Ultraconserved elements support the elevation of a new avian family, Eurocephalidae, the white-crowned shrikes

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ABSTRACT

In this study, we infer genus-level relationships within shrikes (Laniidae), crows (Corvidae), and their allies using ultraconserved elements (UCEs). We confirm previous results of the Crested Shrikejay (*Platylophus galericulatus*) as comprising its own taxonomic family and find strong support for its sister relationship to laniid shrikes. We also find strong support that the African-endemic genus *Eurocephalus*, which comprises two allopatric species (*E. ruppelli* and *E. anguitimens*), are not “true-shrikes”. We propose elevating the white-crowned shrikes to their own family, Eurocephalidae.

Keywords: African birds, classification, molecular systematics, taxonomy, ultraconserved elements, white-crowned shrikes

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LAY SUMMARY

- Understanding how species are related (systematics) and classified (taxonomy) is important to the study of the world‘s biodiversity.
- Recent work has raised doubt about the phylogenetic placement of the Crested Shrikejay (*Platylophus galericulatus*) and *Eurocephalus*, the white-crowned shrike genus, traditionally considered within the crow and jay family, Corvidae, and the shrike family, Laniidae, respectively.
- We collected a genome-wide dataset for all genera of shrikes, crows, and jays to determine their evolutionary histories with phylogenetic methods.
- We confirm that the Crested Shrikejay constitutes a family-level lineage most closely related to Laniidae, not Corvidae. We show for the first time that *Eurocephalus* also represents a family-level lineage separate from shrikes and more closely related to crows and jays.
- We propose a new avian family, Eurocephalidae, the white-crowned shrikes, for these two African-endemic birds.

Des éléments ultraconservés soutiennent la création d’une nouvelle famille d’oiseaux, les *Eurocephalidae*

RÉSUMÉ

Dans cette étude, nous inférons les relations à l'échelle du genre chez les *Laniidae*, les *Corvidae* et leurs alliés à l'aide d'éléments ultraconservés (EUC). Nous confirmons les résultats antérieurs concernant *Platylophus galericulatus* comme constituant sa propre famille taxonomique et nous trouvons un fort soutien de sa relation de sœur des *Laniidae*. Nous trouvons également un soutien solide que le genre endémique africain *Eurocephalus*, qui comprend deux espèces allopatriques (*E. ruppelli* et *E. anguitimens*), n'est pas composé de « vraies pies-grièches ». Nous proposons d'élever ces espèces au rang de leur propre famille, les *Eurocephalidae*.

Mots-clés : Oiseaux africains, classification, systématique moléculaire, taxonomie, éléments ultraconservés, *Eurocephalidae*

INTRODUCTION

Molecular phylogenetics has revolutionized our understanding of the evolutionary relationships of birds. Its application to avian systematics has resulted in large-scale taxonomic reorganization due to deep genetic divergences and rampant paraphyly within morphologically defined clades (Cracraft et al. 2004, Reddy et al. 2017, Braun et al. 2019). This taxonomic reordering is most obvious when considering the number of families ornithologists recognize. In 1980, the first Howard and Moore checklist recognized 175 avian families, whereas in 2014, the fourth edition recognized 234 families, a 34% increase (Howard and Moore 1980, Howard et al. 2013, Dickinson and Christidis 2014). Today, upwards of 253 families are recognized by some authorities (IOC v. 12.1; Gill et al. 2022).

One superfamily of oscine passerines, Corvoidea, has received considerable attention with regards to higher-level taxonomic restructuring. Corvoidea comprises many family-level groups and includes fantails, drongos, birds-of-paradise, monarchs, shrikes, and crows and jays. Examples of this restructuring include the bushshrikes (now Malaconotidae) and helmetshrikes (now Vangidae), which were once thought to be closely related to ~~tr~~ue-shrikes” (Laniidae; (Howard and Moore 1980). Today, these groups are no longer treated within Corvoidea and are instead considered members of the superfamily Malaconotoidea (Aggerbeck et al. 2014, McCullough et al. 2022). Other taxonomic rearrangements have moved genera between families, for example *Chaetorhynchus* from Dicruridae to Rhipiduridae (Irestedt et al. 2008) and *Grallina* from what is now known as Corcoracidae to Monarchidae (Filardi and Moyle 2005). Finally, *Ifrita* and *Melampitta* have been aligned with various families outside of Corvoidea, including Orthonychidae and Timaliidae (Schodde and Christidis 2014, Fjeldsa et al. 2020). These genera are now treated as their own families within Corvoidea (Aggerbeck et al. 2014, Schodde and Christidis 2014, Winkler et al. 2015, Oliveros et al. 2019). This taxonomic restructuring is a result of past groups being defined on morphological and behavioral similarities that were not supported by molecular phylogenetics.

Shrikes have long been considered close relatives of crows and jays and many modern systematic treatments consider these families to be sister groups. Shrikes comprise 34 species of passerine birds that are distributed across Africa, Eurasia, and North America. Shrike genera include *Urolestes*, *Corvinella*, *Eurocephalus*, and the species-rich *Lanius*, but recent work on this group found *Urolestes* and *Corvinella* are best treated as *Lanius* (Fuchs et al. 2019). Corvidae is a cosmopolitan family and comprises 135 species in 24 genera (IOC v. 12.1; Gill et al. 2022). Though some species have been the foci of genomic studies (Kearns et al. 2018, Slager et al. 2020, Weissensteiner et al. 2020), the genus-level relationships of Corvidae remain unresolved due to limited genetic character sampling (Cibois and Pasquet 1999, Ericson et al. 2005, Jønsson 2016, Fernando et al. 2017, Garcia-Porta et al. 2022, McCullough et al. 2022).

