a hard minimum bound for a gamma (2,10) distribution. To determine if divergence time estimates were driven by any single calibration point, we performed a jackknife cross-validation, removing each of the five fossil calibrations, producing five replicates. To reduce the number of parameters estimated and improve MCMC performance, we selected the HKY + G model for each partition. All BEAST analyses used a Birth-death tree prior and an uncorrelated lognormal (UCLN) relaxed clock. We executed two independent MCMC runs of 50,000,000 generations for each iteration, and examined convergence of parameter estimates using Tracer 1.5 (Rambaut and Drummond, 2007) resulting in effective sample sizes (ESS) of greater than 200 following removal of the first 25% of samples as burnin. Chains were sampled every 50,000 states, resulting in 1500 post burnin samples from the combined two independent MCMC runs.

2.5. Biogeographic reconstructions

We used BioGeoBEARS to infer the ancestral distribution of cracids. BioGeoBEARS fits probabilistic biogeographic models to phylogenies given user-defined geographic areas (Matzke, 2014). We fitted six probabilistic models that treat geographic range evolution through time as a series of anagenetic (range expansion and range contraction) and cladogenic events (where daughter lineages inherit all or a portion of the ancestor range) given a phylogeny and tip ranges. The DEC (Dispersal Extinction Cladogenesis; Clark et al., 2008; Ree and Sanmartín, 2009) model allows all anagenetic and cladogenic events. DIVA-LIKE (likelihood implementation of Dispersal-vicariance analysis; Ronquist, 1997; Yu et al., 2010) is similar to DEC but does not allow daughter lineages to each inherit the ancestor's entire range. BAYAREA-LIKE (likelihood implementation of BAYAREA; Landis et al., 2013); is similar to DEC but does not allow daughter lineages to inherit portions of their ancestor's range. Each of these models can be modified with the +*j* founder event speciation modifier, which models daughter lineages inheriting a novel area unoccupied by the ancestor (Matzke, 2014).

To implement BioGeoBEARS, we used the time-calibrated, ultrametric, maximum clade credibility tree inferred with BEAST, and selected the best-fit biogeographic model (DEC, DIVA-LIKE, BAYAREA-LIKE; each with and without +*j*) using BIC. We coded cracid and outgroup distributions to represent established biogeographic regions relevant to cracid diversification: Old World, Nearctic, Central America, trans-Andean South America (excluding the Atlantic forest region of eastern Brazil, Argentina, Paraguay, and Uruguay), and Atlantic forest.

3. Results

3.1. Phylogenetic results

DNA sequence alignments contained between 4815 (introns) and 246,701 (mtDNA + introns + UCEs) bp, and between 1479 (introns) and 19,061 (mtDNA + introns + UCEs) informative characters for analysis (Table 3). PartitionFinder selected between three (introns) and 23 (mtDNA + introns + UCEs) partitions for each alignment (Table 3). ML and SVDquartets analyses generally produced similar and congruent phylogenetic hypotheses, although bootstrap support was generally greater using ML (Figs. 1 and 2; Supplemental Figs. S2 and S3). There were some differences in trees based on the total evidence matrix (Fig. 2B; mtDNA + introns + UCEs, see below).

Cracid genera formed four strongly supported groups: the curassows (*Crax*, *Mitu*, and *Pauxi*), the chachalacas (*Ortalis*), horned guan (*Oreophasis*), and the remaining guans (*Penelope*, *Penelopina*, *Pipile*, *Chamaepetes*, and *Aburria*; Figs. 1 and 2). Amongst these major lineages, we found *Ortalis* sister to curassows, and the monotypic *Oreophasis* sister to *Ortalis* + curassows. Greatest bootstrap support for these relationships was in the inference of the UCE and the mtDNA + intron + UCE matrices. Bootstrap support among

Table 2
Fossils used to time-calibrated the cracid phylogeny in BEAST.

Taxon	Locality	Stratigraphy	Node calibrated	Hard minimum (Mya)	Soft maximum (Mya)
Gallinuloides wyomingensis	Green River, Wyoming, USA	Late Oligocene	Galliformes + Anseriformes	51.6	75.3
Palaeortyx gallica	Enspel, Germany	Late Oligocene	Numididae + Phasianidae	28.0	51.7
Schaubortyx keltica	Armissan, France	Oligocene	Odontophoridae + Phasianidae	23.0	47.7
Rhegminornis calobates	Gilchrist Co., Florida, USA	Early Miocene	*Meleagris* + *Tympanuchus*	18.0	41.7
Boreortalis laesslei	Gilchrist Co., Florida, USA	Early Miocene	*Ortalis* + *Crax*	18.0	41.7
Callipepla shotwelli	Umatilla Co., Oregon, USA	Middle Pliocene	*Callipepla* + *Colinus*	3.5	27.2

Table 3
DNA Sequence summary statistics for the five alignments of three different data classes: mitochondrial DNA, nuclear introns, and ultraconserved elements.

