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Investigations

What Is an Eared Nightjar? Ultraconserved Elements Clarify the Evolutionary Relationships of *Eurostopodus* and *Lyncornis* Nightjars (Aves: Caprimulgidae)

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Abstract

Nightjars (Aves: Caprimulgidae) are a species-rich family of birds, with the "eared nightjars" (Eurostopodinae) being an early-branching group endemic to the Indo-Pacific. While much research has focused on species-rich nightjar genera and their higher-level relationships, the evolutionary history of Eurostopodinae (*Eurostopodus*, *Lyncornis*) remains understudied. We generated a genome-scale dataset to produce the first fully sampled phylogeny of all *Eurostopodus* and one *Lyncornis* species, including sequencing two type specimens of critically endangered and extinct species. Tree-building methods inferred concordant, well-resolved topologies that reveal intriguing biogeographic patterns within *Eurostopodus*. Our results show *Eurostopodus* as sister to all other nightjars, while *Lyncornis*, previously considered related, is more closely allied with other caprimulgids. We propose that the term "eared nightjars" should apply only to the two *Lyncornis* species, which should be classified within the subfamily Caprimulginae. Accordingly, since only *Eurostopodus* species remain in Eurostopodinae, we recommend renaming this subfamily "Indo-Pacific nightjars" to reflect their geographic distribution in this significant region.

Introduction

Phylogenetic reconstruction of the avian superorder Strisores, the 'nightbirds', has proven to be contentious and difficult (Braun & Huddleston, 2009; Ericson et al., 2006; Hackett et al., 2008; Prum et al., 2015; Reddy et al., 2017; Sibley et al., 1990; White & Braun, 2019). Though its name suggests otherwise, this cosmopolitan avian superorder comprises both diurnal and nocturnal taxa that are divided among eight taxonomic families. These families range from the species-rich nightjars (Caprimulgidae) to the enigmatic and monotypic Oilbird (*Steatornis caripensis*; Steatornithidae) of South America to the unique treeswifts (Hemiprocnidae) and owlet-nightjars (Aegothelidae) of the Indo-pacific. Strisores also includes one of the most species-rich avian families: hummingbirds (Trochilidae) with 363 species (Winkler et al., 2015).

Nightjars (Caprimulgidae, 98 species) are a group of obligate aerial insectivores, commonly known as "goatsuckers." They have soft, cryptic brown plumage, distinctive nocturnal vocalizations, and large mouth openings (gapes) that they use to catch flying insects (del Hoyo & Collar, 2014). Research on their systematic relationships has primarily focused on the species-rich and widespread genus *Caprimulgus*, which accounts for nearly 40% of the species diversity in the family (Gill et al., 2022). This genus has been the subject of multiple studies using small multi-locus datasets to assess relationships within the family (Barrowclough et al., 2006; Braun & Huddleston, 2009; Han et al., 2010; Sigurðsson & Cracraft, 2014; White et al., 2016). However, the limited number of studies using genome-wide markers have focused on the difficult-to-resolve higher-level relationships within the Strisores (Chen et al., 2019; White & Braun, 2019).

Eurostopodus, commonly known as the 'eared nightjars', is an early diverging and poorly studied group of nightjars. As the only nightjar genus endemic to the Indo-Pacific region, it includes seven species distributed from Wallacea eastward through Australia and Melanesia (Fig. 1). Early systematic studies suggested that eared nightjars were distinct enough to warrant either family-level ("Eurostopodidae"; Mariaux & Braun, 1996) or even superfamily-level status ("Eurostopodoidea"; Sibley & Ahlquist, 1990). Currently, they are considered a subfamily, Eurostopodinae, along with *Lyncornis* (Winkler et al., 2015). However, the va-

