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A Laurasian origin for a pantropical bird radiation is supported by genomic and fossil data (Aves: Coraciiformes)

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The evolution of pantropically distributed clades has puzzled palaeo- and neontologists for decades regarding the different hypotheses about where they originated. In this study, we explored how a pantropical distribution arose in a diverse clade with a rich fossil history: the avian order Coraciiformes. This group has played a central role in the debate of the biogeographical history of Neoaves. However, the order lacked a coherent species tree to inform study of its evolutionary dynamics. Here, we present the first complete species tree of Coraciiformes, produced with 4858 ultraconserved elements, which supports two clades: (1) Old World-restricted bee-eaters, rollers and ground-rollers; and (2) New World todies and motmots, and cosmopolitan kingfishers. Our results indicated two pulses of diversification: (1) major lineages of Coraciiformes arose in Laurasia approximately 57 Ma, followed by independent dispersals into equatorial regions, possibly due to tracking tropical habitat into the lower latitudes—the Coracii (Coraciidae + Brachypteraciidae) into the Afrotropics, bee-eaters throughout the Old World tropics, and kingfishers into the Australasian tropics; and (2) diversification of genera in the tropics during the Miocene and Pliocene. Our study supports the important role of Laurasia as the geographical origin of a major pantropical lineage and provides a new framework for comparative analyses in this charismatic bird radiation.

1. Introduction

Biogeographical patterns—both past and present—can illuminate mechanisms of biological diversification. One such pattern is a pantropical distribution, which refers to clades with disjunct, equatorial distributions across the world's tropical regions. Pantropical clades are observed across the tree of life, from plants [1,2] to insects [3] and birds [4,5]. This pattern is diversity independent—for example, it spans a diversity continuum in birds from three species of finfoots to hundreds of parrots [6]. Originally, two competing hypotheses explained how pantropical clades arose: continental breakup of Gondwana isolated organisms via vicariance [7,8] or clades originated in Laurasia and subsequently dispersed into the Southern Hemisphere [9–11]. Based on fossil histories of plants, the Boreotropics hypothesis [12,13] suggests that these disjunct clades arose in the warm, tropical habitats characteristic of the early to middle Palaeocene of Laurasia. As the tropical climate deteriorated after the Palaeocene–Eocene Thermal Maximum and continental land bridges were severed, these clades tracked tropical habitats southward and became isolated across the equatorial tropical zone.

A general pattern emerges in the fossil record of tropical, non-passerine landbirds that is difficult to reconcile with their modern distributions. Lineages with Old World distributions are known from fossils in North America and vice versa. Mousebirds [14], turacos [15], rollers [16] and the cuckoo roller

[17,18]—all restricted to the Old World today—have stem-fossil representatives in the Paleogene of North America. Even trogons [19,20] and hornbills [21], modern tropical clades, have fossil representatives far outside their current range. Conversely, Palaeogene stem representatives of extant New World clades are found in Europe (e.g. hummingbirds [22,23] and todies [24]). These fossils suggest that earlier ancestors of these clades had more widespread, Holarctic distributions than their more range-restricted modern relatives [16,25]. Recently, Claramunt & Cracraft [26] proposed the 'North American Gateway Hypothesis', which posits that a major pathway of avifaunal dispersal existed in the early Palaeogene, out of West Gondwana and into North America. Major lineages of Neornithine birds thus originated in mesic environments of North America and subsequently colonized the Old World via land bridges [13] across Greenland and into Eurasia. One of the aims of this study is to investigate these hypotheses in the context of a well-sampled phylogeny of a clade that is at the centre of this debate, the Coraciiformes [16,27–31].

Due to its diversity, fossil history and modern ranges, Coraciiformes (177 species, six families) presents an opportunity in which to elucidate how pantropical clades evolved throughout the Cenozoic. Its fossil record is rich compared to other bird lineages (all but one of the six families in the order, bee-eaters, are represented). Today, it is distributed pantropically, but five of the six coraciiform families are largely restricted to specific tropical regions: Neotropical motmots (Momotidae, 15 sp.), Caribbean todies (Todidae, five sp.), African and Asian bee-eaters (Meropidae, 27 sp.) and rollers (Coraciidae, 12 sp.), and Malagasy ground-rollers (Brachypteraciidae, five sp.) [32–34]. Kingfishers are the most species-rich family (Alcedinidae, 113 sp.), comprising two-thirds of coraciiform diversity, and are the only family that is distributed across all three disjunct tropical regions [6,33]. Kingfishers have received the most attention from systematists [35–39], whereas the remaining families are understudied by comparison (bee-eaters [40], ground-rollers [41], todies [42], rollers [43]). Indeed, the relationships among coraciiform families are unresolved [26,30,44,45] and the ongoing debate about their biogeographical origins continues to be hampered by the lack of a comprehensive species tree of the group.

Here, we investigated the evolutionary relationships and biogeographical origins of Coraciiformes with both new and long-standing hypotheses into the evolution of pantropical clades. We used thousands of ultraconserved elements (UCEs [46]) and fossil calibrations to generate a fully sampled time-calibrated tree of Coraciiformes. Ultraconserved elements are short genomic regions with a conserved core and variable ends that are scattered throughout the genome and are conserved across the tetrapod tree of life; they are powerful molecular markers with high resolving power [47–49]. With this robust phylogenomic hypothesis of Coraciiformes, we inferred biogeographical ancestral ranges to assess competing hypotheses regarding the origins of the clade. Next, we estimated the tempo of macroevolutionary diversification to assess potential shifts in the pace of diversification that produced clades with disparate species richness and geographies. By leveraging phylogenomic and paleontological data, we demonstrate how temporal and spatial diversification during the radiation of a major avian clade gave rise to the enigmatic biogeographical pattern of a pantropical distribution.

