

Rapid Laurasian diversification of a pantropical bird family during the Oligocene–Miocene transition

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Disjunct, pantropical distributions are a common pattern among avian lineages, but disentangling multiple scenarios that can produce them requires accurate estimates of historical relationships and timescales. Here, we clarify the biogeographical history of the pantropical avian family of trogons (Trogonidae) by re-examining their phylogenetic relationships and divergence times with genome-scale data. We estimated trogon phylogeny by analysing thousands of ultraconserved element (UCE) loci from all extant trogon genera with concatenation and coalescent approaches. We then estimated a time frame for trogon diversification using MCMCTree and fossil calibrations, after which we performed ancestral area estimation using BioGeoBEARS. We recovered the first well-resolved hypothesis of relationships among trogon genera. Trogons comprise three clades, each confined to one of three biogeographical regions: Africa, Asia and the Neotropics, with the African clade sister to the others. These clades diverged rapidly during the Oligocene–Miocene transition. Our biogeographical analyses identify a Eurasian origin for stem trogons and a crown clade arising from ancestors broadly distributed across Laurasia and Africa. The pantropical ranges of trogons are relicts of a broader Afro-Laurasian distribution that was fragmented across Africa, Asia and the New World in near coincident fashion during the Oligocene–Miocene transition by global cooling and changing habitats along the Beringian land bridge and North Africa.

Keywords: Beringian land bridge, historical biogeography, pantropical distribution, Trogonidae, ultraconserved elements.

The occurrence of the disjunct pantropical biota has been of wide interest to ornithologists. The Boreotropics hypothesis (Wolfe 1975, Tiffney 1985), which was borne out by studies of plant taxa and their fossils but has since been invoked in animal groups (e.g. Sanmartín *et al.* 2001), represented a major advance in our understanding of

disjunct distributions across the Old and New Worlds. This hypothesis ascribes disjunct distributions to a Laurasian origin in the early/middle Palaeocene, during which lineages attained a broad distribution under favourable tropical and sub-tropical climatic conditions and suitable land connections across Laurasia before subsequently becoming isolated by high-latitude climatic deterioration and the severing of continental land bridges. The Boreotropics hypothesis provides a framework that describes the divergence of plant

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and animal lineages across the North Atlantic (Lavin & Luckow 1993, Sanmartín *et al.* 2001) and Beringia (Beard 1998, Donoghue *et al.* 2001, Beard *et al.* 2016) and has even been invoked to explain an Africa–South America disjunction of an angiosperm clade (Davis *et al.* 2002). Although the large-scale geographical and climatic events driving diversification are the same for all groups, the pattern and timing of divergence in individual lineages vary; thus, an accurate estimate of phylogeny and divergence times for each lineage is essential for deciphering various patterns and individual causes of their spatial history (Donoghue *et al.* 2001, Sanmartín *et al.* 2001), and ultimately for understanding the development of modern pantropical biota.

Independent of the Boreotropics hypothesis, many tropical avian lineages are considered relicts of ancestors with broader distributions in Laurasia in the Palaeocene (Olson 1985, Blondel & Mourer-Chauviré 1998, Feduccia 2003). These relicts include: mousebirds (Coliiformes); the cuckoo roller (Leptosomiformes); hornbills (Bucerotiformes); rollers and allies (Coraciiformes); woodpeckers and allies (Piciformes); and trogons (Trogoniformes). All of these bird groups have been traditionally considered members of the ‘higher non-passerines’ (Sibley & Alquist 1972) and have recently been found to constitute a major clade of land birds, the Coraciimorphae (Jarvis *et al.* 2014, Prum *et al.* 2015). Coliiformes and Leptosomiformes, groups currently confined to Africa and Madagascar, respectively, had much wider distributions in North America and Europe during the Eocene based on the fossil record (Weidig 2006, Ksepka & Clarke 2009). Bucerotiformes at present occur in the Old World tropics, but hornbill fossils are known from the Eocene and Miocene of Europe. Coraciiformes, Piciformes (including barbets) and Trogoniformes, each of which has a contemporary pantropical distribution, had broader distributions in the Cenozoic. Eocene/Oligocene coraciiform fossils are known from Europe; piciforms are known from the Eocene of North America and the Miocene of Europe (Brodkorb 1971); and trogoniform fossils are known from the Palaeogene of Europe (Kristoffersen 2002, Mayr 2005, 2009). Among these groups, trogons have been the subject of especially intense phylogenetic and biogeographical study (Espinosa de los Monteros 1998, Johansson & Ericson 2005, Moyle 2005, DaCosta & Klicka 2008, Ornelas *et al.* 2009, Hosner *et al.* 2010).

Reconstructing the early biogeographical history of the trogons has been a major challenge, even with DNA sequence data. The trogons, in the family Trogonidae, consist of 43 species in seven genera distributed throughout much of the Old World and New World tropics (Dickinson & Remsen 2013; Fig. 1). Diversity is greatest in the New World (29 species), followed by Asia (12 species) and Africa (three species). Trogons are generally considered poor long-distance dispersers, although some species exhibit seasonal movements and one species has colonized the oceanic Philippine islands. Multiple, conflicting biogeographical histories have been proffered for the group because of differences in phylogenetic estimates (Espinosa de los Monteros 1998, Johansson & Ericson 2005, Moyle 2005, Ornelas *et al.* 2009, Hosner *et al.* 2010). For instance, some studies recovered distinct clades of African, Asian and Neotropical taxa (Espinosa de los Monteros 1998, Johansson & Ericson 2005, Ornelas *et al.* 2009), whereas others suggested paraphyly of the Neotropical taxa (Moyle 2005, Hosner *et al.* 2010). These conflicts probably resulted from the use of a few, different molecular markers, each supporting different topologies or providing little or no branch resolution. Support for intergeneric relationships was low in all the studies except one (Ornelas *et al.* 2009), in which Bayesian posterior probabilities were high (100%) but maximum likelihood bootstrap values were < 50%. Moreover, with the exception of Hosner *et al.* (2010), previous work did not include the distinctive Asian genus *Apalharpactes*, whose placement with other Asian trogons was equivocal.