Recently, the phylogenetic placement of 2 genera within both of these families—*Platylophus* and *Eurocephalus*—have rendered the traditional sister relationship of Laniidae and Corvidae as paraphyletic (Figure 1). The Crested Shrikejay (*Platylophus galericulatus*) is a lowland forest species found in Indomalaya and has been historically considered within Corvidae (Sibley and Monroe 1990, Clements 2007, Dickinson and Christidis 2014, Gill et al. 2021). Oliveros et al. (2019) used thousands of ultraconserved elements (UCEs, Faircloth et al. 2012) to infer higher-level relationships of all passerine families and found a sister relationship of *Platylophus* and *Lanius*, to the exclusion of *Corvus*. This result rendered Corvidae paraphyletic with respect to *Platylophus* but relied on limited taxon sampling (1–2 representative taxa per family). When more species in both Laniidae and Corvidae have been included in molecular analyses, albeit with limited character sampling, *Platylophus* is either inferred to be sister to the African-endemic genus *Eurocephalus* (Jønsson et al. 2016, Garcia-Porta et al. 2022) or Corvidae (Fuchs et al. 2019). Although its exact relationships are uncertain, *Platylophus* is now treated in its own family—Platylophidae—and is widely considered to be closely related to shrikes (Winkler et al. 2015, Gaudin et al. 2021, Gill et al. 2022). Most recently, McCullough et al. (2022) combined a family-level UCE matrix and species-level 12-gene supermatrix for the infraorder Corvides and found that *Platylophus* is sister to Laniidae, but to the exclusion of *Eurocephalus.* Yet, the single *Eurocephalus* tip included in this matrix was represented by only 3 genes, pointing to the need for further genetic character sampling to help solve the puzzle of family-level diversity within the superfamily Corvoidea.

Eurocephalus comprises 2 species of African passerines that have long been considered part of Laniidae, but whose traits have set them apart from the other ―true-shrikes.” The Northern (*E. ruppelli*) and Southern (*E. anguitimens*) White-crowned Shrikes are allopatric inhabitants of arid thorn savanna in Eastern and Southern Africa (Harris and Franklin 2000). Though once considered the same species, they were split based on plumage differences and because they occupy non-overlapping, allopatric ranges (Clancey 1965, Hall and Moreau 1970). Both species have vocalizations that separate them from all other species within Laniidae, described as harsh bleating and lacking a whistled or warbling song that is emblematic of ―true-shrikes” (Harris and Franklin 2000). Behaviorally, white-crowned shrikes are distinct from all other laniids by spending more time on the ground, not impaling prey items, and living permanently in small groups (Yosef 2008). Both species are also cooperative breeders, a behavior that is rare within ―true-shrikes” to the extent that it led earlier taxonomic authorities (Mayr 1943) to consider *Eurocephalus* as more closely related to *Prionops* helmet-shrikes (now within Vangidae, which is in a different superfamily, Malaconotoidea; Aggerbeck et al. 2014, Jønsson et al. 2016, McCullough et al. 2022). However, DNA-DNA hybridization studies placed *Eurocephalus* within Laniidae (Sibley and Ahlquist 1990), where it has remained regardless of taxonomic implications highlighted by past work (Sorenson and Payne 2001, Fuchs et al. 2019, McCullough et al. 2022).

To resolve family-level and inter-generic relationships within these cosmopolitan clades, we collected the first genus-level UCE dataset of shrikes and crows and jays. We include all genera and use an updated target-capture probe set that was refined to better capture UCEs from degraded, toepad-sourced samples. We confirm previous studies and show *Platylophus* as sister to ―true-shrikes” and thus deserving recognition as a family-level lineage, Platylophidae. Moreover, we find strong support for the elevation of *Eurocephalus* to its own family-level group.

METHODS

Sampling and Laboratory Methods

Following the taxonomy of Gill et al. (2022), we collected genus-level UCE data for Corvidae, Laniidae, and their allies (Supplementary Material Table 1). In total, our dataset comprised 47 samples and every genus within Laniidae and Corvidae. We downloaded raw reads from recent, higher-level UCE studies of passerines ($n = 23$; Moyle et al. 2016, Oliveros et al. 2019, McCullough et al. 2022). For all other samples ($n = 24$), we extracted DNA from ethanol- or frozen-preserved tissue samples loaned from natural history collections. However, for some rarely collected taxa, we relied on specimen toepad clippings (14% of samples, denoted in Supplementary Material Table 1). Because this source of genetic material is well known to be degraded, we treated samples derived from frozen or ethanol preserved samples differently than those derived from museum toepad clippings. For tissue-derived samples, we used the Qiagen DNeasy kit to extract genomic DNA and estimated fragment size using gel electrophoresis. For toepad-derived samples, we used a phenol-chloroform DNA extraction with gel phase-lock tubes. This method has been shown to produce higher yields of DNA than silica columns of Qiagen kits (Tsai et al. 2019). Prior to library prep, we quantified DNA concentrations with a Qubit 3.0 Fluorometer (ThermoFisher Scientific) for all samples.

We followed established protocols for library preparation and target capture of UCEs (Faircloth et al. 2012, McCormack et al. 2016). We made toepad-specific modifications to improve yields, following McCormack et al. (2016); these included increasing concentrations of AMPure bead (Beckman Coulter) cleanups to 3X, extending ligation times, and using Eppendorf Lo-Bind tubes to increase retention of DNA. We pooled tissue (8 libraries per pool) and toepad-derived (5–6 per pool) libraries separately for UCE enrichment. We used an updated version of the Arbor Biosciences MYbaits kit for Tetrapods UCE-5Kv2b probe set, which includes a larger number of baits per locus designed from both chicken and Zebra Finch (*Taeniopygia guttata*) genomes. We hybridized probes at either 65ºC (tissues) or 62ºC (toepads) for 24 hr. We sequenced samples either on an Illumina HiSeq 2500 System at the University of Kansas Genome Sequencing Core or an Illumina NovaSeq 6000 at the Oklahoma Medical Research Foundation (sequencing technology is denoted in Supplementary Material Table 1).

Data Processing and Phylogenetic Analyses

To process UCE data, we used the Phyluce v1.7.0 (Faircloth 2016; described in full at https://github.com/faircloth-lab/phyluce) Python package with the University of New Mexico‘s Center for Advanced Computing (CARC) cluster. We trimmed adaptor sequences and low-quality sites from demultiplexed raw reads with Illumiprocessor v2.1 (Faircloth 2013, Bolger et al. 2014), assembled clean reads into contigs with Spades v1.7 (Prjibelski et al. 2020), and extracted UCE loci with this updated probe set.