2. Material and methods

(a) Sampling, DNA extraction and quantification

We sampled 196 ingroup and four outgroup taxa (electronic supplementary material, table S1), including every extant coraciiform species recognized by the International Ornithological Congress (IOC v. 8.2 [34]). Our sampling also included phenotypically divergent subspecies that are sometimes considered distinct species [33,38,39,50] (electronic supplementary material, table S1). We included these taxa as terminal units in downstream biogeographical and macroevolutionary analyses. We extracted UCEs from published genomes for our outgroup species: cuckoo roller (*Leptosomus discolour*; Leptosomiformes), bar-tailed trogon (*Apaloderma vittatum*; Trogoniformes), rhinoceros hornbill (*Buceros rhinoceros*; Bucerotiformes) and downy woodpecker (*Picoides pubescens*; Piciformes) [51].

Eighty per cent of taxon sampling was derived from frozen or ethanol-preserved muscle tissue with museum-vouchered specimens (electronic supplementary material, table S1). We extracted DNA from toepad clippings of museum study skins from the remaining species for which no tissue was available (see toepad specific modifications in electronic supplementary material, appendix S1). We extracted genomic DNA from frozen or ethanol-preserved muscle tissue with the Qiagen DNeasy extraction kit (Qiagen, Valencia, CA) following the manufacturer's protocol. We used a Qubit 3.0 fluorometer (Thermo Fisher Scientific) to quantify all samples prior to library prep.

(b) Ultraconserved element data capture and analysis

We used established sequence capture protocols to target 5060 UCE loci with toepad specific modifications [47]. We used the python bioinformatics pipeline PHYLUCE v.1.5.0 [52] to clean, assemble and align Illumina-sequenced reads. For four outgroup taxa, we downloaded genome assemblies from the NCBI database [51] (downloaded 26 November 2017), identified and extracted UCE loci with 500 bp flanking regions following established protocol [53]. See electronic supplementary material, appendix S1 for details on wet laboratory and bioinformatic protocols. We assembled three separate UCE datasets that varied in completeness. Our datasets comprised: (1) a 90%-complete matrix (at least 180/200 taxa were present at each UCE); (2) a 75%-complete matrix; and (3) a 75%-complete matrix with well-performing toepads and all tissue samples (referred to as the 75%-193 species dataset; electronic supplementary material, table S1). After concatenating locus-specific alignments, we determined the best-fit partitioning scheme for the concatenated loci with PartitionFinder2 [54] and its rcluster [55] search algorithm, then evaluated partitioning schemes using AIC.

(c) Phylogenetic analysis

We inferred concatenated maximum-likelihood (ML) phylogenies of each UCE subset using RAxML 8.2.4 [56] with the best-fit partitioning scheme, using a general time-reversible model of rate substitution and gamma-distributed rates among sites (GTR + G). We evaluated node support using 1000 bootstrap replicates, summarized using SumTrees v. 4.3.0 [57,58]. For the 90%-complete matrix, we additionally conducted 15 ML searches for the best-fit phylogenetic tree and reconciled the tree with 108 non-parametric bootstrap replicates as determined by RAxML's AutoMRE function.

To take gene-tree heterogeneity into account, we inferred species trees from individual gene trees under the multispecies coalescent model (MSC [59,60]). We used SVDquartets [61], implemented in PAUP* [62], to estimate a species tree without using summary-statistic MSC methods. We analysed all possible quartets for the 90%-complete matrix, and 10^6 quartets for the

75%-complete matrix and 75%–193 matrix, assessed with 100 bootstrap replicates each. Moreover, we estimated a species tree for the 90%-complete matrix and 500 multi-locus bootstrap replicates with ASTRAL III v. 5.6.1 [63,64] implemented from PHYLUCE scripts.

We conducted time-calibrated Bayesian analysis in BEAST 2.4.8 [65] with CPU acceleration in BEAGLE [66]. Due to the large size of the dataset, we conducted independent Markov chain Monte Carlo (MCMC) runs of 10^7 generations for 10 subsets of 50 loci (500 loci total) chosen at random without replacement from the 90%-complete matrix. With unlinked site models, we applied an uncorrelated lognormal clock model and birth–death tree model to linked partitions. With the well-supported topology inferred from concatenated and species tree analyses, we fixed relationships to the genus-level with a series of nested monophyly statements in BEAUti 2.4.8. For fossil calibrations (electronic supplementary material, table S2), we used a stem roller (clade Coracii, i.e. Coraciidae + Brachypteraciidae [67]), a crown roller (Coraciidae [68]) and a stem tody fossil [22] as minimum ages [69]. We used two secondary calibrations from the recent, fossil-calibrated avian time tree [26] by assigning normal distributions on: (1) the node representing the split of the cuckoo roller (Leptosomiformes) from Trogoniformes, Bucerotiformes, Piciformes and Coraciiformes (mean = 61.6 Ma, 95 CI = 57.7–65.5); and (2) the node of the most recent common ancestor of Coraciiformes and Piciformes (mean = 55.9 Ma, 95 CI = 53.0–58.7). Convergence of chains and parameters was assessed in Tracer 1.6 [70], then we discarded ≥ 30% of MCMC generations as burnin. The remainder was summarized in a maximum clade credibility tree with LogCombiner 2.4.8 and TreeAnnotator 2.4.8 [65].