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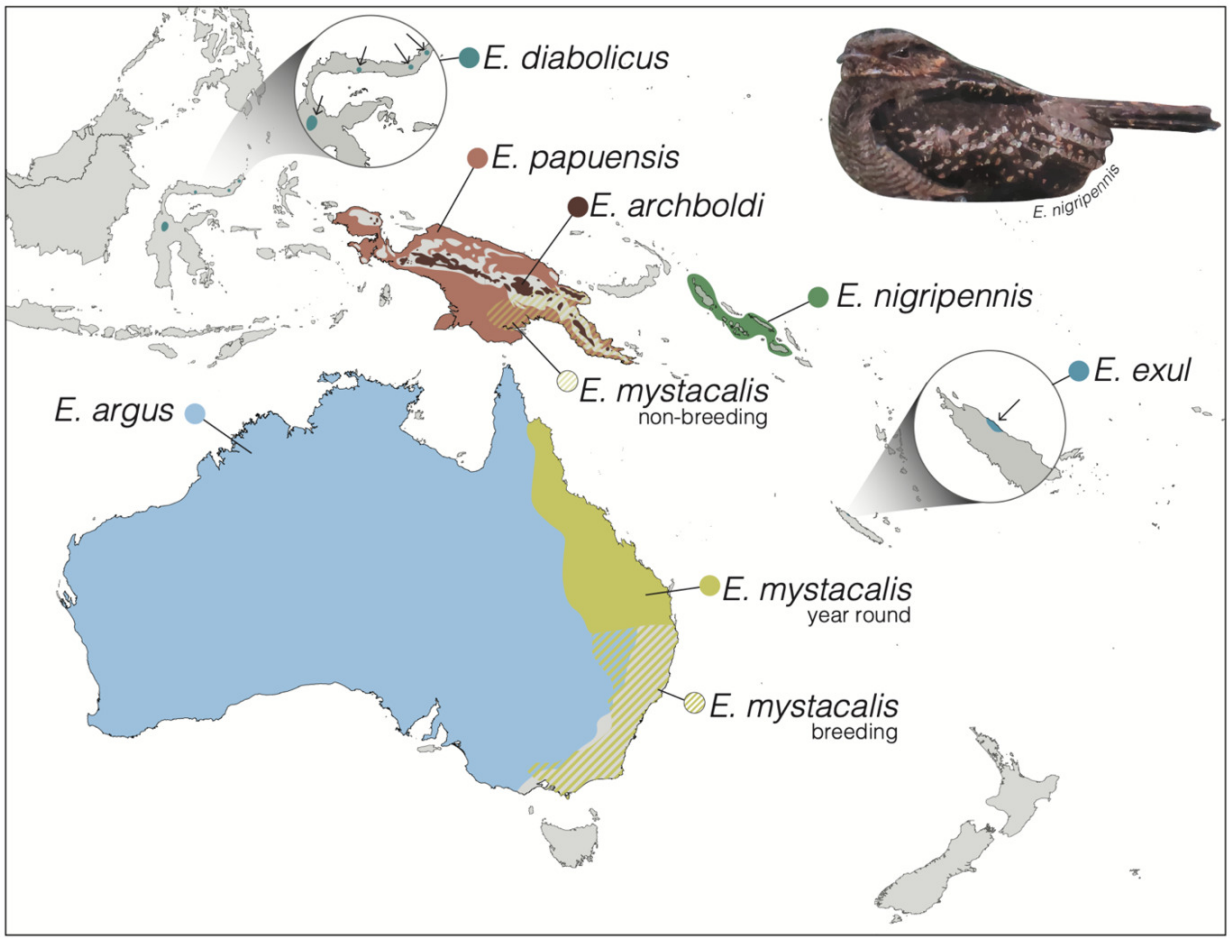

Figure 1. Range map of all *Eurostopodus* species. Diagonal green bars for the migratory White-throated Nightjar (*E. mystacalis*) indicate breeding or non-breeding ranges. Arrows are for emphasis for extremely range restricted species. Illustration of Solomons Nightjar (*E. nigripennis*) created by Jenna McCullough.

lidity of this subfamily is uncertain, as *Eurostopodus* is often treated as an outgroup in studies that primarily focus on other Caprimulgids (Barrowclough et al., 2006; Braun & Huddleston, 2009; Han et al., 2010; Sangster et al., 2022; Sigurðsson & Cracraft, 2014). Few taxa from Eurostopodinae have ever been included in molecular phylogenies, yet species limits of some *Eurostopodus* have recently been revised. For example, two subspecies of the White-throated Nightjar (*E. mystacalis mystacalis* and *E. m. nigripennis*), were elevated to species rank based on differences in plumage and vocalizations (Dutson, 2011; Holyoak, 2001). Three island-endemic species—the New Caledonian Nightjar (*E. exul*), Solomons Nightjar (*E. nigripennis*), and Satanic Nightjar (*E. diabolicus*)—have not previously been included in molecular phylogenies due to lack of available genetic material.