The difficulty in resolving trogon phylogeny stems from two factors. First, the base of the trogon tree is characterized by short successive internodes, indicating a rapid initial burst of lineage formation. Phylogenies with such a structure are difficult to resolve with limited data, as in all previous studies of trogons, because of the low probability of informative substitutions occurring along these short internodes (Lanyon 1988) and the high probability of gene tree discordance (Degnan & Rosenberg 2006). Secondly, trogons have no close, living sister-group to break up the long branch leading to their rapid radiation (Johansson & Ericson 2005, Moyle 2005, Hackett *et al.* 2008, Prum *et al.* 2015). This long branch, combined with subsequent short internodes at the base of the trogon clade, obfuscates the root of

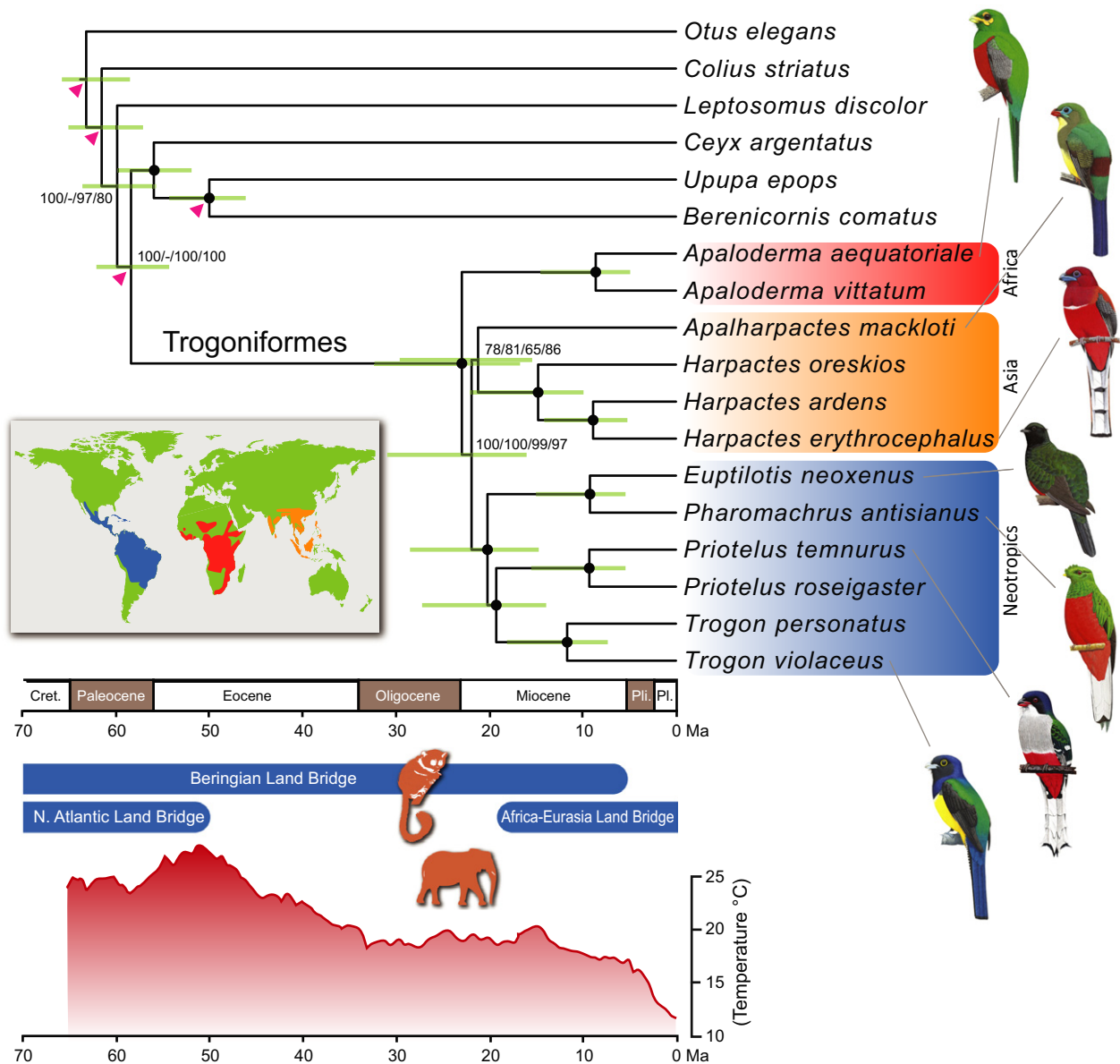


Figure 1. Estimate of phylogenetic relationships of trogons based on concatenated and coalescent approaches. Nodes with dots correspond to 100% bootstrap support from all methods of analysis. Numbers next to nodes indicate support from analyses using ML, SVDQuartets, ASTRAL and ASTRID, respectively. The chronogram is based on divergence time estimation with MCMCTree using four fossil calibrations on nodes indicated by arrows. Bars across nodes indicate 95% credible intervals for node age estimates. Inset map depicts the present distribution of trogons. Abbreviations in geological time scale are Pli, Pliocene; PI, Pleistocene. The bottom graph shows estimated Cenozoic surface temperature changes adapted from Hansen *et al.* (2013). Trogon images reproduced with permission from HBW Alive (del Hoyo *et al.* 2015). [Colour figure can be viewed at wileyonlinelibrary.com]

trogon phylogeny (Johansson & Ericson 2005, Moyle 2005) and any ensuing biogeographical inference. An additional factor that may have confounded phylogeny estimation in trogons is that the successive short internodes may place the species tree within the anomaly zone (Degnan & Rosenberg 2006), a situation in which the most

common gene trees inferred from sampled loci are expected to be incongruent with the species tree. To solve this problem, methods based on the multi-species coalescent may be more appropriate than concatenation (Degnan & Rosenberg 2006, Kubatko & Degnan 2007), but so far these have not been applied.

Conflicting estimates of trogon phylogeny have resulted in two alternative hypotheses of crown trogon origin (Espinosa de los Monteros 1998, Moyle 2005). Espinosa de los Monteros (1998) favoured an African origin based on topology and the geographical proximity of Africa to Palaeocene fossils from Europe. Alternatively, Moyle's (2005) tree supported a New World origin of crown trogons, which had been proposed previously because of higher trogon diversity in the Neotropics than in Africa and Asia (Mayr 1946). Since the publication of these two studies, additional stem trogon fossils from the Eocene of Europe have been described and phylogenetically analysed (Mayr 2005, 2009), providing new evidence on crown trogon origins that has not been formally included in previous biogeographical reconstructions (Espinosa de los Monteros 1998, Moyle 2005). Specifically, the fossil taxa *Masillatrogon* and *Primotrogon* were found to be successive sister taxa to crown trogons (Mayr 2009). In addition, an unpublished record of a putative stem trogon from the early Eocene of North America also apparently exists (Weidig 2003), albeit from a partial skeleton. These Northern Hemisphere fossils and the Boreotropics hypothesis point to a different explanation: trogons originated in Laurasia and later invaded southern latitudes concomitant with global cooling. The critical step in distinguishing among these possibilities is to reconstruct phylogeny and the timing of diversification accurately, as well as to incorporate fossil taxa in biogeographical analysis.

Recent studies using sequence capture of ultra-conserved elements and their flanking regions (UCE loci) have helped clarify phylogenetic relationships in regions of the avian tree that previously were recalcitrant because of successive short internodes (e.g. Sun *et al.* 2014, Moyle *et al.* 2016). In addition, advances in analytical methods now allow coalescent-based approaches to species-tree inference from thousands of loci (Liu *et al.* 2009, 2010, Chifman & Kubatko 2014, Mirarab *et al.* 2014, Vachaspati & Warnow 2015). In this paper, we utilize these sequencing and analytical methods to re-examine phylogenetic relationships within trogons. We then estimate the timing of diversification among trogon clades and evaluate hypotheses of the origin, timing and mode of their diversification using recent advances in our knowledge of the trogon fossil record.