Alignment	Taxa included (total)	Taxa included (ingroup)	Bp of alignment	Informative characters	Uninformative characters	Partitions	% Missing
mtDNA	58	47	5247	1981	490	6	27.3
introns	46	35	4815	1479	1025	3	30.7
UCEs	23	12	236,539	15,601	18,288	14	11.2
mtDNA + introns	58	47	10,162	3460	1515	9	35.9
mtDNA + introns + UCEs (total evidence)	58	47	246,701	19,061	19,803	23	63.6
mtDNA + introns + UCEs (pruned - taxa with UCEs)	23	12	246,669	18,669	19,894	23	15.8

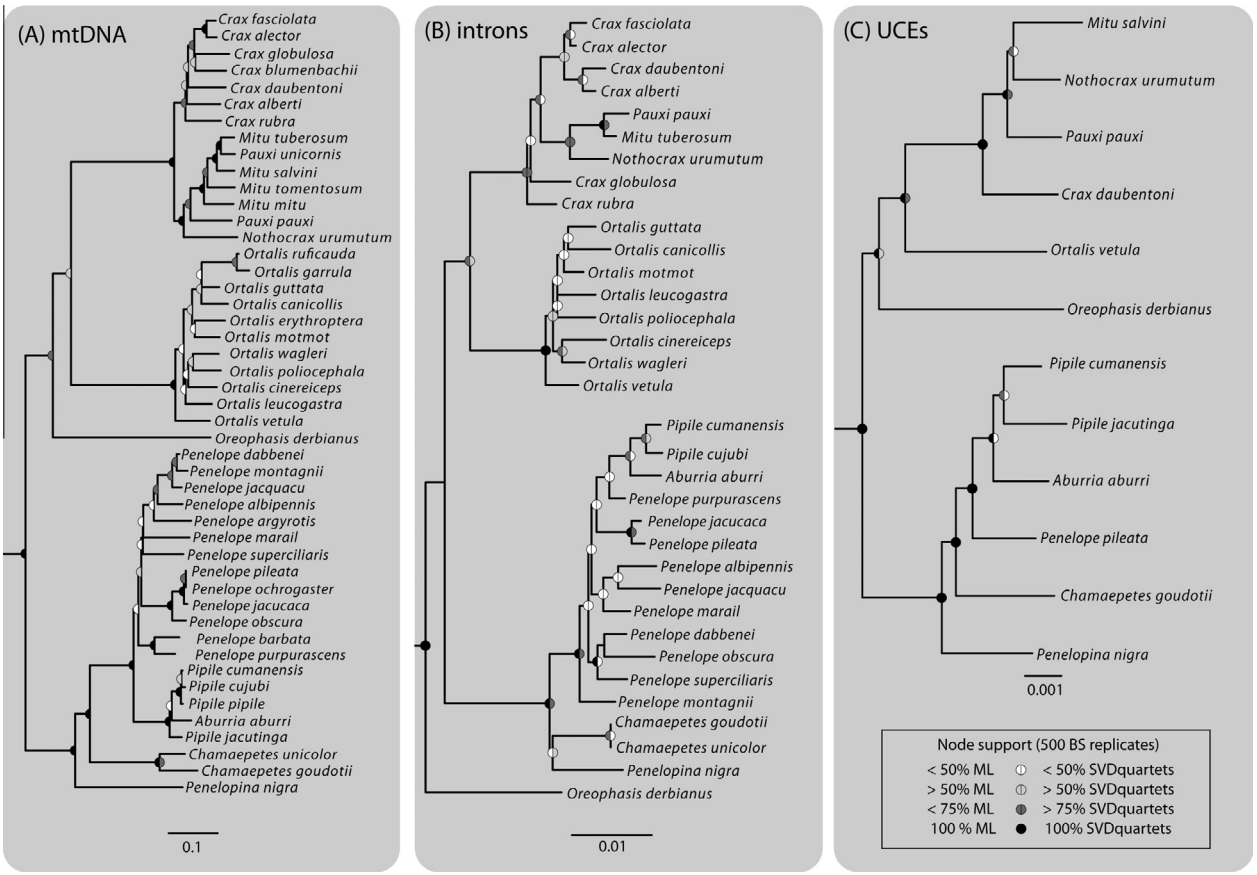

Fig. 1. Maximum likelihood phylogenies inferred from individual data types: mtDNA (A), nuclear intron (B), and UCE (C). Node support icons represent ML bootstrapping % (left semicircle) and SVDquartets bootstrapping % (right semicircle). SVDquartet analysis requires multilocus data, hence we omitted this analysis for mtDNA.

