Biological Journal of the Linnean Society, 2024, **XX**, 1–17
https://doi.org/10.1093/biolinnean/blae028
Advance access publication 22 March 2024
Original Article

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Enigmas no longer: using ultraconserved elements to place several unusual hawk taxa and address the non-monophyly of the genus *Accipiter* (Accipitriformes: Accipitridae)

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ABSTRACT

Hawks, eagles, and their relatives (Accipitriformes: Accipitridae) are a diverse and charismatic clade of modern birds, with many members that are instantly recognized by the general public. However, surprisingly little is known about the relationships among genera within Accipitridae, and several studies have suggested that some genera (in particular, the megadiverse genus *Accipiter*) are not monophyletic. Here, we combine a large new dataset obtained from ultraconserved elements, generated from whole genome sequencing of 134 species, with publicly available legacy markers (i.e. a suite of commonly sequenced mitochondrial and nuclear genes) to infer a well-supported, time-calibrated phylogeny of 237 extant or recently extinct species. Our densely sampled phylogeny, which includes 90% of recognized species, confirms the non-monophyly of *Accipiter* and provides a sufficient basis to revise the genus-level taxonomy, such that all genera in Accipitridae represent monophyletic groups.

Keywords: birds of prey; eagle; harrier; hawk; phylogenomics; raptor; systematics; vulture; whole genome sequencing

INTRODUCTION

Systematists generally agree that genus-rank categories should be composed of monophyletic groups of species, and this is a central tenet of the synapomorphy-based system of classification (Hennig 1965, Dubois 1982, Stevens 1985). However, there is often disagreement about how inclusive such groups should be and what criteria should be applied to determine generic limits. Some authors have proposed that genera should reflect 'adaptive zones' (e.g. Dubois 1982, 1988, Lemen and Freeman 1984, Miller and Wenzel 1995), age of divergence (Hennig 1965, Avise and Johns 1999), or the overall degree of morphological divergence (e.g. Dubois 1982). However, each approach has its drawbacks. For example, molecular clocks can produce wildly different estimates for divergence times at a given node, even within the same dataset, depending upon calibration methods (Oatley *et al.* 2015, Mindell *et al.* 2018), and 'morphological gaps' between monophyletic groups can result simply from incomplete sampling of taxa (e.g. owing to extinction; see Marshall 2017). Seeking a practical compromise, Isler *et al.* (2013: 469) encouraged taxonomists to recognize clades at generic rank when they '[provide] recognition of phylogenetic relationships, synapomorphic characters, and phenotypic distinctiveness that will best facilitate understanding and communication of relatedness of taxa among analysts, field workers and conservationists'.

We investigated the systematics of a particularly challenging group—the cosmopolitan family Accipitridae (Aves: Accipitriformes), hawks and eagles—which includes multiple large, morphologically diverse genera (e.g. *Accipiter* and *Buteo*) and a plethora of monotypic genera defined by relatively narrow criteria (e.g. *Micronisus*, *Megatriorchis*). The inconsistency of taxonomic practice in Accipitridae has long been a source of frustration for systematists, and a critique written two centuries ago still rings true:

> [Authors] are at full liberty to make as many genera or subgenera as they please.… But the human mind is ever prone to extremes, and the passion for dividing and subdividing, and giving names, may become as great an evil as that which

Received 26 June 2023; revised 31 January 2024; accepted 7 February 2024

> led the followers of Linnaeus to deprecate *all* division, and to view with abhorrence the slightest attempt to break up the old groups.… Fortunately, the only group in Ornithology which has apparently suffered from this evil is that of the *Falconidae* [*sensu lato*, including modern Accipitridae]. (Swainson 1831: lvii)

Before the mid-20th century, most systematists assumed that falcons (Falconidae) and hawks and eagles (Accipitridae) were sister groups and thus classified both in the order Falconiformes (e.g. Mayr 1959, but see Starck 1959). However, based on electrophoretic profiles of egg-white proteins, Sibley (1960) proposed that 'Falconiformes [*sensu lato*] may be polyphyletic, the Falconidae possibly being unrelated to the other diurnal birds of prey'. This hypothesis, controversial in its time, has been confirmed repeatedly with molecular data (Hackett *et al.* 2008, Jarvis *et al.* 2014, Prum *et al.* 2015); falcons are more closely related to perching birds (Passeriformes) and parrots (Psittaciformes) than to hawks. This is corroborated by evidence from the feather-chewing louse genus *Degeeriella* (Phthiraptera), a parasite of hawks and falcons, which is also non-monophyletic; the clade parasitizing falcons is more closely related to the genus *Picicola*, which parasitizes woodpeckers (Catanach and Johnson 2015). Likewise, the 'New World' vultures (Cathartidae), long thought to be related to storks (Garrod 1874, Ligon 1967, Sibley and Ahlquist 1990, Avise *et al.* 1994), are now hypothesized to be the sister group of Accipitriformes (Jarvis *et al.* 2014, Prum *et al.* 2015).