METHODS

Sampling

The monophyly of all seven trogon genera is well established (DaCosta & Klicka 2008, Ornelas *et al.* 2009, Hosner *et al.* 2010). Because this study focuses on inter-generic relationships and broad-scale biogeographical patterns, we sampled 12 trogon species that included at least one representative of each genus and one or two additional species from species-rich genera (Table 1). Species from six closely related orders were used as outgroups.

Laboratory techniques

We extracted and purified DNA from fresh muscle or liver tissue using the Qiagen DNeasy Blood and Tissue Kit following the manufacturer's protocol. We sheared 500 ng of DNA of each sample in a 50- μ L volume using a Covaris S220 sonicator. We performed $\frac{1}{4}$ reactions of end-repair, A-tailing and adapter-ligation using Kapa Biosystems Library Prep kits. To allow for dual indexing, we ligated universal iTru stubs (Glenn *et al.* 2016) and incorporated iTru dual-indexes (Glenn *et al.* 2016) to library fragments using a 17-cycle PCR with NEB Phusion High-Fidelity PCR Master Mix. Libraries were combined in pools of eight equimolar samples for enrichment. We performed target enrichment using the Mycarray MYbaits kit for Tetrapods UCE 5K version 1, which targets 5060 UCE loci. Fragments recovered were amplified in a 17-cycle PCR amplification step, quantified using an Illumina Eco qPCR System, and sequenced in a high-output paired-end run of 100 cycles on an Illumina HiSeq 2500 System.

Data assembly

Raw reads were de-multiplexed using CASAVA ver. 1.8.2 (Illumina, Hayward, CA, USA). Low-quality bases and adapter sequences were trimmed from reads using ILLUMIPROCESSOR ver. 1 (<https://github.com/faircloth-lab/illumiprocessor>). Subsequent data processing was performed using the python package PHYLUC 1.5 (Faircloth 2015) as outlined below. Cleaned reads were assembled into contigs using Trinity (Grabherr *et al.* 2011). Contigs matching UCE loci were extracted for each taxon. For Speckled Mousebird

Table 1. Sampling and contig characteristics.

| Species | Accession number | Locality | Number of UCE contigs | Mean and (range) UCE contig length (bp) | Mean UCE coverage |
|----------------------------------|---|--------------------|-----------------------|---|-------------------|
| Ingroup | | | | | |
| <i>Apalharpactes mackloti</i> | LSUMNS B49104 | Indonesia | 4192 | 957.9 (201–2125) | 38.6 |
| <i>Apaloderma aequatoriale</i> | KUNHM 8461 | Equatorial Guinea | 4082 | 790.6 (201–1819) | 35.5 |
| <i>Apaloderma vittatum</i> | Downloaded from NCBI Genome (Jarvis <i>et al.</i> 2014) | Tanzania | 4680 | 2074 (275–2751) | – |
| <i>Euptilotis neoxenus</i> | AMNH DOT11081 | USA | 4078 | 881.3 (201–2067) | 42.3 |
| <i>Harpactes ardens</i> | KUNHM 26958 | Philippines | 4288 | 890.8 (203–1900) | 37.4 |
| <i>Harpactes erythrocephalus</i> | KUNHM 9970 | China | 3882 | 792.6 (201–1892) | 32.1 |
| <i>Harpactes oreskios</i> | KUNHM 23185 | Vietnam | 3695 | 799.3 (201–1890) | 26.2 |
| <i>Pharomacrus antisianus</i> | LSUMNS B22870 | Bolivia | 4201 | 1017.5 (201–2199) | 42.5 |
| <i>Priotelus roseigaster</i> | KUNHM 6363 | Dominican Republic | 4105 | 684.8 (201–1799) | 41.6 |
| <i>Priotelus temnurus</i> | ANSP 5565 | Cuba | 4264 | 1003 (201–2172) | 47.7 |
| <i>Trogon personatus</i> | AMNH DOT4266 | Venezuela | 3935 | 911.7 (202–2489) | 34.1 |
| <i>Trogon violaceus</i> | AMNH DOT11951 | Venezuela | 3195 | 748.7 (201–2097) | 31.1 |
| Outgroup | | | | | |
| <i>Berenicornis comatus</i> | AMNH DOT14737 | Captive | 4342 | 644 (201–4950) | 51.1 |
| <i>Upupa epops</i> | KUNHM 26612 | Mongolia | 3865 | 914.2 (201–2071) | 29.7 |
| <i>Ceyx argentatus</i> | KUNHM 19269 | Philippines | 4278 | 951.8 (201–2199) | 55.6 |
| <i>Leptosomus discolor</i> | FMNH 449184 | Madagascar | 4306 | 945.8 (202–1829) | 37.2 |
| <i>Otus elegans</i> | KUNHM 10975 | Philippines | 4225 | 955.2 (201–2026) | 46.8 |
| <i>Colius striatus</i> | Downloaded from NCBI Genome (Jarvis <i>et al.</i> 2014) | Captive | 4872 | 2113.8 (204–2752) | – |

AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Drexel University; KUNHM, University of Kansas Natural History Museum; LSUMNS, Louisiana State University Museum of Natural Science.

Colius striatus and Bar-tailed Trogon *Apaloderma vittatum*, UCE loci were obtained by *in silico* alignment of UCE probes with the full genome sequence (Jarvis *et al.* 2014) and taking the matched region along with 1000 bp of flanking nucleotides on each side of the matched region. We then assembled a dataset containing UCE loci that were present in at least 90% of taxa. Each locus was aligned using MAFFT (Katoh & Standley 2013) and trimmed using Gblocks (Castresana 2000) using default parameters with the exception of the minimum number of sequences for a flank position in Gblocks, which we set at 75% of taxa. The alignments were formatted to phylip and nexus files for phylogenetic analysis.

Phylogenetic analysis

We performed maximum likelihood (ML) inference on the concatenated dataset using ExaML ver. 3.0.15 (Kozlov *et al.* 2015) assuming a general time-reversible model of rate substitution and gamma-distributed rates among sites. We performed 20 ML searches and evaluated node support using 100 bootstrap replicates. We employed

three coalescent-based approaches to estimate a species tree. First, we used SVDQuartets (Chifman & Kubatko 2014, 2015), as implemented in PAUP* ver. 4.0a157 (Swofford 2003), to estimate phylogeny from the concatenated dataset using default parameters. We evaluated all quartets and performed analysis on 100 bootstrap replicates. We also employed two species-tree methods that use unrooted gene trees as input, ASTRAL III ver. 5.5.9 (Zhang *et al.* 2017) and ASTRID ver. 1.4 (Vachaspati & Warnow 2015). We performed gene-tree inference using RAxML 8.2.8 (Stamatakis 2014) on the individual locus alignments as well as on 100 multi-locus bootstraps of the data (Seo 2008) that were generated using PHYLUC. Consensus trees were generated for ExaML, ASTRAL and ASTRID using the sumtrees.py program in Dendropy (Sukumaran & Holder 2010). We followed the approach of Esselstyn *et al.* (2017) to examine topological concordance of individual gene trees with estimated species relationships. Using a custom Python script, we summarized the proportion of gene trees supporting bipartitions corresponding to trogon clades, as well as the average bootstrap

support for these clades among bootstrap replicates generated for multi-locus bootstrapping above. Command line, Python and R scripts used to process data and run species tree analyses are available at <https://github.com/carloliveros/trogons>.