(d) Biogeographical analysis of ancestral ranges

To infer the origins of Coraciiformes, we estimated the probability of their ancestral ranges and historical biogeography using BioGeoBEARS [71] in R v. 1.1.44 [72]. This program infers ancestral geographical ranges on a phylogeny using user-defined geographical areas in a likelihood framework [73]. We tested six probabilistic models for historical biogeography that are implemented in BioGeoBEARS. The DEC [74] model allows for range expansion and regional extinction given the pattern of cladogenetic events represented by the phylogeny. In this model, daughter lineages generally do not inherit identical copies of the ancestral range (i.e. through allopatric or sympatric cladogenesis). We allowed for long-distance dispersal and founder-event speciation with the +*j* [75] model, which allows a daughter species to move into an area outside its ancestor's range. In addition, we tested the DIVA [76,77] and BayArea [78] models both with and without +*j* and we assessed model fitness with AIC. The DEC +*j* model has the tendency to explain all biogeographical variation through the jump parameter [79]. However, we believe the +*j* parameter is germane to Coraciiformes because many lineages are accomplished dispersers. For example, some bee-eaters (e.g. *Merops apiaster* and *M. ornatus*), rollers (*Coracias garrulus* and *Eurystomus orientalis*) and the sacred kingfisher (*Todiramphus sanctus*) are long-distance migrants [29], and numerous species of kingfishers have colonized oceanic islands in Wallacea and the Pacific [39].

We assigned extant coraciiform species to one or more biogeographical regions according to their current distribution [32]. In the New World, we coded three regions: the Nearctic (inclusive of North America and Central America); South America; and the Caribbean Islands. We also ran analyses with Central America—defined from the Isthmus of Tehuantepec to the Isthmus of Panama—split out from North America, because more recent reconstructions [80] suggest Central America was subaerial much longer than previously considered [81]. We split up the Old World into six regions: Palaearctic, Africa and Madagascar, Indomalaya, Wallacea and the Philippines, Australia and Papua New Guinea, and Oceania (electronic supplementary material, table S3, figure 1). Our four outgroup taxa were coded to represent the full range of all extant members of that particular taxonomic order.

We added nine fossils to the time-calibrated tree to improve representation of ancestral biogeographical ranges, as most Palaeogene fossil coraciiforms exist outside of extant ranges [25] (electronic supplementary material, table S4). We added fossils as terminal tips to our time-calibrated tree via midpoint rooting with the R function Fossil.graft [26]. In doing so, we were able to incorporate the Holarctic fossil record in our biogeographical analysis. There are no Palaeogene coraciiform fossils known from outside of the Holarctic, therefore we incorporated nine fossils that represented their oldest respective genus and had comparable geographical representation of Holarctic fossils (electronic supplementary material, tables S3 and S4). To explore how fossil taxa affect biogeographical reconstructions, we also analysed our dataset with: (1) only extant taxa (no fossil histories); (2) outgroup stem fossils incorporated into their respective extant group's range, rather than as a separate branch; and (3) fossil ranges coded as uncertain rather than absent, so as to account for the incomplete fossil record. To accommodate wide-ranging outgroups, we set the maximum range size to seven, though only three ingroup taxa exist in more than three areas.

(e) Macroevolutionary dynamics

In conjunction with our inferences of biogeographical history, we investigated the mode of macroevolutionary diversification of Coraciiformes to determine how speciation rates have changed throughout the Cenozoic. To distinguish and quantify heterogeneity of evolutionary rates, we estimated rates and rate shifts of diversification (speciation, extinction, net diversification) across the tree with Bayesian analysis of macroevolutionary mixtures v. 2.5.0 (BAMM [82,83]). Due to the sensitivity of posterior estimates of diversification rate shifts [84,85], we explored ranges of priors for diversification (expectedNumberOfShifts = 0.1, 1, 3, 5, 8, 10). For each, we ran 100 million generations, sampling every 100 000 generations with four chains. Similar to other rate-based comparative phylogenetic methods [86,87], there is ongoing debate regarding its statistical underpinnings [88]. We followed additional guidelines for running and interpreting BAMM (http://bamm-project.org). These included assessing MCMC convergence and exploring a series of credible rate shifts for all BAMM analyses.

3. Results

We obtained on average 4.8×10^6 reads per individual (tissue-derived libraries: 5×10^6 reads; toepad-derived libraries 4.1×10^6 reads). These reads mapped to 1739–4858 UCE loci (3607 average) for each individual with a mean length of 749 bp (electronic supplementary material, table S5). Coraciiformes comprise two major clades: (1) bee-eaters are sister to the Coracii (rollers + ground-rollers), and (2) todies are sister to motmots + kingfishers. Within kingfishers, we recovered the three monophyletic subfamilies as Alcedininae sister to Cerylinae + Halcyoninae. Coalescent and concatenated methods yielded identical topologies at the family and genus level with high support for most nodes (electronic supplementary material, figures S1–S9). See electronic supplementary material, appendix S1 for the full description of systematics results.