During initial phylogenetic exploration, we identified 5 toepad-derived (2 *Temnurus* and 3 *Zavattariornis*) samples that had extraordinary long branches in concatenated RAxML analyses (see below for more depth on these phylogenetic methods and Supplementary Material Table 1 for these problematic samples). These long branches are biologically unlikely and this problem has been shown to be an artifact of poor trimming and ―dirty ends" of UCE loci from degraded toepad-sourced samples (Smith et al. 2020). To remove these problematic artifacts that contribute to artificially long branches, we followed the bioinformatic pipeline by Smith et al. (2020). In detail, we identified our reference samples by expanding *fastas* (with *phyluce_assembly_explode_get_fastas_file*) and chose a closely related, tissue-derived sample. We chose *Platysmurus atterimus* (LSU B58660) as a reference for *Temnurus* samples and *Podoces hendersoni* (KU 20444) for *Zavattarriornis* samples based on an initial concatenated RAxML analyses (Kozlov et al. 2019). With bwa, SAMtools, and GNU parallel (Li and Durbin 2009, Li et al. 2009, Tange 2021), we indexed the reference samples (UCE contigs) and aligned cleaned reads of the problematic toepad-derived samples to these references. To remove the low-quality data in the flanking regions that were contributing to spurious inferences, we dropped sites with <5x coverage and quality scores <20. We incorporated these cleaned samples back into the pipeline with the other samples by manually adding (1) the nucleotide data into the combined, unaligned *fasta* file; (2) names of samples into the .conf file; and (3) adding the list of loci for each sample into the incomplete matrix conf file; all these files are originally produced from the *phyluce_assembly_get_fastas_from_match_counts phyluce* script. Together with these cleaned toepad-based samples, we aligned all 47 samples with MAFFT (Katoh and Standley 2013) without initially trimming. Instead, we used TrimAl v1.4.rev15 (Capella-Gutiérrez et al. 2009) to trim UCE loci with the ―automated1" flag. Finally, we produced a 100% complete matrix, in which all samples are present at each UCE locus.

We implemented both concatenated maximum likelihood (ML) and species tree methods. We estimated the ML tree with RAxML-ng v 1.0.1 (Kozlov et al. 2019) and evaluated support with bootstrap replicates with the autoMRE function (set to 100 BS). We accounted for gene tree heterogeneity with SVDquartets (Chifman and Kubatko 2014) implemented in Paup*v4.0a166 (Swofford 2003). SVDquartets is a concatenated quartet method that does not rely on individual gene trees and has recently been shown to perform better for large multilocus datasets than other coalescent based tree-building programs (Wascher and Kubatko 2021). We analyzed all possible quartets ($n = 169{,}661$ quartets) and performed 100 bootstrap replicates to assess nodal support.

Time Calibration

To infer a time calibrated tree, we used BEAST v2.6.7 (Bouckaert et al. 2014). We created 6 randomized subsets of 50 UCE loci each without replacement (a total of 300 loci) from our complete matrix (Supplementary Material Table 2). We ran 2 independent MCMC chains per dataset for 10 million generations, sampling every 5,000 generations. We used a relaxed log normal clock, a birth-death tree prior, and assigned the HKY+G sequence model to each UCE locus. We constrained the BEAST topology to the RAxML-inferred topology using a multi-monophyletic constraint prior. We used 2 secondary calibrations from Oliveros et al. (2019) to date the phylogeny. This comprehensive phylogeny used 13 fossil calibrations to date a family-level UCE tree of all songbirds. For this study, we assigned a normal distribution for the split between *Rhipidura* and the rest of our sampled taxa with a mean date of 18.93 Ma (confidence interval = 22.0–15.9, standard deviation (sigma value) of 1.5). The second calibration point was assigned to the split between *Dicrurus* and all other taxa with a normal distribution and a mean date of 18.46 Ma (CI = 21.4–15.6, sigma value of 1.5). We visualized posterior estimates in Tracer v 1.7.1 (Rambaut et al. 2018) to assess convergence of chains and that ESS values were >200. We discarded the first 25% of trees as burn-in and first combined the 2 runs from each dataset, then we combined those 6 tree files into one final maximum clade credibility (MCC) tree using *TreeAnnotator* v 2.6.7 (Bouckaert et al. 2014).

ND2 P-distances

To assess relative divergences between major clades within our dataset, we compared uncorrected *p*-distances in the mitochondrial ND2 gene for representative taxa. We used *Mitofinder* v 1.4 (Allio et al. 2020) to extract mitochondrial genomes from cleaned UCE reads using a complete mitochondrial genome of *Corvus corax* as a reference (PRJNA321255; Johnsen et al. 2017). Next, we extracted ND2 from these mitochondrial genomes and used PAUP* v 4a168 (Swofford 2003) to generate *P*-distances.

RESULTS

Genomic Data Matrix

The 100% complete matrix comprised 2,500 UCE loci and totaled 2,565,469 base pairs (bp), of which 184,345 sites were parsimony informative. UCE loci averaged 1,026 ± 15 bp in length with a range of 218–3,464 bp. Newly generated raw read data is available on NCBI SRA (Bioproject PRJNA964785; see Acknowledgments).

Genomic Support for Four Families within Traditional Crows and Shrikes

Our ML and SVQuartets analyses strongly supported the relationship of *Platylophus* as sister to a clade comprising *Lanius*, *Urolestes*, and *Corvinella* (Figure 2, Supplementary Material Figure 1), but not *Eurocephalus*. Instead, we inferred *Eurocephalus* as deeply divergent and sister to Corvidae. In our MCC tree, we inferred the split between *Eurocephalus* and Corvidae at 13.9 Ma (11.5–16.2 Ma 95% HPD; Figure 3). This divergence date is similar to when Platylophidae and Laniidae are estimated to have diverged at 14.1 Ma (11.8–16.5 Ma). We inferred the crown age of Corvidae at 11.2 Ma (8.9–13.3 Ma). Uncorrected *P*-distances of ND2 between Eurocephalus and all other family-level groups, including representative clades within Corvidae, ranged from 17.1 to 20.6% (Supplementary Material Table 3).