We used the approximately unbiased (AU) test (Shimodaira 2002) to test alternative topologies in an ML framework. In addition to the ML search above, we performed 20 ML searches in ExaML ver. 3.0.15 (Kozlov *et al.* 2015) for each alternative topology with the alternative topology as a constraint. We then calculated site-wise likelihoods for each topology (ML and alternatives) using RAxML 8.2.8 (Stamatakis 2014). Using these site-wise likelihood scores we conducted the AU test in CONSEL ver. 0.20 (Shimodaira & Hasegawa 2001). To explore the strength of support of individual loci between topologies, we compared site-wise likelihoods of the ML topology and alternative topologies following the general approach of Shen *et al.* (2017). From the site-wise likelihoods above, we calculated a site-wise $\Delta\ln L$ by subtracting the value obtained for the alternative topology from the value for the ML topology. We summed site-wise likelihood differences over the length of individual loci to obtain a locus-specific $\Delta\ln L$ for each comparison between the ML solution and an alternative topology (Shen *et al.* 2017). As a result, locus-specific $\Delta\ln L$ is positive when it supports the ML hypothesis but negative when it favours the alternative topology.

Divergence time estimation

We used the program MCMCTree in the PAML ver. 4.8 package (dos Reis & Yang 2011) to estimate absolute divergence times among trogon genera. The complete dataset was concatenated and treated as a single locus in the analysis. The tree topology was fixed to the well-supported topology inferred from both concatenated and species tree analyses. A model of independent rates among lineages drawn from a lognormal distribution was used with gamma-distributed hyper-priors for the mean and variance of rates. The hyper-prior parameters for *rgene_gamma* were selected using estimates of the overall substitution rate on the tree obtained by the PAML program BASEML. A birth-death-sampling model of lineage diversification was used with sampling rate of 0.28 (12/43 trogon species). Date estimates were robust to

changing initial values for the hyper-prior parameter β in *rgene_gamma* (between 0.45 and 2) and *sigma2_gamma* (between 1 and 0.5), as well as in the birth rate (between 2 and 1) and death rate (between 1.3 and 1). An HKY85 substitution model with gamma-distributed rates in five categories was arbitrarily chosen to account for substitution rate variation among sites. Two independent Markov chain Monte Carlo (MCMC) chains were run with parameters sampled every 10^4 generations, 1.5×10^4 times after discarding 5×10^4 generations as burn-in. Convergence of likelihood and parameters was assessed by examining trace plots using the program Tracer ver. 1.6.0 (Rambaut & Drummond 2014) and by comparing results between the two independent runs.

Although a number of stem trogon fossils are known, no fossils appropriate for calibrating divergences among extant genera are available (Mayr 1999, 2005, 2009, 2017, Kristoffersen 2002, Mayr & Smith 2013). Thus, four fossil calibrations from closely related bird orders and one calibration from a stem trogon were used (Table 2). A maximum bound of 65.6 Ma was applied to the root of the tree, which corresponds to the higher end of the confidence interval for the same node from a recent phylogenomic study of all bird orders (Jarvis *et al.* 2014, see also Claramunt & Cracraft 2015).

An alternative set of dating analyses was performed using two secondary time calibrations from a recent chronogram of avian bird orders based on genome-wide data and multiple fossil calibrations (Jarvis *et al.* 2014). Normally distributed priors were assigned to both calibrations: one with mean of 59.942 Ma with sd 1.675 Ma at the split of Coliiformes and its sister clade; and the other with mean 51.985 Ma and sd 1.55 Ma at the split of Bucerotiformes and its sister clade. We used means and standard deviations in our calibration priors that reflected their posterior distribution in Jarvis *et al.* (2014). Age estimates based on these calibrations did not differ substantially from those derived with fossil calibrations and are thus not shown.

Ancestral area estimation

We performed biogeographical analyses using BioGeoBEARS ver. 0.2.1 (Matzke 2013) to estimate the ancestral area of stem and crown trogons. We coded each taxon according to the distribution of

Table 2. Fossil calibrations for divergence time estimation.

| Taxon | Phylogenetic position | Constraint | References |
|------------------------------|--|---|--|
| <i>Ogygoptynx wetmorei</i> | Stem-Strigiformes | Lower bound 56.8 Ma and upper bound 65.6 Ma | Rich and Bohaska (1976) |
| <i>Sandcoleus copiosus</i> | Sister to Colii (<i>sensu</i> Ksepka & Clarke 2009) | Lower bound 55.4 Ma ^a | Houde and Olson (1992), Ksepka and Clarke (2009) |
| <i>Messelirrisor grandis</i> | Stem-Upupidae | Lower bound 49 Ma ^a | Mayr (2000, 2006) |
| <i>Septentrogon madseni</i> | Stem-Trogoniformes | Lower bound 54.5 Ma ^a | Kristoffersen (2002), Mayr (2009) |

^aLower bounds were used with offset parameter $P = 0.1$, and scale parameter $c = 0.5$.

the clade it represents using three broad geographical areas: the New World, Africa + Madagascar and Eurasia. We assigned the outgroups *Colius striatus* and *Leptosomus discolor* to all three areas because stem fossils of both taxa are known from Europe and North America (Weidig 2006, Ksepka & Clarke 2009, Mayr 2013), in addition to their present-day distributions in Africa and Madagascar, respectively. Several fossils from the Palaeogene of Europe have been proposed as trogons (Brodkorb 1971, Olson 1976, Mayr 1999, 2001, 2005, 2009, Kristoffersen 2002, Weidig 2003, Mayr & Smith 2013). However, only two of these have been successfully placed in the trogon phylogeny, *Masillatrogon pumilio* from the middle Eocene (c. 47 Ma) of Germany (Mayr 2009) and *Primotrogon wintersteini* from the middle Oligocene (c. 30 Ma) of France (Mayr 1999). Because these are thought to be successive sister taxa of crown trogons (Mayr 2009), we added two branches corresponding to them to the phylogram output of MCMCTree using an R script that was modified from Claramunt and Cracraft (2015). These branches were inserted arbitrarily at the midpoint of the appropriate edge and served as representatives of Palaeocene trogon fossils from Europe. We compared biogeographical reconstructions using the DEC (Ree & Smith 2008) and DEC+ j (Matzke 2014) models of ancestral area evolution. We chose the DEC model *a priori* because it includes all biogeographical processes available in the DIVALIKE and BAYAREALIKE models of BioGeoBEARS with the exception of widespread sympatry and widespread vicariance at cladogenesis (Matzke 2013), scenarios which are not biologically realistic across the three broad geographical areas. To test the sensitivity of our results to model choice we also performed biogeographical reconstructions using the DIVALIKE (Ronquist 1997, Yu *et al.* 2010) and BAYAREALIKE (Landis *et al.* 2013) models of ancestral area evolution, as well as versions of these

models with the jump-dispersal parameter j (Matzke 2014). We also performed the same biogeographical analysis with the MCMCTree phylogram, which did not contain the fossil taxa, to examine the sensitivity of reconstructions to the addition of fossil taxa.