Modern world checklists, including the checklist of Clements *et al.* (2021), whose nomenclature we follow in this study, recognize three families in Accipitriformes: (i) Sagittariidae, a group with unique cranial morphology (Huxley 1867: 441), consisting of one extant species, the Africa-endemic secretarybird *Sagittarius serpentarius* (Miller, 1779), and some extinct taxa from the Oligocene and Miocene (Mourer-Chauviré and Cheneval 1983); (ii) Pandionidae, a group consisting of one extant species, the cosmopolitan osprey *Pandion haliaetus* (Linnaeus, 1758), and some extinct taxa from the Miocene of North America (Warter 1976, Becker 1985); and (iii) Accipitridae, a hyper-diverse (249 species in 68 genera) and globally distributed family that includes hawks, vultures, eagles, and harriers. Accipitridae has been divided into several subfamilies and tribes, but these groupings vary widely from study to study. For example, Lerner and Mindell (2005) listed 14 subfamilies, whereas Peters (1931) and Mindell *et al.* (2018) each recognized only eight, the make-up and names of which do not match completely. Mindell *et al.* (2018) also recognized a non-monophyletic group that they referred to as the 'transitory Accipitrinae'. Hereafter, for clarity and consistency, we place English and Latin group names within quotation marks when they are widely used to refer to non-monophyletic groups. Furthermore, when there is uncertainty about the generic placement of a particular species, we place its traditionally used genus name in square brackets.

Relative to Sagittariidae and Pandionidae, extant members of Accipitridae exhibit a wide array of morphological, ecological, and behavioural characteristics (del Hoyo *et al.* 1994). Some species have restricted ranges and narrow ecological requirements (e.g. the Madagascar serpent-eagle, *Eutriorchis astur* Sharpe, 1875; see Kemp and Christie 2020), whereas others are ecological generalists with trans-hemispheric distributions [e.g. the golden eagle, *Aquila chrysaetos* (Linnaeus, 1758); see Katzner *et al.* 2020]. Most species are solitary predators, with monogamous social and genetic mating systems, but some exhibit cooperative parental care [e.g. Galapagos hawk, *Buteo galapagoensis* (Gould, 1837); see Faaborg *et al.* 1980, DeLay *et al.* 1996], cooperative hunting behaviour [e.g. Harris's hawk, *Parabuteo unicinctus* (Temminck, 1824); see Bednarz 1988], and even partial frugivory [e.g. the palm-nut vulture, *Gypohierax angolensis* (Gmelin, 1788); see Carneiro *et al.* 2017]. Despite this considerable diversity, ornithologists have struggled to resolve relationships within Accipitridae because of high levels of apparent convergence in external morphology and skeletal structure, which might be caused by shared selective pressures that are inherent to a predatory lifestyle (Holdaway 1994, Pecsics *et al.* 2019).

Molecular tools have advanced knowledge of some higher-level relationships within Accipitridae, but the phylogenetic positions of many taxa are unresolved. Complete or nearly complete taxon sampling has been achieved in some genera, but these phylogenies are based on Sanger sequencing of a small number of markers and often lack statistical support for the branching order between genera or groups of genera (e.g. Lerner and Mindell 2005, Amaral *et al.* 2009). In other bird groups, higher-level relationships have been resolved by sequencing large numbers of genes, either via genome reduction methods [e.g. ultraconserved elements (UCEs)] or by mining data from whole genome sequencing (WGS) (Prum *et al.* 2015, Chen *et al.* 2021, Hruska *et al.* 2023). These methods are more amenable to the use of degraded and highly fragmentary samples, such as the toepads of study skins (e.g. Burrell *et al.* 2015, Catanach *et al.* 2021). This is crucial for studies of Accipitridae systematics because high-quality tissues are lacking for several genera, owing to challenges associated with collecting diurnal birds of prey (e.g. heightened legal protection and low population densities). Furthermore, to deal with the scarcity of tissue samples, new methods have been developed to combine 'legacy markers' (i.e. Sanger data) with datasets obtained via next generation sequencing (NGS) analyses (Kimball *et al.* 2021). Here, we took advantage of these recent breakthroughs to reconstruct a time-calibrated phylogeny of Accipitridae and resolve the genus-rank taxonomy.