The goal of this study is to assess the evolutionary history of this understudied group of nightjars using a genome-scale dataset. We sampled all *Eurostopodus* species, including three species that have never been part of a molecular analysis before—two of which (*E. exul* and *E. diabolicus*) were sourced from toepad clippings of type specimens housed at the American Museum of Natural History. We collected a comprehensive genome-scale dataset of ultraconserved elements (UCEs; Faircloth et al., 2012), utilizing an updated probe set specifically refined to better capture UCEs from degraded, toepad-sourced samples. This approach allowed us to produce a fully sampled phylogeny of *Eurostopodus* nightjars.

Methods

Sampling and laboratory techniques

Following the taxonomy of Gill et al. (2022), we sampled all seven *Eurostopodus* species, including representatives of three additional genera that have shown to be recalcitrant at the base of Caprimulgidae (Table S1; White & Braun, 2019). We extracted genomic DNA with the Qiagen DNeasy kit from frozen or ethanol-preserved tissue samples that were loaned from natural history collections. However, samples representing three species, Archbold's Nightjar (*E. archboldi*), Satanic Nightjar (*E. diabolicus*), and New Caledonian Nightjar (*E. exul*), were derived from toepad clippings of museum specimens from the American Museum of Natural History. Notably, *E. diabolicus* and *E. exul* are derived from type-specimens and those we sampled here are the only study skins in existence for these species (Table

S1). For increased taxonomic sampling, we downloaded raw reads (White & Braun, 2019) or genomes (Jarvis et al., 2014; Zhang et al., 2014) for ten additional species from GenBank for a total of 27 samples used in this study.

Due to the fragmented nature of DNA derived from museum specimens, we treated these three toepad samples differently from tissue-derived samples in several ways. For toepad-derived libraries, we instead extracted DNA with a phenol-chloroform protocol, which has been shown to produce higher yield DNA extractions than Qiagen kits (Tsai et al., 2019). To increase yields and limit chloroform exposure to samples during the extraction, we used phase lock gel tubes. Prior to library preparation, we estimated fragment size using gel electrophoresis (tissue-derived samples only) and quantified DNA concentrations with a Qubit 3.0 Fluorometer (ThermoFisher Scientific).

For library preparation and target capture of UCEs, we followed established protocols (Faircloth et al., 2012; McCormack et al., 2016). For toepad-derived samples, we followed McCormack et al. (2016) for specific modifications to improve yields for library preparation. Specifically, we performed all AMPure bead cleanups at 3X the sample volume, doubled adapter ligation times (30 minutes), and performed all non-PCR steps with samples in Eppendorf Lo-Bind tubes to increase retention of historical DNA. We pooled dual-indexed tissue- and toepad-derived libraries separately (but with samples from other unrelated projects) for UCE enrichment, including either six (toepad) or eight libraries (tissue) per pool. We used an updated version of the Arbor Biosciences MyBaits kit for Tetrapods UCE-Kv2b probe set, which is different from the widely used 5K probe set because it includes more baits per locus designed from both chicken and Zebra Finch (*Taeniopygia guttata*) genomes (published prior in McCullough et al., 2023). We hybridized probes at either 65°C (tissues) or 62°C (toepads) for 24 hours. We sequenced samples on a single lane of an Illumina NovaSeq 6000 with a PE150 flow cell at the Oklahoma Medical Research Foundation (OMRF).

Bioinformatics

We used the Phyluce v1.7.1 Python package to process UCE data (Faircloth, 2016; described in full at https://github.com/faircloth-lab/phyluce) with the University of New Mexico Center for Advanced Research Computing (CARC) high performance cluster. With Illumiprocessor v2.1, we trimmed adaptor sequences and low-quality bases from demultiplexed raw reads (Bolger et al., 2014; Faircloth, 2013). We used Spades v1.7 (Prjibelski et al., 2020) to assemble cleaned reads into contigs and extracted UCE loci with the updated probeset.