genera was moderate to strong in all analyses, being strongest in the UCE, the mtDNA + intron + UCE, and the mtDNA + intron datasets. However, the intron dataset lacked power to resolve the position of *Oreophasis*.

Within the typical guan lineage (*Aburria*, *Chamaepetes Penelope, Penelopina,* and *Pipile*), our analyses found strong support for monophyly of all genera (Figs. 1 and 2). We found Central American *Penelopina* sister to all other guans with moderate to strong support, and the two species of *Chamaepetes* sister to a clade containing *Penelope, Aburria,* and *Pipile*. Using only mitochondrial data, *Pipile* monophyly was questionable, with *Aburria* sometimes nesting within *Pipile*. However, the addition of UCEs convincingly placed *P. jacutinga* sister to *P. cumanensis* to the exclusion of *Aburria* in both ML and SVDquartet analyses (Fig. 2). The Atlantic forest *Pipile jacutinga* was sister to the three 'pale-fronted' *Pipile* species of the Amazon/Orinoco basins and Trinidad.

Within *Penelope*, the most diverse guan genus, relationships were generally poorly resolved. The combined mtDNA + intron tree (Fig. 2A), the most resolved phylogenetic hypothesis, placed the widespread *P. purpurescens* sister and the range-restricted *P. barbata* sister to all other *Penelope*. Among the remaining species, two other well-supported clades emerged. One comprised Amazonian species *P. pileata, P. ochrogaster,* and *P. jacucaca* and the more temperate *P. obscura,* and a second clade comprised *P. dabbenei*, *P. jacquacu*, and *P. montagnii*. In the mtDNA + intron + UCE tree, support for *P. purpurescens* and *P. barbata* sister to all other *Penelope* evaporated, leaving an unresolved 6-way polytomy in a majority-rule consensus.

Relationships were also partially resolved in the other large cracid genus, *Ortalis* (chachalacas; Figs. 1 and 2). Analyses recovered *O. vetula* sister to all other *Ortalis*. Otherwise, analyses recovered a South American clade of *O. erythroptera, O. motmot, O. guttata, O. canicollis, O. ruficauda, and O. garrula* sister to or nested within Central American species *O. leucogastra, O. wagleri, O. poliocephala,* and *O. cinereiceps*, albeit with weak to moderate support. Bootstrap support for all relationships within *Ortalis* were weak in separate