RESULTS

We obtained an average of 4058 UCE loci per individual with an average UCE contig length of 868 bp and average coverage of 39 \times (Table 1). The assembled dataset included data from 3581 loci with a total alignment length of 2 915 690 bp and included nucleotide data in 94.5% of the data matrix. Raw reads are available from NCBI SRA and UCE sequence data are available at NCBI GenBank accessible through the NCBI Project (PRJNA494020) and NCBI BioSamples (SAMN10147543–SAMN10147558). Alignments are available from Figshare (<https://doi.org/10.6084/m9.figshare.7356191>).

Concatenation and coalescent phylogenetic approaches, with the exception of ASTRAL, yielded the same topology with high support for most nodes (Fig. 1). The earliest split in crown-clade trogons involved the African genus *Apaloderma*, which was sister to a clade that included two radiations, one in Asia and the other in the New World. Within the Asian clade, *Apalharpactes* was sister to *Harpactes*. In the New World, the quetzal genera *Euptilotis* and *Pharomachrus* formed a clade sister to *Trogon* and *Priotelus*. With two exceptions, all nodes in the ingroup had 100% bootstrap support across the different analytical approaches. The node that unites the Asian and New World clades (Fig. 1) received 100% bootstrap support in both ML and SVDQuartets analyses, and 99% and 97% bootstrap support in ASTRAL and ASTRID analyses, respectively. In

contrast, the node that unites the Asian genera *Apalharpactes* and *Harpactes* (Fig. 1) received moderate bootstrap support of 78%, 81% and 86% in ML, SVDQuartets and ASTRID analyses, respectively. Although ASTRAL analysis of multi-locus bootstraps yielded a low bootstrap support of 65% for this node, ASTRAL analysis of gene trees inferred from the original locus alignments found a sister relationship between the genus *Harpactes* and New World trogons.

The alternative ASTRAL topology had lower support for the monophyly of the Asian genera *Apalharpactes* and *Harpactes*, suggesting that relationships among three trogon lineages, the genus *Apalharpactes*, the genus *Harpactes* and the New World trogons, needed closer scrutiny. We performed the AU Test (see above) to compare our primary topology in which the Asian genera were monophyletic (T1) with two alternative topologies: (T2) *Harpactes* sister to New World trogons, and (T3) *Apalharpactes* sister to New World trogons. With our data, we could not reject a sister relationship between *Harpactes* and New World trogons ($P = 0.2$). However, a sister relationship between *Apalharpactes* and New World trogons was rejected ($P = 10^{-10}$). A few loci contributed substantially large $\Delta\ln L$ values but removing these outlier loci did not change the sign of the total $\Delta\ln L$ and, consequently, the preferred ML topology (Fig. 2). Examination of gene trees inferred from the individual locus alignments showed that gene tree discordance at these nodes was high (Table 3). Among the three possible relationships among these three lineages, the monophyly of Asian trogon genera (T1; Fig. 1) received the highest support (but from only 12.9% of gene trees) and highest resolution (45.4% average bootstrap support). Each of the alternative topologies, T2 and T3, was supported by a lower proportion of gene trees ($< 10\%$) and by an average of 40% or less of bootstraps. By comparison, the monophyly of well-known trogon clades was supported by 27–91% of gene trees (Table 3). The low proportion of gene trees supporting our primary and alternative topologies is not surprising given the rapid nature of splitting events among the main trogon lineages.

The trogons were found to be sister to a clade consisting of Bucerotiformes (hornbills) and Coraciiformes (rollers, bee-eaters and allies; Fig. 1) in ML, ASTRAL and ASTRID analyses with 100% bootstrap support, a topology consistent with results of recent phylogenomic studies (Jarvis *et al.* 2014, Prum *et al.* 2015, Reddy *et al.* 2017). This

Trogoniformes + Bucerotiformes + Coraciiformes clade was in turn sister to Leptosomiformes (cuckoo-roller) with high bootstrap support in ML and ASTRAL analyses (100% and 97%) and with moderate support in ASTRID analysis (80%). SVDQuartets, however, recovered a topology in which trogons and Coliiformes (mousebirds) formed a clade, and which in turn was sister to Bucerotiformes + Coraciiformes, both nodes with a moderate 87% bootstrap support.

Our dating analysis estimated that crown trogon lineages from Africa, Asia and the New World diverged rapidly *c.* 23 Ma within a few million years around the Oligocene–Miocene transition, *c.* 35 million years after trogon ancestors diverged from their closest relatives in the Palaeocene (Fig. 1). Our age estimate of crown trogons is within the confidence intervals of previous estimates (Espinosa de los Monteros 1998, Moyle 2005) but is at the younger end of these ranges (19.7–35.6 and 23.9–35.1 Ma, respectively).

Biogeographical analyses using the DEC and DEC+*j* models estimated that crown trogons were present in an area encompassing the New World, Africa and Eurasia with high probability before splitting between Africa and Eurasia + New World (Fig. 3). We obtained the same result whether fossil taxa were included or excluded. However, the estimated origin of stem trogons changed from Eurasia, when fossil taxa were included in the analysis (Fig. 3a), to equivocal between Africa and Eurasia, when fossil taxa were excluded (Fig. 3b). The DIVALIKE and DIVALIKE+*j* models yielded ancestral reconstructions identical to our DEC results. The BAYAREALIKE and BAYAREALIKE+*j* models produced different reconstructions but with lower likelihood values and higher Akaike information criterion (AIC) scores (Table 4). We focus our discussion on DEC results that include fossil taxa because ignoring them changes ancestral area estimates as seen in our data. Biogeographical models with the jump-dispersal parameter *j* as well as statistical comparisons of models that include this parameter have been criticized as inappropriate (Ree & Sanmartín 2018), but these criticisms are moot with respect to our results because we obtained identical biogeographical reconstructions for the nodes of interest in both DEC and DEC+*j* analyses. In fact, analyses with the DEC+*j* model produced likelihood values identical to the DEC model and a zero estimate for *j*, indicating that the more complex models were reduced to the simpler model in the analyses that included the *j* parameter (Table 4).