One particularly challenging group is *Accipiter*, a catch-all genus for (usually) forest-dwelling hawks, into which ~50 species have historically been placed (Peters 1931). For decades, researchers have debated the morphological boundaries of *Accipiter* and its relationship to other genera in Accipitridae (Roberts 1922). Olson (1987) noted that the procoracoid foramen, which is absent in '*Accipiter*' but present in nearly all other hawk genera, is also absent in some members of *Harpagus* ('kites') and *Circus* (harriers). However, at the time, this was not considered to be strong evidence of a close relationship between '*Accipiter*' and *Circus*, because they are extremely divergent in behaviour and ecology (Olson 1987). A subsequent study, focused primarily on osteological characters, concluded that *Accipiter* and *Harpagus* were closely related to the exclusion of *Circus* (Holdaway 1994). Testing these hypotheses with three molecular markers (*ND2*, *cyt-b*, and one nuclear intron), Lerner and Mindell (2005) found support for a sister relationship between

Accipiter and *Circus*, which convinced Olson (2006), but this finding was soon followed by a wave of evidence that *Accipiter*, as traditionally defined (Peters 1931), does not form a monophyletic group (e.g. Griffiths *et al.* 2007, Hugall and Stuart-Fox 2012, Oatley *et al.* 2015, Mindell *et al.* 2018). As more genes were added to phylogenetic analyses, it became evident that *Circus*, *Megatriorchis*, and *Erythrotriorchis* are nested within a larger '*Accipiter*' clade, which does not include several other species traditionally placed in *Accipiter*. Furthermore, chewing lice (*Degeeriella*) obtained from the northern goshawk, [*A.*] *gentilis* (Linnaeus, 1758), and Cooper's hawk, [*A.*] *cooperii* (Bonaparte, 1828), were shown to be more closely related to lice from *Circus* species than from other '*Accipiter*' species (Catanach and Johnson 2015).

Despite these findings, previous authors have been hesitant to revise the genus-level taxonomy and nomenclature of Accipitridae, for a variety of reasons. Most evidence that *Accipiter* is non-monophyletic has been an incidental byproduct of studies focused on more distantly related clades, which happened to include '*Accipiter*' taxa as outgroups in phylogenetic analyses. When the relationships of '*Accipiter*' were addressed explicitly, authors have been unwilling to take nomenclatural action because of relatively sparse species-level sampling (e.g. Oatley *et al.* 2015) or uncertainty caused by the exclusion of (or scarcity of available data from) certain enigmatic taxa (Mindell *et al.* 2018). To our knowledge, there have been no attempts to reorganize broadly (under criteria of monophyly) the generic classification of *Accipiter* and related genera. The only case in which '*Accipiter*' species were reclassified in a new genus, after molecular data showed that they were not members of the larger *Accipiter* (*s.l.*) clade (Hugall and Stuart-Fox 2012, Oatley *et al.* 2015), is the osteologically divergent clade containing the sister species tiny hawk, [*Accipiter*] *superciliosus* (Linnaeus, 1766), and semicollared hawk, [*Accipiter*] *collaris* (Sclater, 1860), which are now placed by some authors in the genus *Microspizias* Sangster *et al.* (2021).

Here, we estimated phylogenetic relationships among species and genera in Accipitridae by assembling and analysing multiple molecular datasets: UCEs and legacy markers (nuclear DNA and mitochondrial genomes). Our primary objective was to test the monophyly criterion for each genus-rank taxon, to inform a potential revision of the generic classification of Accipitridae, such that each genus refers to a monophyletic lineage.

MATERIALS AND METHODS

Sample selection

We selected 107 species for WGS and an additional eight species for UCE sequencing. All our samples were obtained from vouchered museum specimens, sourced from frozen tissues (*n* = 76), study skin toepads (*n* = 37), or dried bloodspots (*n* = 2). All toepads were sampled from preserved study skins, not living or recently deceased individuals. We supplemented this dataset by downloading all publicly available raw data (*n* = 19 samples) from the European Nucleotide Archive (https://www.ebi.ac.uk/ena/browser/), resulting in a combined dataset (Supporting Information, Table S1) that included samples from 45 genera in Accipitridae (ingroup) and seven genera in Pandionidae, Sagittariidae, and Cathartidae combined (outgroup). When multiple genomes were available for the same species, we selected (for the UCE analysis) the sample with most UCEs assembled, but we included all available samples for gene tree analyses involving publicly available sequence data ('legacy markers').