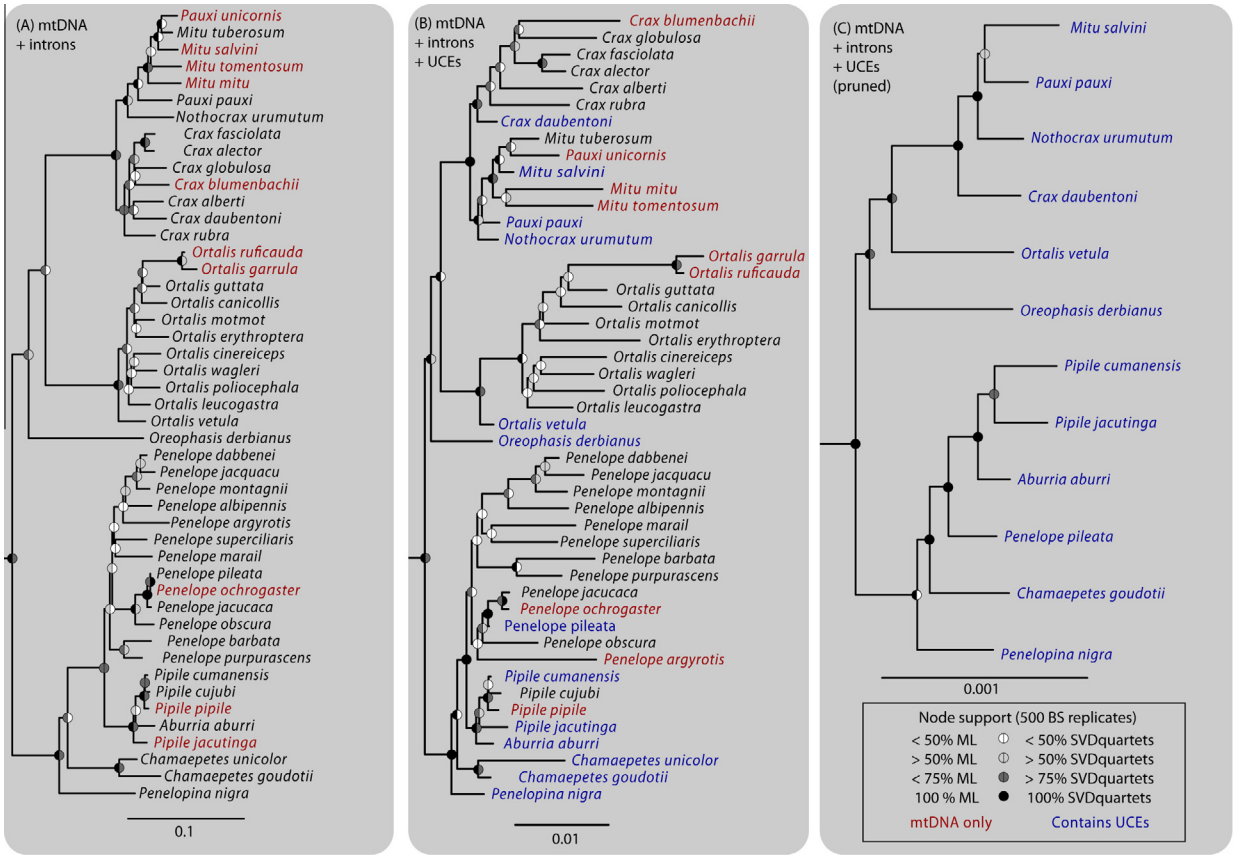

Fig. 2. Maximum likelihood phylogenies inferred from combined datasets. Node support icons represent ML bootstrapping % (left semicircle) and SVDquartets bootstrapping % (right semicircle). Taxa highlighted in red have only mtDNA data, taxa highlighted in blue include UCE data. Note distorted branch lengths when taxa sampled for UCEs are combined with taxa not sampled for UCEs (B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

mtDNA and intron analyses (Fig. 1), but it improved when we combined mtDNA and introns (Fig. 2A).

Within the curassows, we found a division between *Crax* and *Nothocrax*, *Pauxi*, and *Mitu* (Figs. 1 and 2). Mitochondrial and intron data strongly supported *Nothocrax* sister to *Pauxi* and *Mitu*. However, UCE data supported a different topology, with *Nothocrax* sister to *Mitu*. When these data sources were combined, the mtDNA/intron topology of *Nothocrax* + *Mitu/Pauxi* was supported, despite the fact that the mtDNA + intron dataset had an order of magnitude fewer informative characters than the UCE dataset (Table 3). We recovered *Pauxi* paraphyletic, with *Pauxi unicornis* sister to *Mitu tuberosa* and *Pauxi pauxi* sister to all other *Mitu* + *P. unicornis*. However, this result is based purely on previously sequenced mtDNA for *P. unicornis* (Pereira et al., 2004) rather than new data.

The mtDNA + introns + UCE dataset recovered several relationships that conflicted with those from other analyses (Fig. 2B). Within *Crax*, *C. rubra* was sister to all other *Crax* in the mtDNA, intron, and mtDNA + intron dataset. However, in the mtDNA + intron + UCE dataset, *C. daubentoni* – the only taxa for which UCEs were included, was sister to all other *Crax*. Similarly, when we added UCEs to mtDNA + introns, there was a topological rearrangement with regards to *P. pileata*, the only *Penelope* species for which we sequenced UCEs. We also observed odd results when estimating branch lengths in the mtDNA + intron + UCE dataset. Taxa that lacked UCE sequences featured unrealistic long terminal branch lengths when compared to taxa for which UCEs were sequenced, justifying our use of mtDNA + introns only for time-calibrated analyses. This problem was most obvious with taxa for which only mtDNA was available such as *Mitu mitu/tomentosum*, *Ortalis garrula/ruficauda*, and *Penelope argyrotis*.