(a) Divergence timing, biogeography and rates of diversification

With all nine fossils included in our analysis, we inferred a Palaearctic origin for Coraciiformes during the late Palaeocene

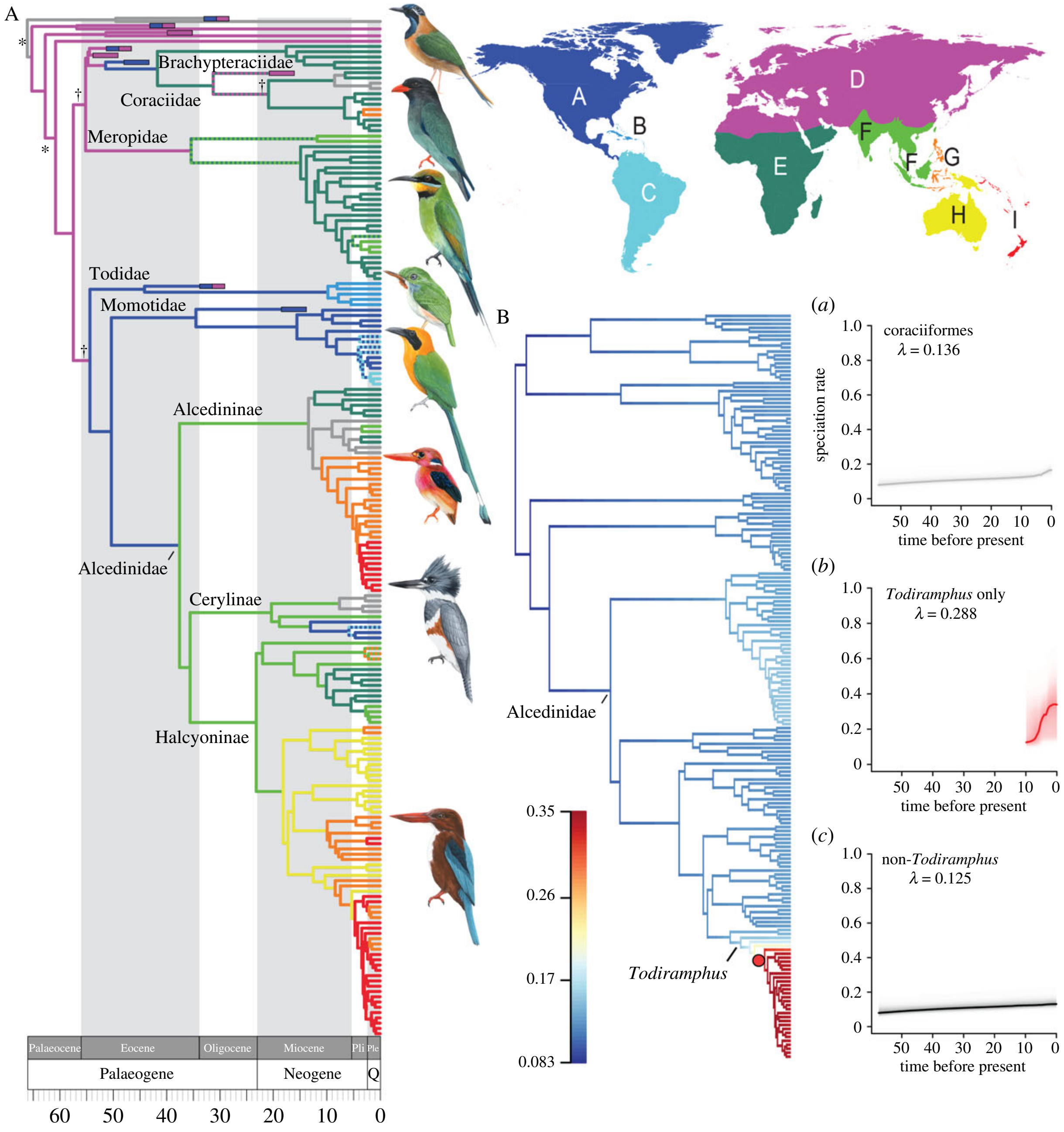

Figure 1. Biogeography and macroevolutionary dynamics of Coraciiformes. (*a*) Time-calibrated, maximum clade credibility tree showing species-level relationships of Coraciiformes based on 500 ultraconserved elements, fossil calibrations and maximum-likelihood topology constraints. Node ages were estimated in BEAST with three fossil calibrations (electronic supplementary material, table S2), indicated by daggers (†), and two secondary calibrations indicated by asterisks (*). Representative taxa are illustrated (from top to bottom): pitta-like ground-roller (*Atelornis pittoides*); Oriental dollarbird (*Eurystomus orientalis*); rainbow bee-eater (*Merops ornatus*); Cuban tody (*Todus multicolor*); rufous motmot (*Baryphthengus martii*); north Philippine dwarf kingfisher (*Ceyx melanurus*); belted kingfisher (*Megaceryle alcyon*); and white-breasted kingfisher (*Halcyon smyrnensis*). Biogeographical information is summarized from the full results (see electronic supplementary material, figure S9). Branch colours represent the most recent ancestral node's range reconstruction and correspond to the following areas on the map: (*a*) Nearctic, (*b*) Caribbean islands, (*c*) South America, (*d*) Palaearctic, (*e*) Africa and Madagascar, (*f*) Indomalaya, (*g*) Wallacea and the Philippines, (*h*) New Guinea and Australia and (*i*) Oceania. Grey branches indicate a broad distribution of three or more areas. (*b*) Results from macroevolutionary rate analysis in BAMM. The phylorate plot depicts an inferred core rate shift in *Todiramphus*. Clade-specific rate through time plots are shown for (*a*) all Coraciiformes, (*b*) all *Todiramphus* and (*c*) the background rate of Coraciiformes excluding *Todiramphus* with mean evolutionary rates (λ), respectively. Original artwork by Madison E. Mayfield. (Online version in colour.)