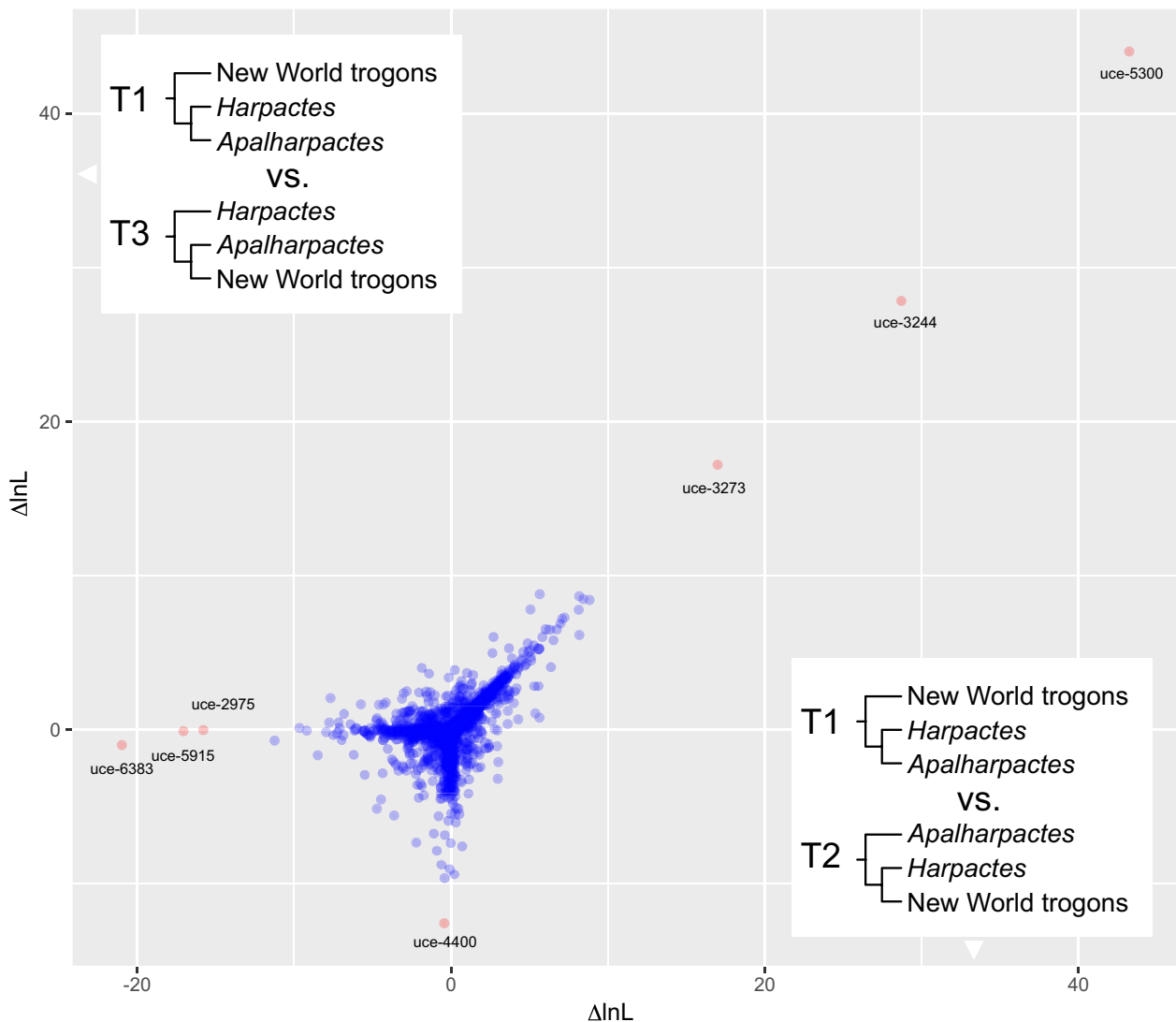


Figure 2. Differences in site-wise log likelihood ($\Delta\ln L$) showing the strength of phylogenetic signal supporting (positive $\Delta\ln L$ values) or contradicting (negative $\Delta\ln L$ values) our primary topology (monophyly of Asian trogons, T1; Fig. 1) over two alternative topologies (x-axis: monophyly of *Harpactes* and New World trogons, T2; y-axis: monophyly of *Apalharpactes* and NW trogons, T3) for each UCE locus (dots). Removal of outlier loci (labelled dots) does not alter the high likelihood for the monophyly of Asian trogon genera. [Colour figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Trogon relationships

This study is the first to estimate trogon phylogeny based on genome-wide data and to produce a well-resolved tree of generic relationships. Congruence of results among most concatenation and coalescent analyses suggests our estimate of relationships among trogon genera is robust. Support for most nodes in the ingroup was high

(> 97% bootstrap) in both concatenation and coalescent analyses, with one exception. Support for the monophyly of Asian genera *Apalharpactes* and *Harpactes* (T1) was low to moderate in four different analyses (65% in ASTRAL, 78% in ML, 81% in SVDQuartets and 86% in ASTRID) but highest among estimated gene trees. Although the alternative topology of the genus *Harpactes* forming a clade with New World trogons (T2) could not be rejected by the AU test, we consider the sister relationship between the two Asian genera

Table 3. Gene tree discordance among 3581 UCE loci.

| Clade | Proportion of supporting gene trees | Average bootstrap support |
|--|-------------------------------------|---------------------------|
| Crown trogons | 43.0 | 90.8 |
| Genus <i>Apaloderma</i> | 90.6 | 91.5 |
| Genus <i>Harpactes</i> | 65.6 | 74.7 |
| New World genera (<i>Euptilotis</i> , <i>Pharomacrus</i> , <i>Priotelus</i> , <i>Trogon</i>) | 27.4 | 50.6 |
| T1: Asian genera (<i>Apalharpactes</i> , <i>Harpactes</i>) | 12.9 | 45.4 |
| T2: Genus <i>Harpactes</i> and New World genera | 9.6 | 40.2 |
| T3: Genus <i>Apalharpactes</i> and New World genera | 8.6 | 39.2 |

Average bootstrap support from UCE loci that support the clade are also indicated.

as the best estimate of relationships because of moderate support in concatenation and most coalescent analyses. The only other study that included *Apalharpactes* was unable to estimate its position with confidence (Hosner *et al.* 2010). The inclusion of the only other species of *Apalharpactes*, *A. reinwardtii*, in examining trogon phylogenetic relationships would probably not alter these results because the two *Apalharpactes* species are so closely related that they were once treated as conspecific.

The main results of our study, demonstrating the monophyly of trogons in each geographical region – Africa, Asia and the Neotropics – and establishing hierarchical relationships among them, are similar to those of earlier studies (Espinosa de los Monteros 2000, Ornelas *et al.* 2009), but now with strong nodal support across the tree. Our results contradict the outcome of earlier studies that found Asian (Hosner *et al.* 2010) and New World trogons (Moyle 2005, Hosner *et al.* 2010) to be paraphyletic. These earlier studies appear to have suffered largely from inadequate phylogenetic signal in the markers used. For example, analysis of mitochondrial *Cyt-b* gene sequences placed the African genus *Apaloderma* as sister to all other trogons, with low support (Espinosa de los Monteros 1998, Johansson & Ericson 2005). Another mitochondrial gene, *ND2*, and the nuclear *RAG-1* gene, each indicated *Priotelus* and the quetzal genera *Euptilotis* and *Pharomacrus* as the first lineages to sequentially diverge from the base of the tree, again with weak support (Moyle 2005). Interestingly, the study that combined all these markers

arrived at a topology similar to ours, albeit with low ML bootstrap support (Ornelas *et al.* 2009).