3.2. Divergence time estimation

Cross-validation indicated that treating of *Boreortalis* as a stem *Ortalis* resulted in divergence time estimates that were incongruent with other fossil calibrations (Table 4). Removal of the *Boreortalis* calibration shifted the estimate for crown Cracidae from ca. 23 to ca. 13 Mya, and shifted the estimate of crown Galliformes from ca. 82 to ca. 64 Mya. Removal of other fossils (*Callipepla*, *Gallinuloides*, *Palaeortyx*, *Rhegminornis*, *Schaubortyx*) did not shift timing estimates outside of the 95% confidence intervals estimated in the analysis including all fossils (Table 4, Supplemental Fig. S3). Because treatment of *Boreortalis* as a stem *Ortalis* was incongruent with other fossils, we used the analysis lacking the *Boreortalis* calibration for downstream biogeographic reconstructions.

3.3. Biogeographic reconstructions

The best-fit biogeographic model was DEC+*j*, supported by 93% of the relative likelihood (Table 5). Under the DEC+*j* model, we inferred a Central American ancestor of modern Cracidae at 9.9–16 Mya, even though the majority of diversification occurred recently within South America (Fig. 3). Transitions to South America occurred five times: (1) in the curassow ancestor, (2) in the ancestor of the South American *Ortalis* clade, (3) in *Ortalis cinereiceps*, (4) in the ancestor of *Penelope*, *Aburria*, and *Pipile*, and (5) in the *Chamaepetes* ancestor. Secondary colonization of Central America from South America occurred twice, once in *Crax rubra* and once in *Penelope purpurescens*. The timing of South American colonization events inferred with the time-calibrated tree were recent, with transitions from Central to South America in major clades

Table 4
Divergence time estimates (mean and 95% highest posterior density; in Mya) for selected nodes from jackknife cross validation in BEAST. Times estimated without *Boreortalis* were significantly more recent, supporting that placement of *Boreortalis* in crown Cracidae is a poor fit when combined with other fossil calibrations. Hence, the iteration without *Boreortalis* was used for biogeographic analysis (Fig. 3). Curassows represent the earliest inferred cracid divergence in South America.

	Galliform crown		Cracidae stem		Cracidae crown		Curassows	
	Mean	95% HPD	Mean	95% HPD	Mean	95% HPD	Mean	95% HPD
All calibrations	82.3	63.7–99.7	74.6	59.4–91.8	23.3	20.5–26.0	6.3	5.0–7.9
No *Boreortalis*	63.7	52.9–75.8	58.2	47.5–68.6	13.1	9.9–16.0	4.2	3.3–5.2
No *Callipepla*	82.1	65.2–100.3	74.6	58.6–91.4	23.6	20.4–26.6	6.3	4.8–7.8
No *Gallinuloides*	101.2	77.5–124.2	91.3	70.1–110.8	24.3	21.2–27.8	7.1	5.5–8.7
No *Palaeortyx*	88.2	69.6–107.8	80.2	63.4–98.3	23.5	20.8–27.0	6.6	5.1–8.1
No *Rhegminornis*	78.4	58.2–97.0	71.1	53.4–89.5	23	20.3–31.3	6.6	5.1–8.1
No *Schaubortyx*	88	69.8–107.6	80	63.0–98.6	23.6	20.9–27.1	6.1	4.5–7.5

Table 5
BioGeoBEARS model selection summary statistics, including the log-likelihood (LnL), dispersal parameter (*D*), extinction parameter (*E*), jump parameter (*J*), and Bayesian information criterion score (BIC).

Model	LnL	# Parameters	*D*	*E*	*J*	BIC	Delta BIC	BIC weight	Relative likelihood (%)
DEC	−129.322	2	0.00916	0.00988	–	−131.078	8.726	18.4×10^{-4}	0.02
DEC+*J*	−119.718	3	0.00557	1.00×10^{-12}	0.0240	−122.352	–	1	93.05
DIVALIKE	−136.996	2	0.0115	0.0127	–	−138.752	16.400	8.34×10^{-08}	0.00
DIVALIKE+*J*	−124.250	3	0.00606	2.55×10^{-9}	0.0273	−126.884	4.532	0.0106	0.98
BAYAREALIKE	−148.421	2	0.0176	0.0747	–	−150.178	27.825	9.33×10^{-13}	0.00
BAYAREALIKE+*J*	−122.443	3	0.00464	1.00×10^{-7}	0.0326	−125.077	2.725	0.0639	5.95

occurring in the interval between ca. 2.3–2.7 Mya in *Ortalis*, between ca. 4.2–9.8 Mya in the curassow ancestor, and between ca. 3.9–7.0 Mya in guans. Cracid diversity in the Atlantic forest appears to be the result of multiple independent colonization events from *cis*-Andes South America. Alternative biogeographic models DIVALIKE and BAYAREA (Supplemental Fig. S4) produced qualitatively similar results.