To include species for which no WGS sequencing data are yet available, we downloaded all publicly available sequence data ('legacy markers') from Accipitriformes and Cathartiformes from GenBank (https://www.ncbi.nlm.nih.gov/genbank/), with a submission cut-off date of 28 February 2022. We also downloaded sequence data from BOLD (http://www.boldsystems.org/), if they were obtained from a taxon not represented in the GenBank dataset. We included all available mitochondrial data (with the exception of control regions, which are known to be difficult to align confidently when working with taxa that are not closely related, and transfer RNAs), but only five nuclear genes (i.e. those for which broad sampling was available): portions of beta-fibrinogen (*FGB*) 4–8 (exons and introns); myoglobin (*MB*) exon 2 and intron; myelocytomatosis viral oncogene-like protein (c-*myc*); transforming growth factor beta 2 (*TGFb2*) intron 5; and recombination activating protein 1 (*RAG1*).

Extraction, sequencing, and library processing

We extracted DNA from all samples with Qiagen DNAeasy Kits (Germantown, MD, USA) by following the manufacturer's instructions, with the exception of toepad samples used for UCE sequencing, which we extracted using a phenol–chloroform protocol followed by bead clean-up (Tsai *et al.* 2019) or a modified QIAamp DNA Micro Kit (Germantown, MD, USA) protocol developed by Andrés M. Cuervo (Halley *et al.* 2023). For WGS sequencing, Illumina libraries were constructed with the Illumina TruSeq kit with standard adapters, and sequencing was performed on the Illumina X-Ten platform, at Genewiz (South Plainfield, NJ, USA). Before sequencing, extracts prepared for WGS were quantified by Genewiz using a Qubit, and libraries were tested for DNA quality and quantity using an Agilent Tapestation. For UCE samples, library preparation and 150 bp paired-end reads on an Illumina HiSeq 3000/4000 were performed by Rapid Genomics (Gainesville, FL, USA) using either the 2.5k tetrapod kit (which also includes ~100 avian exons) or the 5k tetrapod probe set (Faircloth *et al.* 2012). After sequencing, we used FASTQC to check the quality and duplication levels of our libraries (Andrews 2010). We then removed duplicate reads using the script fastqSplitDups.py from MCSCRIPT (https://github.com/McIntyre-Lab/mcscript), then used bbduk.sh from BBMAP (Bushnell 2014; using the settings ktrim = r, k = 23, mink = 11, and hdist = 1 tpe tbo) to remove adaptors. The only exceptions were some extremely large (>150 Gb) libraries, which we processed without duplicate removal after finding (via FASTQC) that they had low levels of read duplication (Andrews 2010). All samples were uploaded to the Sequence Read Archive, and we examined the produced Taxonomy Analysis, which uses the Sequence Taxonomic Analysis Tool (STAT) to bin reads into a taxonomic hierarchy allowing potential contamination to be identified (Katz *et al.* 2021). Although not used in this study, full genomes were also assembled (Catanach and Piro 2023), and samples that did not produce high-quality genomes were replaced when possible.

After assembly, we estimated sequence coverage using Geneious v.8.1.9 (Biomatters Limited, Auckland, New Zealand).

Ultraconserved element assembly

We assembled UCEs using aTRAM2 (Allen *et al.* 2018). For our target sequences, we selected hawk-specific versions of the probes in the 5k tetrapod probe set. We used the Phyluce pipeline (Faircloth 2016) to assemble UCEs from several high-quality hawk tissue samples, then selected the longest representative of each UCE to serve as a target sequence for UCE assembly for other species in the study (Catanach *et al.* 2021). Using these targets, we then performed five iterations of BLAST queries against each shard (created by partitioning a large dataset into several smaller datasets to ease computational requirements). After the first iteration, the results from the previous iteration were used as the target sequence (i.e. after the first iteration, the target sequence was from the species being assembled rather than the original target species). This feature of aTRAM produces accurate assemblies even for taxa distantly related to the species in the original set of target sequences. Each shard was ~125 Mb and, to decrease runtime, each BLAST query was capped at 4000 sequences per shard. We then created UCE alignments with a set of custom scripts (https://github.com/juliema/phylogenomics_scripts), which extracted the longest assembly from each UCE, combined them across samples, and aligned them using MAFFT v.7.453 (Katoh and Standley 2013). We calculated coverage for five UCEs (selected at random) for the three largest (average coverage of 14.4×) and three smallest libraries (average coverage of 5.6×).