Genus-level Relationships within Corvidae

We inferred *Pyrrhocorax* choughs as sister to all other corvids. We defined 7 major clades (labeled A–F in Figure 2) to facilitate discussion. The first of these clades comprised the treepies, *Dendrocitta* and *Crypsirina*, and a sister relationship between 2 monotypic taxa, Ratchet-tailed Treepie (*Temnurus temnurus*) and Black Magpie (*Platysmurus atterimus*). Clade B comprised 2 colorful, Southeast Asian-endemic magpie genera, *Urocissa* and *Cissa.* Clade C comprised 2 genera that are widely distributed across northern temperate forests: *Cyanopica* magpies and *Perisoreus* jays. The New World jays comprised Clade D, in which the Neotropical-endemic genus *Cyanolyca* was sister to 2 smaller clades comprising (1) *Cyanocorax, Calocitta,* and *Psilorhinus*; and (2) *Aphelocoma*, *Gymnorhinus*, and *Cyanocitta*. Clade E included a sequentially branching relationship pattern of Eurasian taxa *Garrulus* and a clade of largely ground-dwelling corvids: *Ptilostomus*, *Podoces,* and *Zavattariornis.* The last clade (F) comprised another ladderized relationship of *Pica*, *Nucifraga*, and *Coloeus* as sister to the species-rich genus *Corvus*.

Maximum-likelihood and coalescent-based methods yielded highly concordant topologies for all but 2 taxa. First, *Garrulus,* a genus comprising several species of Eurasian jays, was inferred as sister to clade E with ML (Figure 2) or as sister to Clade F with SVDquartets (Supplementary Material Figure 1). Second, the monotypic *Psilorhinus morio* was either inferred as sister to *Calocitta* (ML, Figure 2) or rooted to a three-way polytomy with *Calocitta* and *Cyanocorax* (SVDquartets, Supplementary Material Figure 1).

DISCUSSION

We leveraged a genus-level dataset of UCEs to examine higher-level relationships of shrikes, crows, jays, and allies. We confirmed earlier findings that *Platylophus* is deeply diverged and more closely related to ―true-shrikes” than others in Corvidae, and should indeed be considered its own family, Platylophidae. Moreover, we also found support for *Eurocephalus* as a deeply divergent lineage that is sister to Corvidae, one of similar phylogenetic distance as the relationship between Platylophidae and Laniidae. The 2 species of *Eurocephalus* white-crowned shrikes have many ecological traits that set them apart from these other 3 avian families, which we discuss below. Because of their deep divergence from Corvidae, Platylophidae, and Laniidae, combined with these unique ecological traits, there is a case to be made to raise *Eurocephalus* to a family-level group rather than lumping them within Corvidae. We elaborate on these lines of evidence below and recommend treating *Eurocephalus* in their own taxonomic family.

However, there is no family-level group name available for *Eurocephalus*. The first *Eurocephalus* species described, *E. anguitimens,* was originally included as a new genus within Corvidae (Smith 1836). But it was quickly considered part of Laniidae (Bonaparte 1853) and then Prionopidae based on external morphology (Sharpe 1877, Mayr 1943). Other morphological characters, including tarsal scutellation, hindlimb musculature, and cranial features (Rand 1959, Raikow et al. 1980, Harris and Franklin 2000), behavior (Harris and Arnott 1988, Lefranc 1997), and DNA–DNA hybridization data (Sibley and Ahlquist 1990) consolidated *Eurocephalus* within Prionopinae, a subfamily of Laniidae at the time. When molecular data confirmed that *Prionops* was instead closely allied to vangas (Vangidae; Fuchs et al. 2004, 2012; Moyle et al. 2006, Reddy et al. 2012), *Eurocephalus* remained within Laniidae.

Though the white-crowned shrikes have only ever been considered a peculiar genus in these larger families, their distinctiveness has always been widely appreciated. When first described as a member of Corvidae, Smith (1836) noted ―[*Eurocephalus anguitimens*] true place may be found in another family, and the resemblances, particularly as regards its habits, may be those of analogy and not affinity.” Modern authorities have also questioned its affinities to shrikes: ―Of the genera considered to form Laniidae, *Eurocephalus* is the least shrike-like” (Harris and Franklin 2000, with similar sentiment noted in Yosef 2008). The genetic distinctiveness of the genus was first hinted at with DNA sequence data by Sorsenson and Payne (2001). Recently, Fuchs et al. (2019) and McCullough et al. (2022) both noted that Laniidae was not monophyletic with respect to *Platylophus* and *Eurocephalus,* with Fuchs et al. first noting that the white-crowned shrikes may comprise their own family (though they did not suggest a family-group name). Though *Platylophus* was elevated to a family-level clade, Platylophidae, *Eurocephalus* was not (Clements et al. 2021, Gill et al. 2022).

One could make an argument for lumping the white-crowned shrikes into Corvidae again, nearly two centuries after their original description. General rules of monophyly would consider the sister relationship of *Eurocephalus* and Corvidae as a reason to simply treat the genus as the first branch of Corvidae. Yet, *Eurocephalus* is as genetically diverged as any family-level group within Corvoidea (Figures 2–3; Fuchs et al. 2019, McCullough et al. 2022). This deep divergence is also reflected in the similar dates for the splits between *Eurocephalus* and Corvidae (13.9 Ma) and Laniidae and Platylophidae (14.1 Ma; Figure 3). We inferred the clade including Platylophidae, Laniidae, *Eurocephalus*, and Corvidae to have shared a common ancestor 14.6 Ma, which is 4 million years younger than the crown age of Corvoidea (Oliveros et al. 2019). Moreover, uncorrected pairwise ND2 distances between

Platylophidae, Laniidae, Corvidae, and *Eurocephalus* range from 17.5 to 20.6%, with similar percentages across all family-level groups within Corvoidea (Supplementary Material Table 3). The long branch separating *Eurocephalus* from Corvidae, as well as limited taxon and character sampling in prior studies, is the likely cause of past topological uncertainty. Indeed, both Fuchs et al. (2019) and McCullough et al. (2022) each had <3 gene regions for a single *Eurocephalus* sample to represent this deeply divergent group. In short, the level of molecular divergence for *Eurocephalus* is indicative of family-level status separate from Corvidae.