4. Discussion

4.1. Cracid origin and biogeography

The Cracidae are characteristic birds of South America, but they are relatively recent arrivals on the continent. Concatenated and coalescent data analysis of mtDNA, introns, and UCEs provide a well-supported phylogenetic framework for understanding the timing and geography of cracid diversification. Ancestral area reconstructions (Fig. 3) firmly reject a South American cracid ancestor, and therefore also reject hypotheses that Gondwanan vicariance (H_1) or early Cenozoic dispersal to South America (H_2) influenced cracid diversification. Similarly, ancestral area reconstructions reject a South American crown galliform ancestor (H_4). Consistent with the global cooling hypothesis (H_3), we inferred a Mesoamerican cracid ancestor that diverged from a widespread ancestor ca. 48–68 Mya. The DEC+*j* model reconstructed this node as two disjunct regions– Old World + Central America. However, additional evidence from climate (globally high temperatures during the early Eocene) and geology (existing land connections between North America and the Palearctic), and the fossil record (Miocene *Boreortalis*) suggest this Old World + Central American ancestor is best interpreted as a widespread Laurasian ancestor. We hypothesize that stem cracids were isolated from stem phasianoids (Numididae/Phasianidae/Odontophoridae) by declining global temperatures that restricted the tropical cracids to warmer portions of North America and Mesoamerica during the late Eocene, or possibly the late Miocene.

In addition to ancestral area reconstructions, the fossil record supports a Northern hemisphere cracid ancestor and the global cooling hypothesis (H_3). Fossil cracids ascribed to *Boreortalis* from ca. 18 Mya have been found from various locations in North America (Brodkorb, 1954; Ducey, 1992), well before our inferred age of crown Cracidae (ca. 13 Mya). Tropically-adapted cracids likely enjoyed a larger distribution in North America during the mid-Miocene, given that climates were considerably warmer than present-day climates (Zachos, 2001). *Boreortalis* has been considered a stem *Ortalis* (Brodkorb, 1954), but our divergence time estimation indicates that this treatment was a poor fit to the molecular data given the other galliform fossil calibrations. Although most similar to *Ortalis*, *Boreortalis* also shares at least one character with *Penelopina* (Brodkorb, 1954). *Boreortalis* needs re-evaluation in light of our molecular phylogenetic results to determine if morphological similarities between *Ortalis, Penelopina,* and *Boreortalis* are actually symplesiomorphies, supporting a stem cracid position for *Boreortalis*.

Biogeographic reconstructions and divergence time estimates strongly support a scenario where cracid lineages of Mesoamerican origin colonized and diversified in South America in parallel following uplift of the Panamanian Isthmus (Fig. 3). The exact timing of the closure of the isthmus of Panama remains controversial–conservative estimates place the data of full closure at 3.5 Mya (Coates et al., 2004), but other studies suggest an earlier closure, perhaps ca. 10 Mya (Bacon et al., 2015; Montes et al., 2015, 2012). Considering confidence intervals, our inferred timing estimates for cracid colonization of South America are broadly congruent with a range of isthmus closure date hypotheses. The earliest inferred cracid divergences within South America were in the curassows (3.3–5.2 Mya) and the typical guans (3.0–4.8 Mya).

Our recent estimates of divergence times also supported an alternative mode of diversification in Amazonian curassows. Pereira et al. (2004) assumed a South American cracid ancestor and a Cretaceous origin of crown Cracidae. Based on these assumptions, they concluded that curassow diversification is caused by vicariance due to large-scale changes in Amazonian hydrology associated with Andean uplift. Our estimates instead suggested that Amazonian cracids diversified across a landscape with river basins and hydrology similar to present day, and that differentiation in Amazonian interfluvials is instead due to rare dispersal events across existing biogeographic barriers or headwater areas followed by isolation (Smith et al., 2014).