It is well known that samples sourced from degraded museum samples, such as toepads, can have extraordinarily long branches; this was evident in initial phases of phylogenetic analyses with our toepad-sourced samples (see below for phylogenetic methods and Table S1 for these samples). Smith et al. (2020), using a dataset with many toepad-sourced UCE samples, showed that these extraordinarily long branches are an artifact of poor performance of locus trimming programs for degraded toepad-sourced samples and thus not biologically realistic. Following their bioinformatic pipeline, we removed these problematic regions of UCE loci by aligning cleaned reads of the two toepad-sourced samples to a reference UCE contigs of a closely related species. We expanded fasta files (with the script "phyluce_assembly_explode_get_fastas_file") to get the unaligned UCE contigs for our reference sample, Spotted nightjar (*E. argus*; KU 126607). This sample was chosen as the reference for both our toepad-sourced samples based on our initial concatenated RAxML analysis (Kozlov et al., 2019). Using bwa, Samtools, and GNU parallel (Li et al., 2009; Li & Durbin, 2009; Tange, 2021), we aligned cleaned reads of the problematic toepad-sourced samples to the indexed reference UCE contigs. We then dropped sites that had <5X coverage and quality scores <20 in an effort to remove the low-quality data in the flanking regions that contribute to these spurious long branches.

For wider taxonomic sampling, we downloaded whole genomes from GenBank and followed established pipelines (Faircloth, 2018) to harvest UCE data *in silico*. We aligned the Tetrapods UCE-5Kv2b probes to the genomes (Jarvis et al., 2014; Zhang et al., 2014) and extracted loci with 500 bp flanking regions with the "phyluce_probe_slice_sequence_from_genomes" script. We manually added the nucleotide data for these two samples into the combined, unaligned fasta file of UCE data for all samples (produced by the "phyluce_assembly_get_fastas_from_match_counts" script). We then aligned all 27 samples with MAFFT (Katoh & Standley, 2013) and used TrimAL v1.4.rev15 (Capella-Gutiérrez et al., 2009) with the "-automated1" flag to trim the ends of UCE loci. This produced a 75% complete matrix, in which at least 20 of 27 samples were present at each UCE locus.

We used both maximum likelihood and species tree methods to infer species relationships. For the maximum likelihood tree, we used IQtree 2 v2.0.3 (Minh et al., 2020). We determined the optimal substitution model for each locus (-m TESTONLY) first and then analyzed the partitioned, concatenated alignment with 1000 ultrafast bootstrap replicates (Hoang et al., 2018). We generated a species tree with SVDQuartets (Chifman & Kubatko, 2014) in Paup v4.0a166 (Swofford, 2003). SVDQuartets is a quartet method that accounts for gene tree heterogeneity and has been shown to perform better than other coalescent-based tree-building programs for large multilocus datasets (Wascher & Kubatko, 2021). We analyzed all quartet possibilities (n = 16,356 quartets) and assessed node support with 100 bootstrap replicates.

Results

The 75% complete matrix comprised 27 tips, 4,126 loci (mean loci length = 997 bp), and was 4,910,772 bp in length, of which 401,582 were parsimony informative sites. All newly sequenced UCE raw reads are registered as NCBI BioProject ID PRJNA1170272. The two analyses produced identical topologies and nearly all nodes were supported with 100% bootstrap values (BS; Figs. 2–3). In IQtree, the node uniting *Nyctibius* and *Steatornis* received 84% boot-