In addition to their deep genetic divergence, *Eurocephalus* white-crowned shrikes also possess ecomorphological characteristics that separate them from Corvidae, Laniidae, and Platylophidae (Table 1). Morphologically, *Eurocephalus* species have scuttelation that extends both down the front and sides of their tarsi (Supplementary Material Figure S3). Patterns of scutes along tarsi were historically used in the classification of avian families—described as having the ―utmost consequence in classification, especially among the higher birds, since they are quite significant of genera, families, and even some larger groups" (Coues 1903). Comparatively, this trait is distinctive to *Eurocephalus* when compared to the other three family level-groups, all of which have scuttles only on the front of their tarsi (Table 1, Supplementary Material Figure S3; Harris and Franklin 2000, Yosef 2008, dos Anjos 2009).

Eurocephalus white-crowned shrikes also exhibit different dietary niches than corvids. The majority of corvids are generalists and opportunistic feeders with a variable diet that ranges from foraging for vegetative matter to scavenging carrion. Only a few corvid species possess a specialist foraging niche, such as Pinyon Jay (*Gymnorhinus cyanocephalus*) and Clark‘s Nutcracker (*Nucifraga columbiana*; dos Anjos 2009). Conversely, *Eurocephalus* white-crowned shrikes fill a niche unlike any other corvid: They are largely sit-and-wait predators whose hunting behaviors closely resemble laniid ―true-shrikes" (Keith et al. 1992, Yosef 2008). Both *Eurocephalus* species hunt from elevated perches and can hover in place while hunting, sally for insects, or hawk for aerial arthropods. Unlike most corvids, *Eurocephalus* white-crowned shrikes do not have a wide dietary niche, instead focusing predominately on arthropods and sometimes berries (Keith et al. 1992). Notably, white-crowned shrikes do not impale or cache food items for later consumption, a departure from both members of Laniidae and Corvidae.

Cooperative breeding is a trait that historically was used to separate *Eurocephalus* from Laniidae (Mayr 1943). Though there are ―true-shrikes" species that are considered cooperative breeders, this trait is rare across Laniidae (Harris and Franklin 2000). Cooperative breeding behavior is present in several corvid lineages. The spectrum of this behavior widely varies across the family and includes colonial breeders like the San Blas Jay (*Cyanocorax sanblasianus*) or Rook (*Corvus frugilegus*; dos Anjos 2009). However, the first several branches of Corvidae (e.g., *Pyrrhocorax*, and clades A–B; Figure 2) do not exhibit true cooperative breeding, suggesting that this behavior evolved independently in *Eurocephalus* and Corvidae. Cooperative breeding in the clade Corvides should be reevaluated considering this sister relationship of *Eurocephalus* and Corvidae (Marki et al. 2015). The nest structure is also different between these 2 groups: *Eurocephalus* build well-molded, delicate cup nests that are well-camouflaged, made of cobwebs and grass, and are built perpendicular to a small branch (Keith et al. 1992, Yosef 2008). Corvids build large, bulky stick nests within trees or cliffsides (dos Anjos 2009). In addition to their morphology, ecology, and breeding behavior, *Eurocephalus* white-crowned shrikes have a characteristic flight pattern of ―butterfly-like flight interspersed with long glides on V-shaped wings" (Keith et al. 1992).

Considering the wealth of traits that delineate *Eurocephalus* from Corvidae and deep genetic divergences indicative of family-level distinctiveness, the case to elevate *Eurocephalus* to the family-level is straightforward. As no family-group name for *Eurocephalus* is available, we propose a new family following ICZN (1999) Article 16.1:

Eurocephalidae new family

Type genus: *Eurocephalus* Smith, 1836

Diagnosis: Differs from Corvidae, Laniidae, and Platylophidae by a combination of (1) snow-white plush crown formed with short, stiff feathers and a black facial mask; (2) scutellation extending both distally down the side and ventrally on the tarsus (Supplementary Material Figure S3; Rand 1959, Yosef 2008); (3) sit-and-wait hunting style without impaling or cacheing prey behaviors, with fairly limited diets of mostly arthropods (specifically insects); (4) characteristic shallow wingbeat and gliding flight pattern (Keith et al. 1992, Yosef 2008); (5) cooperative breeding systems in which birds build neat, compact, and camouflaged nests made of grass and cobwebs (Harris and Franklin 2000, Yosef 2008); (6) high degree of sociality, specifically the formation of gregarious small family groups that defend territories and forage together (Yosef 2008); and (7) feathers partially covering the nares and first third of the culmen (Supplementary Material Figure S2).

Genus-level Relationships of Corvidae

Though genus-level relationships of Corvidae largely correspond to those inferred using species-level datasets with limited character sampling, we found highly supported relationships of several difficult-to-place genera for the first time. The relationships of *Pica* magpies and *Garrulus* Eurasian jays within Corvidae have been inferred as 4 different largely equivocal relationships: (1) *Pica* and *Garrulus* are sister and are either within the ―ground jay" clade (*Podoces* and allies; Jønsson et al. 2016); or (2) are the first branch to both ground jay and ―crow" clades (McCullough et al. 2022); (3) *Garrulus* is more closely related to the crow clade (*Nucifraga, Corvus, Coloeus*) and *Pica* within the ground jay clade (Garcia-Porta et al. 2022); (4) there is no ground jay clade, because *Pica* is sister to *Podoces* and *Garrulus* forms a sister relationship with *Ptilostomus* and is the first branch to the crow clade (Fernando et al. 2017). We found a stable relationship for *Pica* across both analyses as the first branch to the crow clade. *Garrulus* was either the first branch of the ground jay clade with ML (Figure 2) or the first branch of the crow clade inferred with SVQquartets (Supplementary Material Figure 1). Since Corvidae harbors extensive behavioral complexity, particularly within *Corvus*, a robust species-level phylogeny of the family will be key for future macroevolutionary analyses. The relationships that we infer here could aid future molecular systematic studies, particularly those that combine both species-level Sanger sequence data and higher-level UCE data (such as in McCullough et al. 2022).

Conclusion

Taxonomic authorities have long questioned to which family the *Eurocephalus* white-crowned shrikes belong. Over the last two centuries, their distinctive morphologies and behaviors have defined them as a peculiar genus within Corvidae, Prionopidae, or Laniidae. We show for the first time, using thousands of genome-wide markers, that *Eurocephalus* is neither sister to *Platylophus* or other members of Laniidae, and instead is deeply divergent from and sister to Corvidae. Our results indicate that white-crowned shrikes should be elevated to their own family-level clade, which we formally propose here as Eurocephalidae.