Origin and diversification of trogons

Inferring the origin of stem trogons is difficult for several reasons. First, trogon distribution has changed considerably during the Cenozoic, as documented in the fossil record. Trogon fossils are known from the late Palaeocene/early Eocene of Denmark (Kristoffersen 2002), the early Oligocene of Switzerland, France, Germany and Belgium (Olson 1976, Mayr 1999, 2001, 2005, Mayr & Smith 2013), and the early Miocene of France (Brodkorb 1971). In addition, a putative stem trogon fossil from the early Eocene of North America (Weidig 2003) might indicate a broader New World distribution, although this unpublished record needs to be confirmed. Secondly, according to our estimates, stem trogons existed for *c.* 35 million years, long enough for their distributions to shift substantially. Thirdly, many lineages most closely related to trogons (Coliiformes, Leptosomiiformes, Bucerotiiformes, Coraciiformes and Piciiformes) also had different or broader distributions in the Palaeocene, thus substantiating the likelihood of a shifting trogon distributional history. Fourthly, as shown in our ancestral area estimates for stem trogons, biogeographical analysis can be sensitive to taxon sampling, including fossil taxa. We found that including fossil taxa yielded a Eurasian origin for stem trogons (Fig. 3a). The outcome was more equivocal with respect to Africa vs. Eurasia when European fossil taxa were excluded (Fig. 3b). Fifthly, the distribution of fossil taxa may be broader than suggested by current records, so biogeographical reconstructions that use them may be biased. Lastly, avian palaeontological work has traditionally been biased toward the Northern Hemisphere (Cracraft & Claramunt 2017), so our estimates could be influenced by this bias.

Despite these challenges and based on our current knowledge of trogon fossils, we consider an African origin of stem trogons unlikely. Although this possibility is partially suggested by the analysis that excluded stem trogon fossils, biogeographical reconstruction with fossil taxa estimates a Eurasian origin for stem trogons with close to 100% probability. In addition, Africa was largely isolated from Europe during the early–middle Palaeocene (Gheerbrant & Rage 2006), when stem trogons occurred in Europe. An African origin for stem

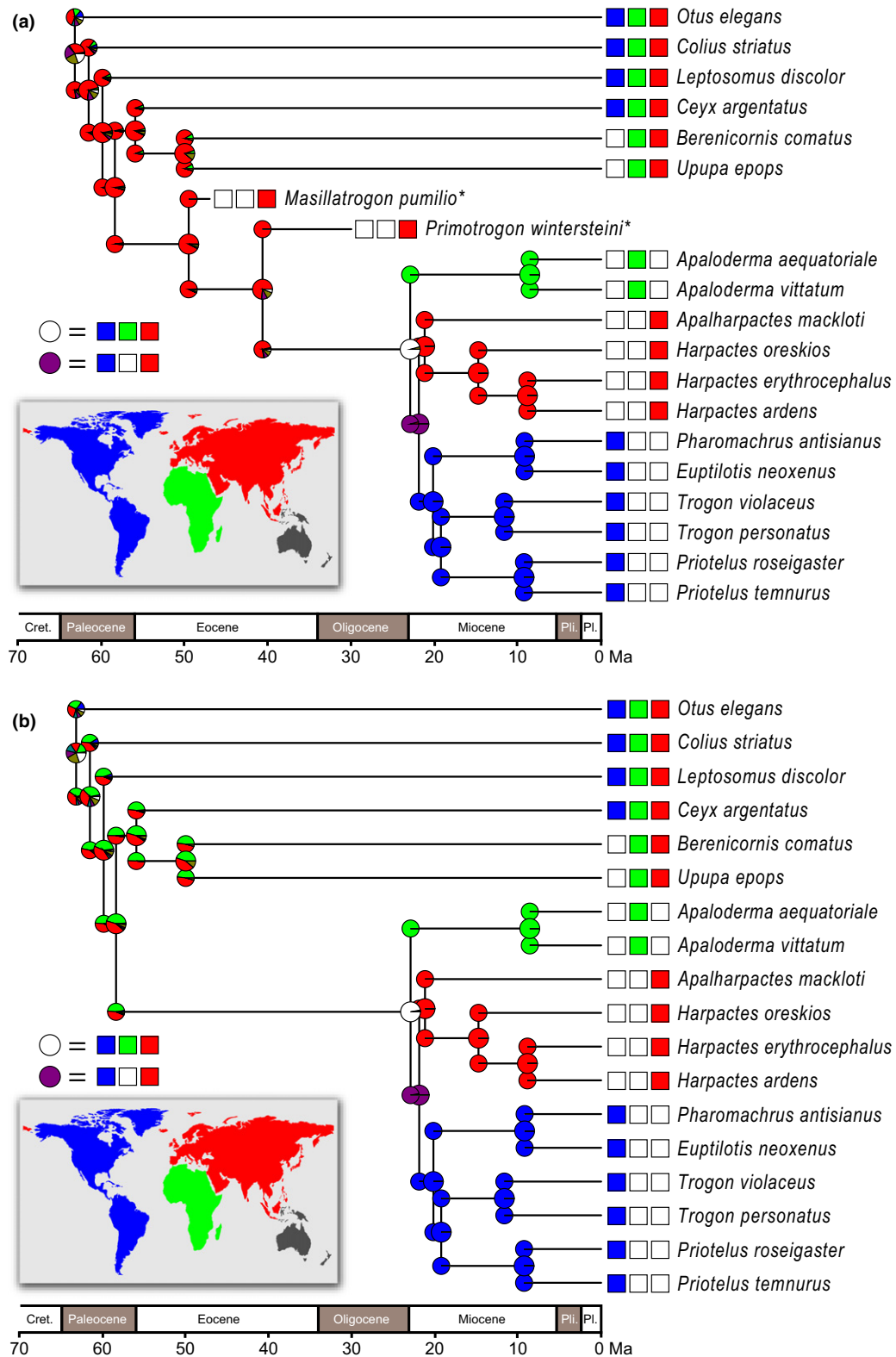


Figure 3. Ancestral area estimates of trogons obtained using the DEC model in BioGeoBEARS. Stem trogon fossils were included and indicated by an asterisk in (a) and excluded in (b). Colours (online version)/shades (print version) of boxes at tips represent distribution of clades represented at the tip. Pie charts at nodes and corners show ancestral area probabilities before and after cladogenesis, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

Table 4. Comparison of biogeographical models in BioGeoBEARS.