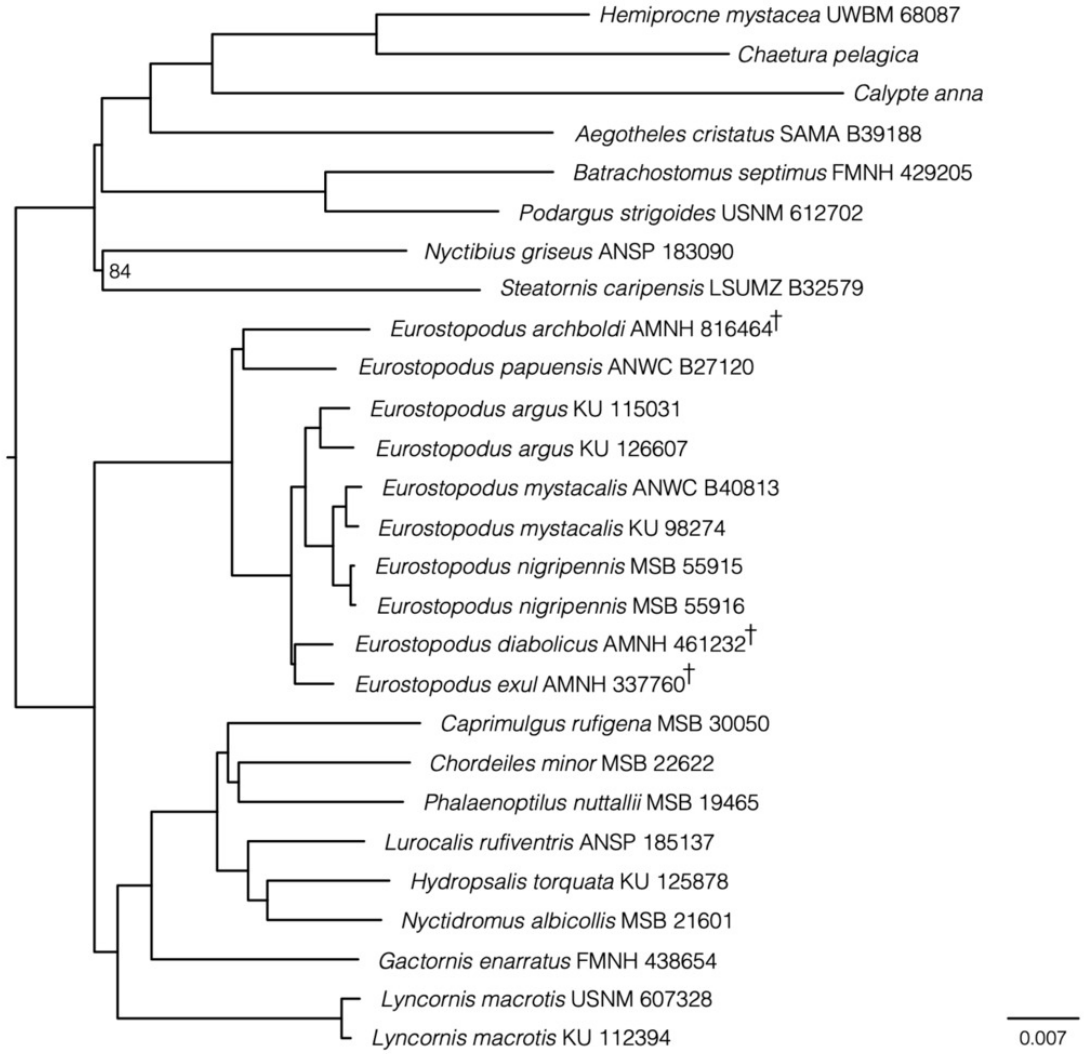

Figure 2. Maximum likelihood phylogeny of *Eurostopodus* nightjars based on the concatenated 75% complete UCE matrix (4,126 loci). Bootstrap support is listed for nodes that received <100. Tips derived from toepad clippings of museum specimens are labeled with a dagger (†).

strap support. In SVDQuartets, it received 77% BS. Two other nodes received low support in SVDQuartets: we recovered 83% BS for the node uniting Podargidae (*Batrachostomus* + *Podargus*) as sister to the clade of owlet-nightjars (*Aegotheles*), hummingbirds (*Calypte*), swifts (*Chaetura),* and treeswifts (*Hemoprocne*). The node subtending *Eurostopodus diabolicus* and *E. exul* was supported with 94% BS. Within Caprimulgidae, *Eurostopodus* was sister to all other caprimulgids and *Lyncornis* and *Gactornis* were each sequentially branching to a clade that comprised *Lurocalis*, *Hydropsalis*, *Nyctidromus* + *Caprimulgus*, *Chordeiles*, and *Phalaenoptilus*.

Within *Eurostopodus*, two taxa from New Guinea were sister: *E. archboldi* and *E. papuensis*. These are elevational replacements of each other, whereby *E. archboldi* inhabits highlands along the Central Cordillera and *E. papuensis* is widespread in the lowlands. This pair was sister to all other taxa in the genus. *Eurostopodus diabolicus* of Sulawesi was sister to *E. exul*, a critically endangered taxon from New Caledonia, which makes for a biogeographically disjunct sister pair. Finally, *Eurostopodus argus*, which is widespread across most of Australia, was sister to the pair of *E. nigripennis* and *E. mystacalis*, which are distributed across the Solomon Islands and Eastern Australia, respectively.