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Ethics statement

The authors have no competing interests.

Author contributions

J.M.M. and M.J.A. designed the study. J.M.M., C.H.O, and M.J.A. collected the data. J.M.M. analyzed the data and wrote the paper. R.G.M. and M.J.A. contributed substantial materials and funding. All authors reviewed and contributed to the study.

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Data availability

All raw read data associated with this project is available on the GenBank SRA database (BioProject PRJNA964785; see Supplementary Material Table S1). Supplementary data, including alignments, tree files, and updated UCE probe set are available at McCullough et al. (2023).

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Table 1. Trait comparisons between Eurocephalidae, Corvidae, Laniidae, and Platylophidae.

Trait	**Corvidae**	**Eurocephalidae***	**Laniidae**	**Platylophidae**
Feathers covering nares	Yes	Partially	No	No
Tarsal scuttelation	Frontal	Scuttles along front and sides	Frontal	Frontal
Foraging style	Largely generalist and opportunistic feeders; rare specialists	Sit-and-wait predators. Will sally and hawk for flying insects	Sit-and-wait predators. Will hover and hawk insects aerially	Forages in leaf litter on forest floor
No	Ranges from leaf matter to carrion	Insects, but have been observed to rarely eat berries	Arthropods, reptiles, small mammals, fruit, birds, fish	Insects and arthropods only
Storage of food	Will cache food	No	Impales prey	No
Sociality	Can be highly social and forage in groups	Gregarious, social birds often in groups	Most species are solitary	Often solitary or in pairs
Breeding system	Most species are monogamous. Many cooperative. Few colonial	Cooperative breeders	Most species are monogamous, rarely cooperative breeders	Solitary, monogamous breeders
Nest structure	Large stick platform or open cup stick nest	Well-molded, delicate, camouflaged cup made of cobwebs and grass	Large untidy, not camouflaged, loosely woven cup nest	Well-made shallow stick cup built low in canopy

Figure 1. Representatives of 4 lineages discussed in this study: (**A**) Southern White-crowned Shrike (*Eurocephalus anguitimens*), (**B**) Loggerhead Shrike (*Lanius ludovicianus*), (**C**) Crested Shrikejay (*Platylophus galericulatus*), and (**D**) Long-billed Crow (*Corvus validus*). Photos are used with permission: (**A**) Alexander Lees, (**B**) Dorian Anderson, (**C**) Alexander Berryman, and (**D**) Jenna McCullough.

Figure 2. Maximum likelihood phylogeny of the superfamily Corvoidea, based on the RAxML analysis of the concatenated 100% complete matrix comprising 2,500 UCE loci and assessed with 100 bootstrap replicates. Bootstrap support is shown for nodes that received <100. Note that we use the family group name, Eurocephalidae, that we propose in this article.

Figure 3. Maximum clade credibility (MCC) tree of 300 ultraconserved loci from the complete UCE matrix and fixed RAxML topology. Node ages are shown for selected clades. Black circles represent nodes in which secondary calibrations from Oliveros et al. (2019) were placed. Note that we use the family group name, Eurocephalidae, that we propose in this article. Artwork by Jenna McCullough.