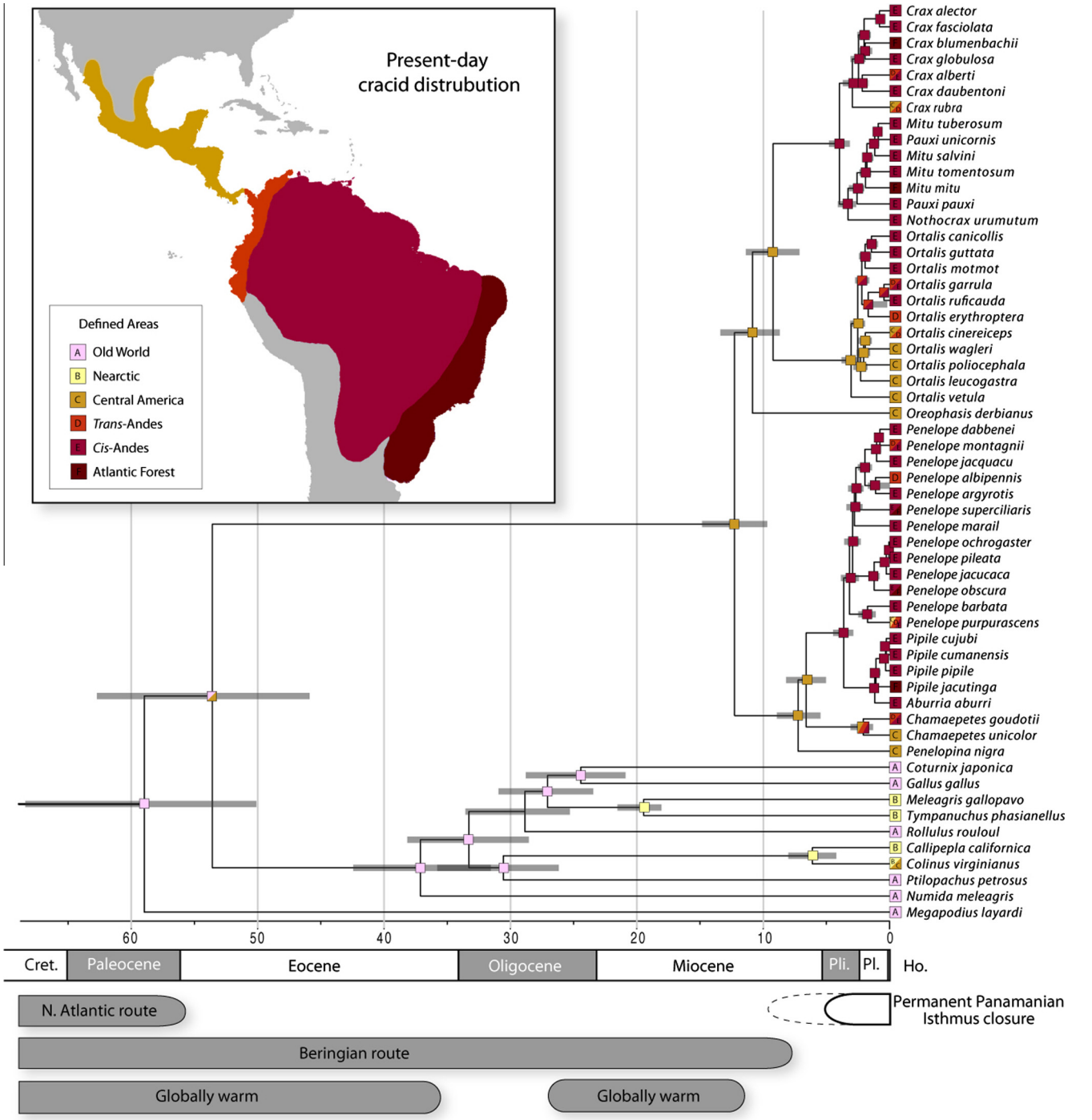

Fig. 3. Time-calibrated cracid phylogeny inferred using BEAST, with ancestral areas inferred from BioGeoBEARS using the DEC+*j* model. Taxa are coded by present-day geographical distribution (inset). Time axis is Mya, along with chronological estimates of geologic and climatic events hypothesized to influence cracid diversification.

Although our combined data phylogenies were generally well resolved, relationships within *Ortalis* and *Penelope* were much less so– being moderately resolved in concatenated analyses and unresolved in SVDquartets analyses. Divergence times indicated that *Penelope* and *Ortalis* are recent and rapid radiations, a challenging problem to resolve in phylogenetics. Resolution within these genera await genome wide sampling to infer relationships with confidence.