between 56.2 and 58.8 Ma (mean 57.4; figure 1; electronic supplementary material, figure S9 and table S6 for probabilities of inferred ancestral ranges) with our best fit biogeographical model, DEC + *j* (electronic supplementary material, table S7). Similarly, we inferred the same ancestral range for the divergence between bee-eaters and the Coracii at 55.6 Ma (52.7–57.4 Ma). Ground-rollers diverged from rollers in Africa/Madagascar 41.7 Ma; bee-eaters dispersed into Africa/Indomalaya between 28.4 and 42.6 Ma (mean 35.4 Ma). We inferred the second clade of coraciiforms in North America: todies diverged at 54.3 Ma (54.1–54.7 Ma), and motmots at 50.3 Ma (47.2–52.9 Ma). Kingfishers dispersed into Indomalaya between 32.6 and 42.6 Ma (mean 37.5 Ma) and split into the three distinct subfamilies by the late Eocene. We inferred a widespread, Old World ancestral range for pygmy-kingfishers (Alcedininae; mean 13.4, 11.1–15.9 Ma). The species-poor 'water kingfishers' subfamily Cerylinae (mean 20.3, 16.0–24.9 Ma) and species-rich 'forest kingfishers' subfamily Halcyoninae (mean 23.2, 18.7–27.5 Ma) both arose in Indomalaya.

We inferred a Palaearctic origin for Coraciiformes across all biogeographical reconstructions that included the fossil record (figure 1; electronic supplementary material, figures S9 and figure S10 for comparison between levels of fossil inclusion). In the light of a recent critique of AIC model selection when assessing DEC and DEC + *j* models [79], we explored ancestral range reconstruction using both models. From a natural history perspective, we *a priori* preferred the DEC + *j* model because of the high number of insular taxa in Coraciiformes. Perhaps unsurprisingly, AIC selected the DEC + *j* model for all our analyses (electronic supplementary material, table S7 and figure S10). According to the DEC + *j* model, the analyses for which we did not include fossils inferred an African origin (electronic supplementary material, figure S10). This inference is not unexpected, given the exceptional species diversity of coraciiforms in Africa (especially of early diverging lineages like bee-eaters, rollers and ground-rollers) and the paucity of these species in northern latitudes today. When we accounted for uncertainty in the fossil record by allowing fossil taxa to possibly exist in ranges from which they are not known, the results were similar to our analysis in which we did not incorporate fossils at all; the only major difference being the inferred Nearctic range of the Todidae and Momotidae nodes in the former analysis (electronic supplementary material, figure S10D). For the analyses in which we incorporated outgroup fossil taxa as their own separate branches, the DEC and DEC + *j* model supported similar inferences, albeit with a Nearctic + Palaearctic range for Crown Coraciiformes (electronic supplementary material, figure S10). When outgroup fossils were coded as part of their crown groups' extant range, we inferred a solely Nearctic origin (see below for further discussion on the impact of fossils). We also investigated how treating Central America separately from North America would affect our reconstructions, which had little effect along the backbone of the tree (electronic supplementary material, figure S11), but as expected, Crown Momotidae was inferred to have a Central American origin due to its high species diversity and endemism in the region.

The mean diversification rate (λ) for Coraciiformes is 0.136 (95% CI: 0.117–0.160), which has remained constant throughout the Cenozoic except for a recent, minor increase within the last 5 Myr. This is most likely to be due to the single inferred core rate shift within *Todiramphus* ($f = 0.33$; figure 1; electronic supplementary material, figure S12), which is the most diverse genus of Coraciifomes and is mostly restricted to Wallacea and the Pacific. Five of the six most frequent shift configurations indicated a rate shift along the first few branches of this genus (cumulative probability 67%; electronic supplementary material, figure S12B).

4. Discussion

Using fossil distributions and modern species' ranges, we inferred a Palaearctic origin for a major pantropical radiation with the first fully sampled, fossil-calibrated phylogeny of Coraciiformes. Our results, fully informed by fossil distributions and our time-calibrated tree, indicate that the major coraciiform lineages arose in Laurasia, diverging between 57 and 50 Ma in the Palaearctic and Nearctic, followed by independent dispersals into lower latitudes by the Miocene (figure 1). Our study adds to the growing body of the literature in support of the Boreotropics Hypothesis [12,13]: early coraciiform lineages originated broadly in Laurasia and as climate deteriorated throughout the Cenozoic, but especially in the Miocene, these lineages tracked tropical climate and habitats southward.