Figure 1

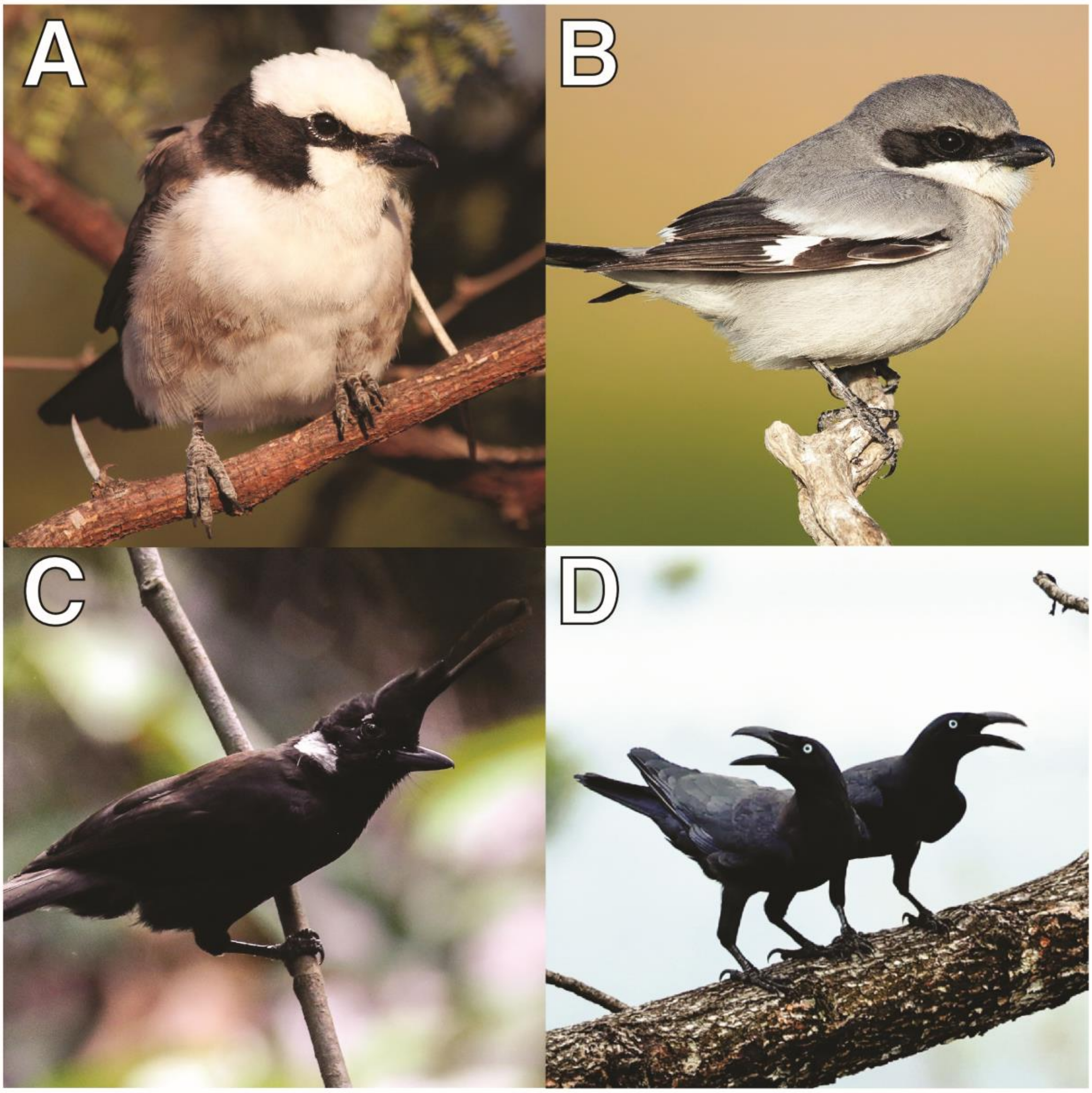


Figure 2

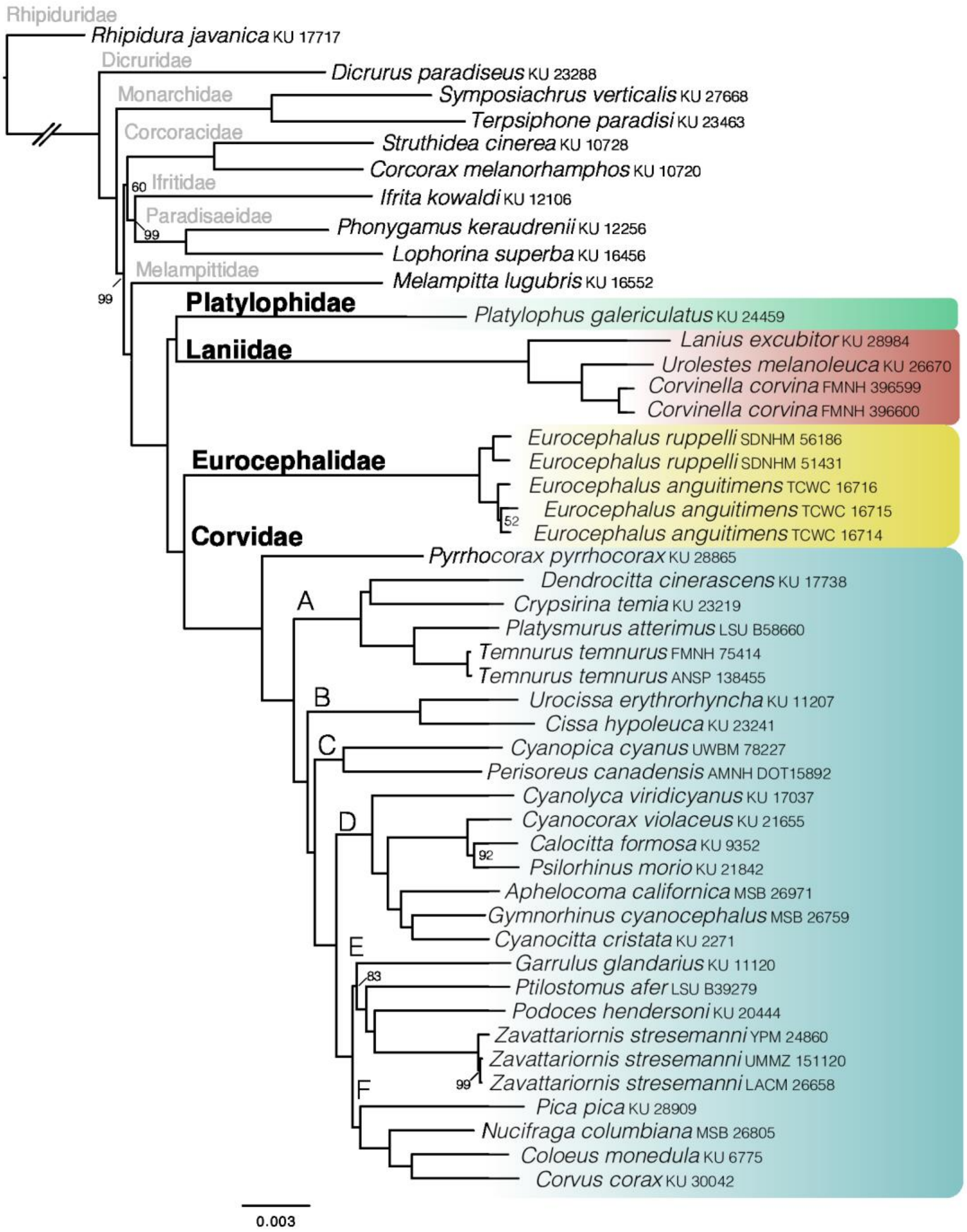
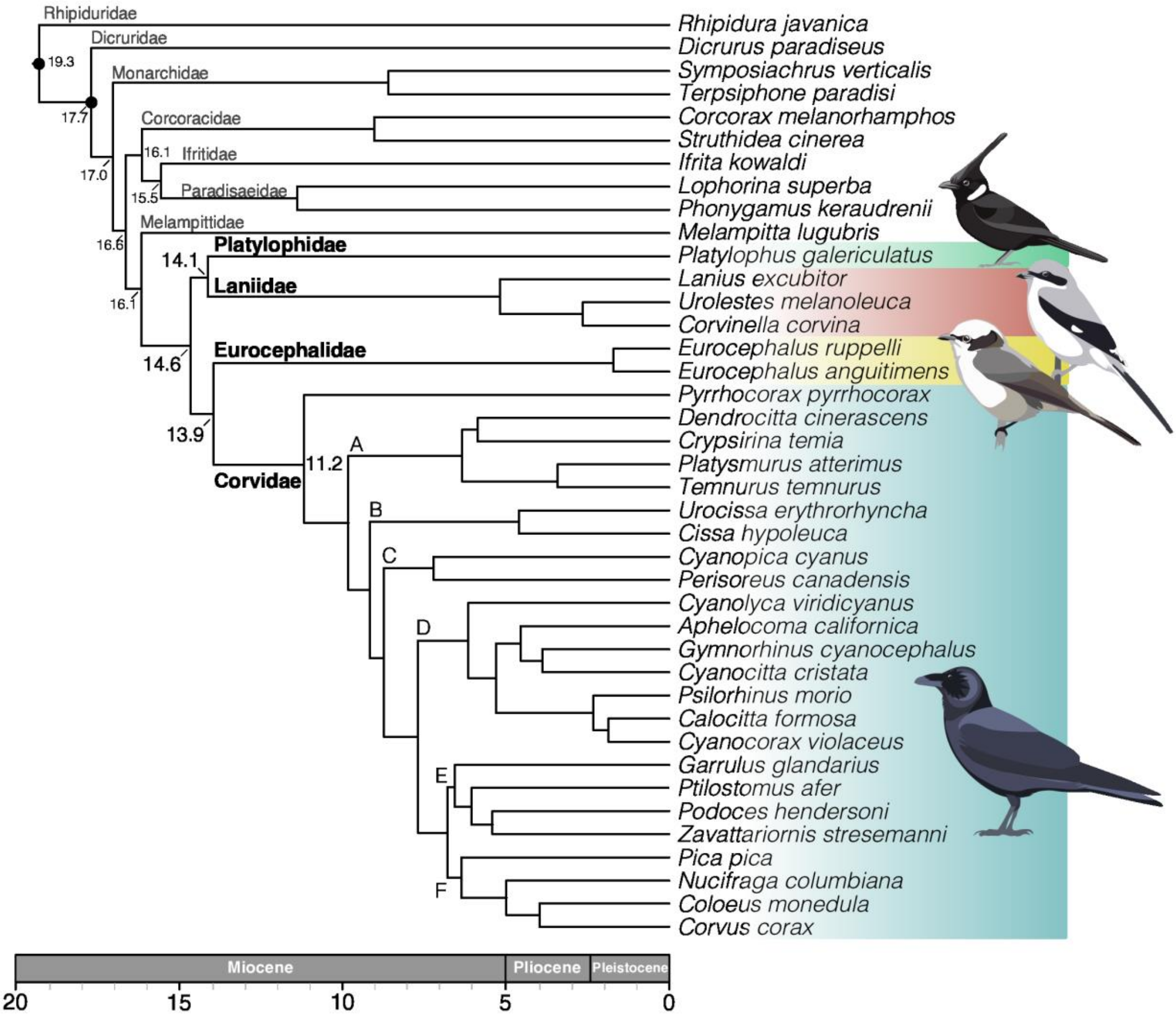