Galliformes are one of the oldest extant bird lineages, and reconstructing their area of origin has strong implications for reconstructing the geography of avian diversification as a whole. Claramunt and Cracraft (2015) coded ranges of higher taxa to reconstruct a Neotropical or North American ancestor for crown gallifomes, and a Neotropical ancestor for all birds. They correctly coded Cracidae as "South America + Nearctic", based on extant and fossil cracid distributions. Here, based on a well-sampled phylogeny, we concluded that crown cracids are Mesoamerican origin, and derived of Laurasian stock. Similarly, Claramunt and Cracraft (2015) correctly coded Odontophoridae as "Neotropical + Nearctic + Afrotropical." Hosner et al. (2015) also determined that Odontophorids, the other widespread Neotropical galliform group in the Neotropics, are of Laurasian ancestry. Contra Claramunt and

Cracraft (2015), who inferred a South American galliform origin (at least in part), our biogeographic reconstructions instead provide little evidence that Galliformes existed in South America prior to the uplift of the Isthmus of Panama. A northern origin of crown Galliformes is further supported by fossil evidence. Stem Galliformes are known from numerous sites in Europe and North America (Mayr, 2005; Mayr and Weidig, 2004; Mourer-Chauviré, 1992). Whether or not coding the galliform ancestor as Laurasian would alter ancestral area reconstructions for all birds is unclear. However, detailed ancestral area reconstructions of Galliformes (this study; Hosner et al., 2015) demonstrate that coding higher taxa (e.g., families, as in Claramunt and Cracraft, 2015) as widespread lineages in higher-level biogeographic studies can mislead ancestral area reconstructions.

4.2. Choice of fossil calibrations

Overall, our estimates of galliform divergence dates are more recent than those from some other studies focused solely on galliforms (Pereira and Baker, 2006; Stein et al., 2015). However, Pereira and Baker (2006) used fossil calibrations that have since been re-evaluated and re-assigned (Ksepka, 2009), whereas Stein et al. (2015) treated *Boreortalis* as a crown cracid, and did not explore congruence of fossil calibrations by jackknifing. When we included a crown *Boreortalis* calibration (Table 4), we inferred Cretaceous divergence dates, similar to those inferred by Stein et al. (2015). Thus, the interpretation of *Boreortalis* appears to have a major impact on the estimates of the timing of galliform diversification. If *Boreortalis* is indeed a crown cracid then our results suggest that cracids exhibit much stronger rate heterogeneity than other galliforms, further complicating divergence time estimation. However, the simpler explanation is that *Boreortalis* has been misplaced. Although our inferred divergences dates were more recent than those inferred by other galliform studies (but see Wang et al., in press), they are in line with avian phylogenomic studies calibrated with fossils throughout the avian tree of life (Claramunt and Cracraft, 2015; Jarvis et al., 2014; Prum et al., 2015). If *Boreortalis* is indeed a crown cracid, then our results would suggest strong rate heterogeneity in the group, further complicating divergence time estimation.

More broadly, our jackknifing results (Table 4) illustrate that fossil choice can be the most important source of error when inferring divergence time estimates in birds. We chose calibrations based on previous morphological phylogenetic studies (Ksepka, 2009) as well as expert opinion (Holman, 1961; Mayr et al., 2006; D. Steadman pers. comm.). However, the ideal method would be to place all fossils by morphological phylogenetic analyses (Ksepka, 2009; Parham et al., 2012; Warnock et al., 2014), and future examination of phylogenetic relationships of additional fossil galliforms may alter and improve the divergence time estimates presented here.

4.3. Branch-length distortion in combined UCE/Sanger matrices

The most striking result of our combined mtDNA + intron + UCE phylogeny was that branch estimates appeared distorted when one or more data types were missing for a taxon. Estimates of substitution rates for mtDNA, introns, and UCEs differed by several orders of magnitude (Fig. 1), which likely results in taxa having biased branch lengths when different data classes were combined (Fig. 2, see also Sun et al., 2014). In two clades (*Crax* and *Ortalis*) topology may also be biased, with taxa including UCEs moved towards the base of the tree when compared to their well-supported positions in the combined mtDNA + intron tree (Fig. 2A–B).

Generation of synthetic large-scale phylogenies (e.g., Burleigh et al., 2015), at least in the near future, will need to draw from heterogeneous sequence data sources like those analyzed here. Full genome sequences are available for some taxa, but most are still limited to one or a few molecular markers. Our observations highlight that caution is needed when analyzing such heterogeneous datasets to minimize biased topologies, and that alternate methods to calculate meaningful branch lengths may be warranted (Sun et al., 2014).

4.4. Conclusions

The cracid phylogenies presented here are the most well-resolved and feature the widest taxon sampling to date. Our time-calibrated phylogeny, in concert with biogeographical reconstructions, indicated that crown cracids originated in Mesoamerica, and multiple lineages diversified rapidly in South American following Panamanian Isthmus uplift. Combining heterogeneous data types such as mtDNA and UCEs causes distorted branch lengths estimates when one data type is missing, and care needs to be taken in these cases to produce robust estimates of divergence times.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2016.06.006.

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