Discussion

Our study provides the first complete species-level phylogeny for *Eurostopodus*, revealing important insights into the evolutionary history of this understudied group of nightjars. The resulting tree provides a well-resolved topology, revealing intriguing biogeographic patterns within *Eurostopodus* and supporting necessary taxonomic revisions concerning the placement of *Lyncornis*. These revisions will, in turn, impact the classification of higher-level clades (subfamilies) within nightjars, which we address below. Fi-

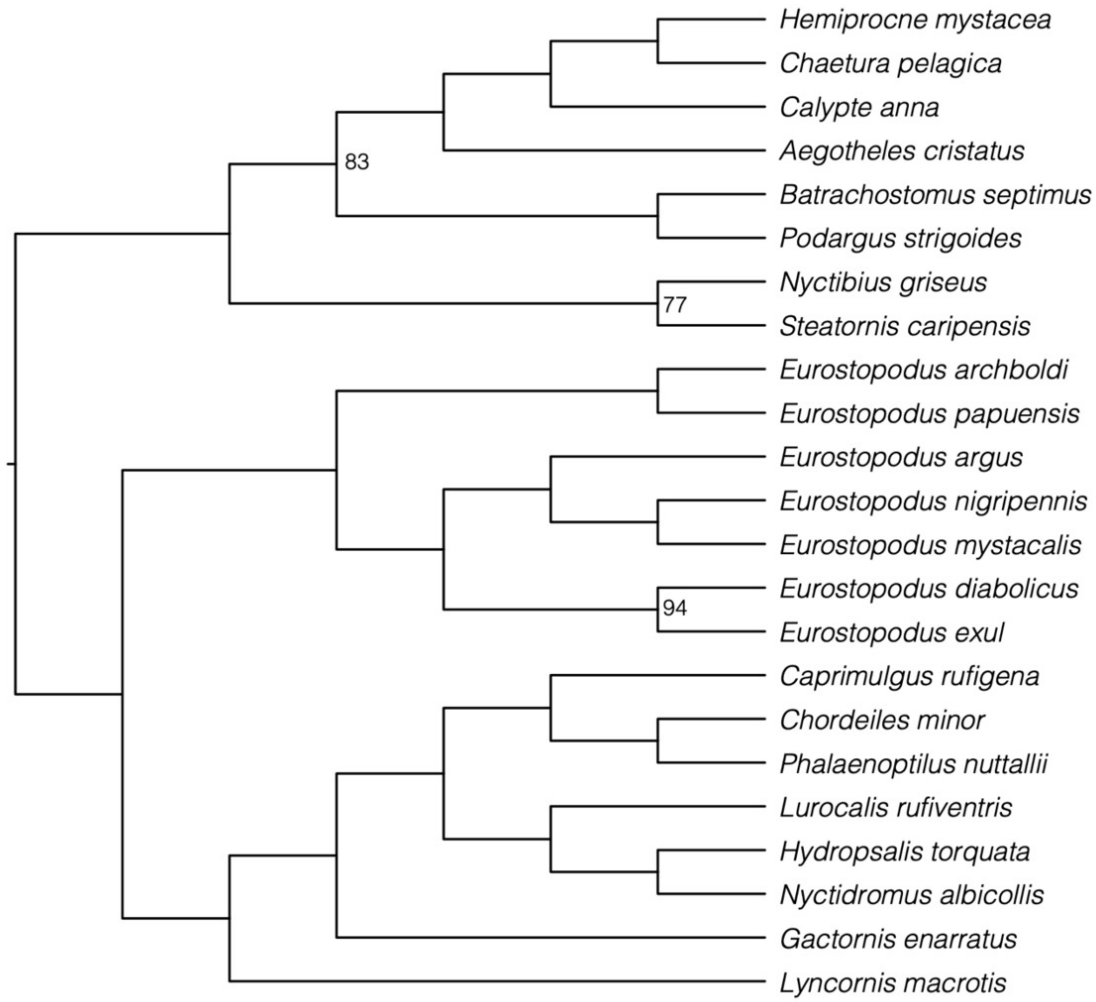

Figure 3. Phylogeny of *Eurostopodus* nightjars, analyzed with all possible quartets and assessed with 100 BS support in SVDQuartets. Bootstrap support is listed for nodes that received <100.

nally, observed variation in nodal support across different phylogenetic methods within outgroup taxa is likely due to uncertainty surrounding the relationships between the potoos (*Nyctibius*) and the monotypic Oilbird (*Steatornis*), a challenge previously noted in the literature (White et al., 2016; White & Braun, 2019).