| Model | lnL | No. of parameters | <i>d</i> | <i>e</i> | <i>j</i> | AIC |
|--|--------|-------------------|----------|----------|----------|-------|
| Tree that includes fossil taxa (Fig. 3a) | | | | | | |
| DEC | -17.78 | 2 | 1.22 | 0.00 | | 39.55 |
| DEC+ <i>j</i> | -17.78 | 3 | 1.22 | 0.00 | 0.00 | 41.55 |
| DIVALIKE | -16.34 | 2 | 1.27 | 0.00 | | 36.68 |
| DIVALIKE+ <i>j</i> | -16.34 | 3 | 1.27 | 0.00 | 0.00 | 38.68 |
| BAYAREA | -29.26 | 2 | 0.89 | 0.35 | | 62.51 |
| BAYAREALIKE+ <i>j</i> | -20.25 | 3 | 0.85 | 0.00 | 0.05 | 46.50 |
| Tree that excludes fossil taxa (Fig. 3b) | | | | | | |
| DEC | -15.43 | 2 | 1.27 | 0.00 | | 34.86 |
| DEC+ <i>j</i> | -15.43 | 3 | 1.27 | 0.00 | 0.00 | 36.86 |
| DIVALIKE | -13.89 | 2 | 1.31 | 0.00 | | 31.77 |
| DIVALIKE+ <i>j</i> | -13.89 | 3 | 1.31 | 0.00 | 0.00 | 33.77 |
| BAYAREA | -28.51 | 2 | 0.21 | 0.84 | | 61.02 |
| BAYAREALIKE+ <i>j</i> | -17.85 | 3 | 0.00 | 0.28 | 0.05 | 41.71 |

lnL, natural logarithm of likelihood; *d*, dispersal rate; *e*, extinction rate; *j*, jump-dispersal rate; AIC, Akaike information criterion.

trogons and other land birds would have required at least two crossings of the Tethys Sea. Unless trogon fossils from the Palaeocene are found in Africa, a region with a sparse avian fossil record, the weight of evidence will remain against Africa as the trogon source. Alternatively, the putative early Eocene trogon fossil from North America (Weidig 2003) would expand geographical possibilities for stem trogon distribution and, depending on its phylogenetic position, might support a Nearctic (Claramunt & Cracraft 2015) or Laurasian origin. Until a North American trogon fossil is confirmed, however, Eurasia remains the most likely site of origin based on our analyses and the current understanding of the fossil record.

Crown, as opposed to stem, trogons appear to have been broadly distributed across the Northern Hemisphere (Fig. 3). This distribution is indicated by the pattern of near-coincident branching into Africa, Asia and the New World. It is also supported by geological and climatic records of appropriate land connections and tropical habitat during the Oligocene–Miocene transition.

The Tethyan Seaway largely hindered colonization between Africa and Eurasia until the early Miocene, when connection through the Middle East allowed vertebrate dispersal between the two continents (Rögl 1999, Gheerbrant & Rage 2006, Harzhauser *et al.* 2007). However, elephantoid mammals appear to have traversed from Africa to Eurasia in the late Oligocene (Antoine *et al.* 2003), suggesting earlier contact between the two continents that might have been exploited by

trogons. Europe was connected to eastern North America by a land bridge in the early Palaeocene, but this link was severed in the early Eocene *c.* 53 Ma (Doré *et al.* 1999), too early for crown trogon exploitation. On the other side of the globe, western North America and east Asia were connected by the Beringian land bridge, at least multiple times, from the mid-Cretaceous until the Pliocene (see summary in Sanmartín *et al.* 2001).

By the Oligocene, global climate began to cool (Fig. 1) and tropical forests across northern latitudes receded southward and were replaced by mixed deciduous hardwood and coniferous forest (Sanmartín *et al.* 2001). However, the period between the late Oligocene and mid-Miocene climatic optima (Fig. 1; Zachos *et al.* 2001, Hansen *et al.* 2013) was notably warmer and might have provided suitable habitat for early crown trogons to move along intercontinental connections. The presence of early Miocene trogon fossils in France (Brodkorb 1971) indicates that early trogons lived during this period at higher latitudes, possibly as high as the Beringian land bridge. Odontophorid quails and strepsirrhine primates also are thought to have crossed the Beringian land bridge from Asia in the Oligocene (Hosner *et al.* 2015, Samuels *et al.* 2015). Climatic cooling during the Oligocene–Miocene transition of the Northern Hemisphere, and the resulting habitat fragmentation, probably isolated trogons in Africa, southern Eurasia and tropical America.

Our hypothesis of crown trogon origins stands in contrast to the African (Espinosa de los

Monteros 1998) and New World (Moyle 2005) origin hypotheses proposed earlier for the group. Although our study yields the same topology as Espinosa de los Monteros (1998), our biogeographical conclusions differ. Espinosa de los Monteros (1998) used an ancestral area estimation method that places more weight on areas associated with lineages that diverge early and assumes that ancestors are no more widespread than current taxa (Bremer 1992, 1995); hence, he estimated an African origin of trogons. The DEC model used in our study makes no such assumptions. The discrepancy between our biogeographical conclusions and those of Moyle (2005), on the other hand, stems largely from the difference in our estimates of trogon phylogeny.

Overall, geological and climate data, along with our divergence date estimates, support the view that crown trogons assumed a wide distribution across Laurasia and Africa during the Oligocene–Miocene transition, probably crossing through the Beringian land bridge and intermittent connections between Africa and Eurasia. Long-distance dispersal need not be invoked to explain their initial diversification in Africa, Eurasia and the New World. However, colonization of the Greater Antillean and Philippine archipelagos probably occurred via overwater dispersal. The Greater Antilles were not connected to North or Central America in the early Miocene (Iturralde-Vinent 2006), the time period when we estimate the ancestors of the Greater Antillean *Priotelus* diverged from other Neotropical trogons. The only trogon species in the Philippines, *Harpactes ardens*, occurs on oceanic islands that have had no land connections to the Asian continental shelf.

Laurasian biogeography

The near-coincident splitting of African, Asian and New World trogons during the Oligocene–Miocene transition helps clarify the timing and pattern of Northern Hemisphere vicariance events among avian lineages and subsequent sequestration of avian lineages in the tropics. Such events appear to have occurred in episodes throughout the Cenozoic in several non-passerine groups. The New World motmots (Momotidae) split from Asian kingfishers (Alcedinidae) in the Late Eocene (Andersen *et al.* 2018), probably across Beringia. The barbets (Ramphastoidea) experienced a near-coincident split among

African, Asian and New World lineages in much the same way as trogons (Sheldon *et al.* 2015). The Asian barbets (Megalaimidae) separated from the African barbets (Lybiidae) and the New World barbets (Capitonidae) in the late Oligocene; subsequently, in the early Miocene, the Lybiidae and Capitonidae split from one another (Prum *et al.* 2015). Unlike trogons, however, the Asian barbets were the first to branch off. Splits between Old and New World lineages within kingfishers and woodpeckers (Picidae) appear to have occurred more recently, i.e. from the mid-Miocene onwards (Shakya *et al.* 2017, Andersen *et al.* 2018). Different habitat requirements in these groups might explain the variations in timing. Episodic vicariance events across Laurasian land bridges have also been hypothesized in angiosperm lineages (Davis *et al.* 2002). Undoubtedly, our understanding of Laurasian vicariance will benefit from further investigations into other groups of organisms distributed across the Old World and New World.

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