Rhipiduridae
Rhipidura javanica KU 17717
Dicruridae
Dicrurus paradiseus KU 23288
Monarchidae
Symposiachrus verticalis KU 27668
Terpsiphone paradisi KU 23463
Corcoracidae
Struthidea cinerea KU 10728
Corcorax melanorhamphos KU 10720
60
Ifritidae
Ifrita kowaldi KU 12106
Paradisaeidae
99
Phonygamus keraudrenii KU 12256
Lophorina superba KU 16456
Melampittidae
Melampitta lugubris KU 16552
99
Platylophidae
Platylophus galericulatus KU 24459
Laniidae
Lanius excubitor KU 28984
Urolestes melanoleuca KU 26670
Corvinella corvina FMNH 396599
Corvinella corvina FMNH 396600
Eurocephalidae
Eurocephalus ruppelli SDNHM 56186
Eurocephalus ruppelli SDNHM 51431
Eurocephalus anguitimens TCWC 16716
52
Eurocephalus anguitimens TCWC 16715
Eurocephalus anguitimens TCWC 16714
Corvidae
Pyrrhocorax pyrrhocorax KU 28865
A
Dendrocitta cinerascens KU 17738
Crypsirina temia KU 23219
Platysmurus atterimus LSU B58660
Temnurus temnurus FMNH 75414
Temnurus temnurus ANSP 138455
B
Urocissa erythrorhyncha KU 11207
Cissa hypoleuca KU 23241
C
Cyanopica cyanus UWBM 78227
Perisoreus canadensis AMNH DOT15892
D
Cyanolyca viridicyanus KU 17037
Cyanocorax violaceus KU 21655
92
Calocitta formosa KU 9352
Psilorhinus morio KU 21842
Aphelocoma californica MSB 26971
Gymnorhinus cyanocephalus MSB 26759
Cyanocitta cristata KU 2271
E
Garrulus glandarius KU 11120
83
Ptilostomus afer LSU B39279
Podoces hendersoni KU 20444
Zavattariornis stresemanni YPM 24860
Zavattariornis stresemanni UMMZ 151120
99
Zavattariornis stresemanni LACM 26658
F
Pica pica KU 28909
Nucifraga columbiana MSB 26805
Coloeus monedula KU 6775
Corvus corax KU 30042
0.003

Figure 3


Rhipiduridae
Dicruridae
19.3
Monarchidae
17.7
Corcoracidae
16.1
Ifritidae
17.0
15.5
Paradisaeidae
Melampittidae
16.6
Platylophidae
14.1
Laniidae
16.1
Eurocephalidae
14.6
13.9
11.2
A
Corvidae
B
C
D
E
F
Rhipidura javanica
Dicrurus paradiseus
Symposiachrus verticalis
Terpsiphone paradisi
Corcorax melanorhamphos
Struthidea cinerea
Ifrita kowaldi
Lophorina superba
Phonygamus keraudrenii
Melampitta lugubris
Platylophus galericulatus
Lanius excubitor
Urolestes melanoleuca
Corvinella corvina
Eurocephalus ruppelli
Eurocephalus anguitimens
Pyrrhocorax pyrrhocorax
Dendrocitta cinerascens
Crypsirina temia
Platysmurus atterimus
Temnurus temnurus
Urocissa erythrorhyncha
Cissa hypoleuca
Cyanopica cyanus
Perisoreus canadensis
Cyanolyca viridicyanus
Aphelocoma californica
Gymnorhinus cyanocephalus
Cyanocitta cristata
Psilorhinus morio
Calocitta formosa
Cyanocorax violaceus
Garrulus glandarius
Ptilostomus afer
Podoces hendersoni
Zavattariornis stresemanni
Pica pica
Nucifraga columbiana
Coloeus monedula
Corvus corax
Miocene
Pliocene
Pleistocene
20
15
10
5
0