Caprimulgidae has traditionally been divided into two subfamilies, either Chordeilinae (nighthawks) and Caprimulginae (nightjars; Cleere, 1998) or Eurostopodinae and Caprimulginae (Sibley et al., 1990; Winkler et al., 2015). Our findings call for a revision of this framework based on the evolutionary relationships we uncovered. In their work on nightbird systematics, White et al. (2016) recommended incorporating additional members of the genera *Lyncornis* and *Eurostopodus* to clarify the early branching pattern of Caprimulgidae. Indeed, our phylogenetic analysis includes all *Eurostopodus* taxa and reveals that *Eurostopodus* is sister to all other nightjars, while *Lyncornis* is sister to the rest of the family Caprimulgidae, exclusive of *Eurostopodus* (*sensu* Han et al., 2010; Sigurðsson & Cracraft, 2014). Contrary to previous classifications, *Lyncornis* and *Eurostopodus* are not each other's closest relatives. Based on these findings, we suggest restricting the subfamily Eurostopodinae to include only the genus *Eurostopodus*, while *Lyncornis* should be reclassified as part of Caprimulginae. This recommendation challenges the traditional English name 'eared nightjars' for *Eurostopodus*, as none of its species possess ear tufts. The term 'eared nightjars' more appropriately applies to *Lyncornis*, which includes two species: the Malaysian Eared Nightjar (*L. temminckii*) and the Great Eared Nightjar (*L. macrotis*), both of which have ear tufts. Consequently, we recommend adopting the name 'Indo-Pacific nightjars' for all *Eurostopodus* species to reflect their biogeographic distribution and the presence of several micro-endemics in this geologically and evolutionarily important region.

Biogeographic patterns within *Eurostopodus*

The biogeography of *Eurostopodus* nightjars reveals complex and often perplexing patterns, particularly regarding island endemics like *E. diabolicus* and *E. exul*. These two enigmatic species, the Satanic Nightjar from Sulawesi and the critically endangered—possibly extinct—New Caledon-

ian Nightjar, respectively, were for the first time included in a molecular phylogeny in this study. Both were sourced from type specimens housed at the American Museum of Natural History, as they are the only known representatives of their species. Our phylogenetic analyses revealed these species as sister taxa, highlighting a disjunct biogeographic pattern between the widely separated islands of Sulawesi and New Caledonia. This raises intriguing questions about the historical dispersal and extinction processes that may have shaped this pattern. Either this pattern is the result of dramatic overwater dispersal, to the exclusion of many intervening landmasses, or, perhaps more likely, the result of extinction having left two widely separated relictual populations on Sulawesi and New Caledonia. Patterns like this have been identified in other birds in this region. For example, the three genera that comprise the subfamily Lamproliinae (Passeriformes: Rhipiduridae), occur on widely separated islands of New Guinea (*Chaetorhynchus*), Fiji (*Lamprolia*), and Sangihe (*Eutrichomyias*; Jønsson et al., 2018).

In New Guinea, two *Eurostopodus* species are elevational replacements of each other. *Eurostopodus archboldi* is a montane species restricted to New Guinea's highlands where it is found above 2400m to treeline (Fig. 1; Beehler & Pratt, 2016). *Eurostopodus papuensis* is widespread across the lowlands of New Guinea, not exceeding 400m elevation. Our results show that *E. archboldi* and *E. papuensis* are deeply diverged sister taxa and confirm long-standing taxonomic treatment as distinct species. Unlike other elevational replacements in New Guinea (e.g., *Syma* kingfishers; Linck et al., 2020) that have parapatric distributions and exchange genes, these *Eurostopodus* taxa are allopatric, absent from mid-elevation forests (ca. 400–2400m), and are unlikely to have ongoing gene flow between them.

Conclusions

Previous work on the relationships of nightjars and other Strisores has focused on species-rich genera or higher-level clades, while relationships within the early-diverging *Eurostopodus* nightjars and their close relatives in the subfamily Eurostopodinae have been largely overlooked. We presented the first fully sampled phylogeny *Eurostopodus* using genome-scale data. Our results show that the so-called 'eared nightjars' of Eurostopodinae lack the namesake ear tufts, which are found only in *Lyncornis*. We also found that *Lyncornis* is more closely related to other caprimulgids than to *Eurostopodus*, suggesting a revision in subfamily taxonomy and a name change for Eurostopodinae. Additionally, we uncovered notable biogeographic patterns, including a close relationship between two relictual, threatened species from Sulawesi and New Caledonia, and an elevational replacement sister pair in New Guinea.

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Supporting Information

Supplementary material, including alignments, tree files, and other information (supplementary table 1) are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xksn02vrh

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