Teasing apart the biogeography of Eocene avifaunas is complicated, as indicated by numerous, conflicting results in the literature. Though we indicate a Palaearctic origin of Coraciiformes, other distantly related groups have fossil representatives in the Nearctic. For example, a recent re-evaluation of a fossil, now attributed to an early stem turaco (Musophagidae) in the Eocene of North America [15], supports the North American dispersal route from South America to the Old World. Although pinpointing the exact origin of Coraciiformes is difficult, we suspect that early coraciifom lineages were widespread across the Holarctic. Fossils of stem rollers [89–93], stem todies [24,27,94], and a motmot-like fossil *Protornis* [95] are known from the Eocene in Europe and North America and confirm avifaunal interchange between Nearctic and Palaearctic. These geographically juxtaposed lineages went extinct, but stem relatives of rollers, todies and motmots moved southward into Africa, the Caribbean and Central America, respectively (electronic supplementary material, figure S9). This broad distribution would have been facilitated by Palaeocene connections via Beringia and North Atlantic land bridges [96–98], a familiar pattern known from plants [12,13], terrestrial animals [99] and other birds [100]. Previous hypotheses about the origin of Coraciiformes focused on Indomalaya or Africa [16,25,29,30,91,93,94,101]. These hypothesized areas of origin are obvious candidates due to their high coraciiform species diversity (electronic supplementary material, table S3), specifically of rollers, ground-rollers, bee-eaters and kingfishers. However, previous ancestral area reconstructions that inferred Indomalayan or African origins were biased due to either (1) not accounting for the fossil record, (2) relying on an unstable topology with respect to bee-eaters as the first branch or (3) sparse ingroup sampling that did not fully appreciate idiosyncrasies of extant species distributions [11,100,102].

Yet, our analyses are not without bias; therefore, it is prudent to interpret our results carefully. Though we were careful to consider how and which fossils we incorporated into our analyses as well as densely sampling across this species-rich clade, there are still unaccounted complexities that limit our inferences about the historical biogeography of Coraciiformes. First, we caution against lumping a widespread outgroup clade into a single representative tip in historical biogeographical analyses, as this could influence ancestral range estimates. Second, it is important to consider biases in the fossil record. The fairly robust and well-characterized fossil record of Coraciiformes is unique for Neoaves; however, there are no known Palaeogene fossils of Coraciiformes outside of the Northern Hemisphere. Some Southern Hemisphere fossils are attributed to crown group kingfishers, the oldest of which are from the middle to late Miocene of Australia [103] and Kenya [104]; however, these fossils reflect modern distribution patterns, and we chose not to include them due to their uncertain phylogenetic placement. The absence of Palaeogene coraciiform fossils in the Southern Hemisphere and tropical regions of Laurasian continents either reflects a real pattern or represents a major bias of fossil preservation, discovery and description [31]. Nevertheless, at this time, we must work with what we know and assume the fossil record is reflective of coraciiform palaeo-distributions, until such time that evidence from the fossil record indicates otherwise.

Additionally, our inclusion of fossils was not without bias. We explored how accounting for the incomplete fossil record affected our biogeographical reconstructions by allowing fossil taxa to possibly exist in areas in which they are unknown from the fossil record (electronic supplementary material, figure S10). Because this approach potentially inflates the false-positive rate by interpreting an absence as uncertain in the model, we do not prefer these results. This way of coding geographical areas allows fossil taxa to have much larger (and potentially widely disjunct) ranges than the data suggest. We argue for a less-biased method—to add fossil data as their own branches and thus accounting for their topology as well as known geographical range from the fossil record (electronic supplementary material, figure S9). In addition, we showed that biogeographical analyses can be sensitive to how outgroup fossil taxa are incorporated into a tree. When outgroup fossil stem taxa were added as separate branches in accordance to their stratigraphic age, we supported a Palaearctic origin of Coraciiformes (electronic supplementary material, figure S9). Alternatively, if fossil distributions were instead merged into the ranges of their respective clades, we inferred a Nearctic origin (electronic supplementary material, figure S10). However, stem and crown taxa are fundamentally different. By treating a stem taxon as part of the crown group, one introduces bias by conflating their palaeo- and modern distributions. For example, the outgroup fossils we included in our analysis, *Plesicathartes* (a stem cuckoo roller), *Septentrogon* (a stem trogon) and *Messelirrisor* (a stem hornbill), are all stem group fossils and are not systematically considered within the crown group clades to which they are attributed (electronic supplementary material, table S4). Therefore, it would be disingenuous to *a priori* assume the distribution of a stem taxon be included in the distribution of its corresponding crown clade. These different results regarding how fossils are included in a biogeographical analysis are interesting, and further work is warranted on both incorporating the biases of the fossil record into historical biogeography and coding outgroup distributions from stem versus crown fossil taxa.

This study is the first biogeographical analysis of Coraciiformes based on a topology in which bee-eaters were sister to Coracii (rollers and ground-rollers), which were in turn sister to the rest of Coraciiformes (*sensu* Prum *et al*. [45]). Other studies supported either the Coracii [30] or bee-eaters [26,44,105] as the first branch. Biogeographical analyses using these topologies support an African ancestral range for Coraciiformes [26], likely because these studies reconstructed bee-eaters—a species-rich clade in Africa—as sister to all other Coraciiformes. This optimization resulted in an unparsimonious biogeographical explanation involving an out-of-Africa colonization of the Nearctic by the ancestor of the Coracii, todies, motmots and kingfishers and an unexpected Malagasy ancestral range inferred for the ancestor of the Coracii. Conversely, biogeographical analyses based on our topology (bee-eaters sister to the Coracii) profoundly changed our inference of early coraciiform evolution. Our results offer a more parsimonious biogeographical history: the major clades of Coraciiformes evolved in Laurasia and dispersed into lower latitudes by the mid-Miocene. Another implication of our topology is the need to re-evaluate several extinct taxa attributed to this group; specifically, two important fossils from the mid-Eocene and early Oligocene of Europe: *Quasisyndactylus* [106,107] and the controversial *Protornis* [16,27,95,108]. These fossils were attributed to the now defunct clade ‘Alcediniformes’, which comprised bee-eaters + todies + motmots + kingfishers and was inferred from an osteological dataset [16,25,67,89,95]. Reclassification of these taxa, in light of our phylogenomic results, will aid future analyses into the historical biogeography of Coraciiformes and the evolution of pantropical distributions.

The evolutionary history of Coraciiformes is characterized by two pulses of diversification. The first pulse saw the origins of all major coraciiform lineages in the Eocene, beginning in the Palaearctic and subsequently in North America. We found older divergence dates for Coraciiformes than previously hypothesized. Recent phylogenomic studies dated the split for Coraciiformes at 42 Ma (48–34.5 Ma [51]), 53 Ma (55–52.1 Ma [45]) and 54 Ma (59–46.5 Ma [26]), whereas we inferred an origin at approximately 57 Ma. Indeed, a recently discovered stem roller fossil, *Septencoracias morensis* [67] (54.04 ± 0.14 Ma) that we included in our calibrations and biogeographical analyses, contributed to pushing back divergence dates for the whole order. Though *Septencoracias* is the oldest known stem roller, other allies are described from the early Eocene [25,89,91,109,110]. As a result, our fossil-calibrated phylogeny inferred older divergence dates than the aforementioned higher-level studies of Neornithine birds.

During the Eocene, the Northern Hemisphere was much warmer and wetter than today—substantially so during the Palaeocene–Eocene Thermal Maximum [111,112] (figure 2). Dispersal into other regions was probably a result of tracking tropical habitat southward [13]. This phenomenon is attributed to a steepening latitudinal climate gradient by the end of the Eocene [26,114,115], precipitated by the opening of the Drake Passage [116]. Within Eurasia, the uplift of the Himalayas [117] starting in the early Eocene, and the closure of the Turgai Strait between northern Africa and Asia at the end of the Eocene [118], significantly impacted climate and biomes of a once subtropical Eurasia. The decline of global temperatures [113] caused temperate forests (i.e. coniferous and mixed deciduous species) to replace tropical and subtropical forests in northern latitudes as the warm tropical biome receded southward [99]. By the late Eocene, ground-rollers and rollers had diverged in Africa, *Nyctyornis* bee-eaters had split from the rest of bee-eaters in the palaeotropics (Africa and Indomalaya), and three major lineages of kingfishers had diverged in Indomalaya, thus supporting tracking of tropical habitat southward.

The second pulse of coraciiform diversification started in the Miocene and extended into the Pliocene (electronic supplementary material, figure S10). During this time, the majority of genera originated and diversified, which is coincident with other upticks in avian diversification patterns (e.g. hummingbirds [119] and songbirds [120,121]). There was significant exchange between Africa and Indomalaya, specifically in the late Miocene, as elucidated by dispersal of *Merops* out of Africa into Indomalaya and vice versa by *Halcyon* (electronic supplementary material, figure S9). Motmots dispersed into South America during the Pliocene, probably precipitated by Panamanian land-bridge connections in the Great American Biotic Interchange [122,123]. Our biogeographical analyses of kingfishers are concordant with recent reconstructions by Andersen *et al*. [39]: crown kingfishers and the three subfamilies

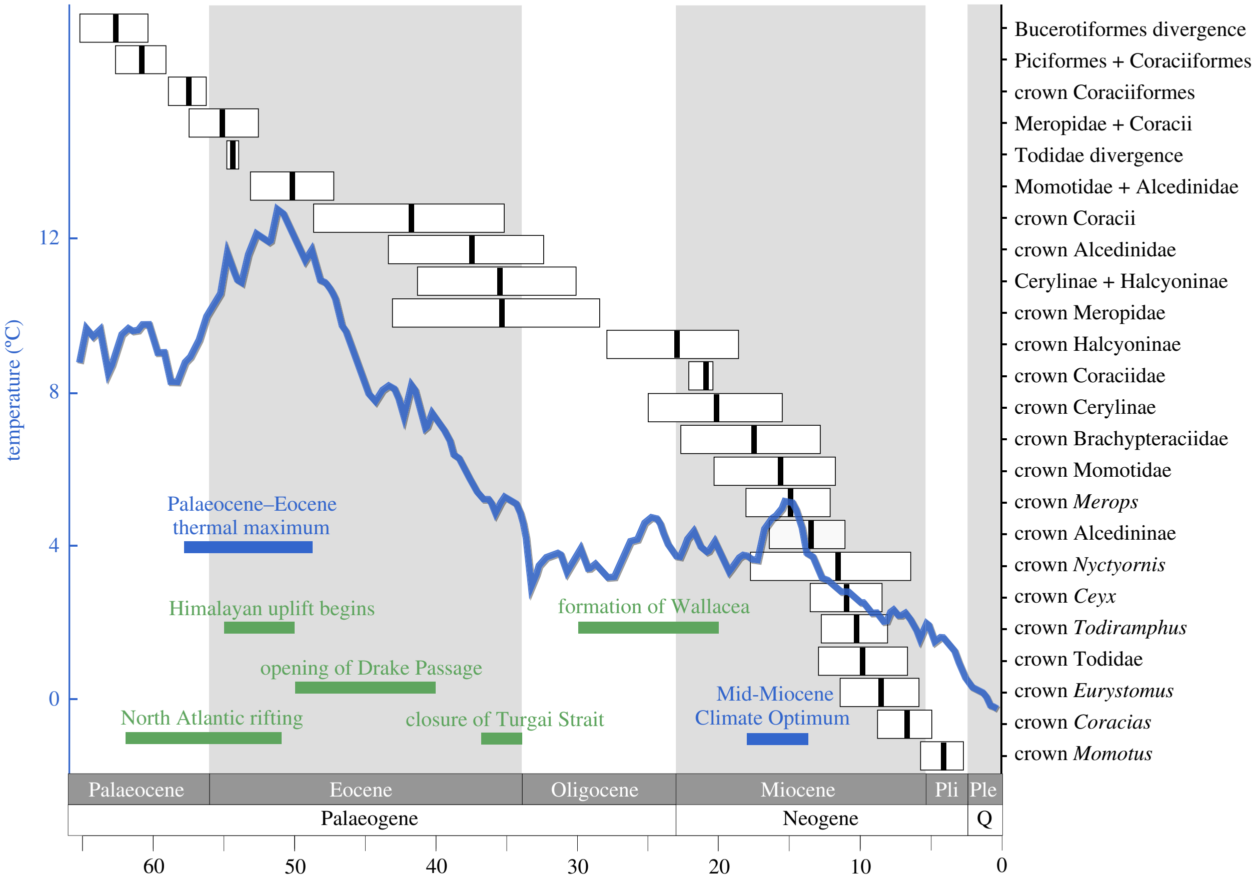

Figure 2. Distribution of coraciiform branching times and palaeogeographical and palaeoclimatological events. White bars indicate the 95% credible intervals of divergence times and mean ages are indicated by a thick black bar for the selected nodes. Estimates of global temperatures throughout the Cenozoic are adapted from Hansen *et al*. [113]. (Online version in colour.)

originated in Indomalaya and diversified largely in the Old World tropics with two independent dispersals by Cerylinae water kingfishers into the New World. During the mid-Miocene, the species-rich kingfisher subfamily Halcyoninae dispersed into Australia and Papua New Guinea with subsequent diversification and colonization of island archipelagos in Wallacea and the Philippines. However, our results did not indicate that elevated diversification rates in kingfishers were related to tectonic uplift of Wallacea, as was shown in songbirds [49]. Instead, we found that upticks in kingfisher diversification rates (specifically related to the oceanic kingfisher genus *Todiramphus*) are coincident with colonization of island archipelagos in Wallacea, the Philippines and the Pacific.

Our older crown age of kingfishers was approximately 10 Ma older than the 27 Ma date reported by Andersen *et al*. [39], which impacted inferences of rate shifts in BAMM. Specifically, our results pulled back the onset of the *Ceyx* radiation approximately 3 Ma than what was previously reported [39]. However, older divergence dates were not as pronounced for the *Todiramphus* radiation, which was dated to be only 1 Ma older than reported by Andersen *et al.* [39]. According to BAMM, there was one core rate shift for *Todiramphus*, and no inferred rate shift for *Ceyx* (figure 1; electronic supplementary material, figure S12). This result is not particularly surprising due to the fact that rate shifts for *Ceyx* were not as consistently supported as those for *Todiramphus*. Similarly, we found a lower diversification rate for *Todiramphus* kingfishers than reported by Andersen *et al*. [39], the inferred core shift and elevated diversification rates for *Todiramphus* are consistent with a recent study that suggested that diversification rates are time-dependent and that younger clades speciate and go extinct faster than older clades [124]. Regardless, our study corroborates that *Todiramphus* has elevated diversification rates compared to background coraciiform rates, irrespective of this study's older divergence dates.

5. Conclusion

In this study, we investigated both new and long-standing hypotheses about the evolution and origins of pantropical radiations. We produced the first completely sampled, fossil-calibrated species tree of Coraciiformes and show an unexpected Palaearctic origin in the Palaeocene. Coraciiforms first attained their current tropical distributions via dispersal events from Laurasia by the end of the Eocene and underwent bouts of increased diversification and dispersal in the Miocene and Pliocene that gave rise to modern diversity patterns. Pantropical distributions can be explained by bouts of increased diversification and dispersal from a single area that falls outside of current ranges. Our study shows that there was significant avifaunal interchange across Laurasia and it contributes to our understanding of how the Palaeogene fossil record helps explain pantropical distributions in modern organisms. To our knowledge, this study represents the first species-level phylogeny of a species-rich avian order (greater than 100 species) using genome-wide data. Beyond the biogeographical implications herein, this phylogenetic framework of species-level relationships will prove useful to future comparative trait evolution studies of this species-rich, ecologically and morphologically diverse bird radiation.

Data accessibility. Raw sequencing reads are available from the NCBI SRA (BioProject PRJNA499128), UCE sequences and mitogenomes are accessioned in NCBI Genbank.

Authors' contributions. J.M.M. and M.J.A. conceived the study. J.M.M. did the laboratory work, data analysis and drafted the manuscript. M.J.A. and B.T.S. funded the laboratory work. All authors contributed to writing and revision of the manuscript.

Competing interests. We declare we have no competing interests.

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