We checked each UCE alignment by eye and removed unalignable portions of individual sequences. In a few cases, we encountered sets of assembled UCE sequences that matched each other but differed drastically from other sequences. We assumed that this was an artefact of assembly and not a biological signal, because UCEs are conserved across all tetrapods (Faircloth *et al.* 2012), and samples from the same avian order (Accipitriformes) are not expected to exhibit extremely different motifs. Therefore, we removed these problematic UCEs. We then used the Python 3 package Fastaq (https://github.com/sanger-pathogens/Fastaq) to create individual UCE alignments with the selected samples. Within each alignment, individual UCE sequences varied widely in length (from ~100 to >6000 bp). Therefore, to limit the amount of missing data, we used trimAL (Capella-Gutiérrez *et al.* 2009) to remove columns with >30% of missing data and excluded all UCEs that did not include ≥132 of the 134 taxa in the dataset. The final dataset consisted of 2360 UCEs and up to 3 535 525 bases of DNA per sample.

Legacy sequence assembly from NGS samples

We used read-mapping in Geneious v.8.1.9 (Biomatters Limited) to assemble mitochondrial genomes (mitogenomes) and legacy markers. We used a set of reference mitogenomes and legacy gene sequences spanning Accipitriformes from GenBank (AF380305, AP010797, AY463690, DQ780884, JN191388, KF682364, KF961184, KX893247, LC541458, MG930481, MK043028, MK860035, and OK662584), set the sensitivity to allow no more than 10% of bases to be mismatches, and ran five iterations of the read-mapping function. During this process, virtually all the legacy markers assembled to completion but, in a few instances, small portions of the mitogenome (excluding the control region) were not assembled. For these samples, we repeated the read-mapping step with the assembled portion of the incomplete gene as the reference, to ensure that no viable data were missed. After the assembly was complete, we annotated the genomes by first creating consensus sequences, then using the 'apply annotation' function, with the source being the same reference mitogenome used for the assembly. Finally, we aligned our genome and the reference genome and checked the annotation by eye. Owing to genome rearrangements and difficulty aligning the control regions, we did not attempt to analyse the mitogenome as a whole. Instead, we extracted each gene and ribosomal RNA, placed them in a file combining all samples, and aligned them using MAFFT.

As expected, coverage was extremely variable in the assembled legacy sequences, especially when comparing nuclear with mitochondrial markers. At the low end, in a few samples, total gene coverage of legacy nuclear markers was <1×. However, these genes were primarily composed of missing data, and non-missing gene portions were in the 3× to 5× range. Conversely, the total gene coverage of most samples was in the 15× to 20× range. Lastly, for mitochondrial genomes, coverage was fairly high, with virtually all samples having coverage >>100×. A few samples, especially those sequenced only for UCEs rather than WGS, had mitochondrial genomes that were more fragmented and represented by fewer reads. In these cases, coverage for assembled portions of the mitochondrial genome were typically in the 5× to 30× range.

Integration of legacy and NGS datasets

Before integrating the data obtained via read-mapping legacy genes to our WGS and UCE libraries, we performed several quality control steps. Initially, we updated the taxonomy to match that of Clements *et al.* (2021) and, where possible, assigned individual samples to subspecies. This step was necessary because some currently recognized species in Accipitridae are evidently not monophyletic (e.g. Kunz *et al.* 2019). To assign subspecies, we extracted the collection locality and date directly from GenBank, associated publication(s), and/or museum databases using the provided voucher information. If subspecies could not be determined conclusively, we assigned the sample to species only. When available, we notated each sample in the alignment with its voucher number or other individual identification information.

Next, we added legacy markers assembled from NGS samples by using the read-mapping process (see above) and aligned individual genes using MAFFT. Then, for quality control, we applied a single model (GTR+I+G, without model testing) to estimate gene trees using IQ-TREE. This enabled questionable sequences to be identified quickly and addressed. After this initial quality control analysis, we removed all samples on extremely long branches, which probably resulted from contamination or poor sequence quality, then investigated each instance where an individual sample was not placed with other samples thought to be its closest relatives. When these errors turned out to be misidentifications, we updated the identification in our dataset. If a problematic sequence was sourced from a specimen that had been sequenced for multiple genes, based on voucher information, we examined its placement in the other gene trees, potentially to shed light on its identity, especially when no other samples of that species were available for that particular gene. If we were unable to identify the cause of the error, despite these efforts, we removed the sample from the dataset. We continued this process until no long branches remained and we were confident that all misidentifications were removed. Lastly, we excluded extremely short samples (<75 bases long).

After the quality control process was complete, we used SEAVIEW v.4 (Gouy *et al.* 2010) to concatenate the legacy data by voucher (i.e. all genes sequenced from a given individual). This produced a single alignment sourced from (potentially) >5000 individual hawks and vultures. This is likely to be an overestimate, because not all GenBank records contained voucher numbers, and we assumed that sequences came from the same individual only when specimen voucher information was stated explicitly or when samples were identified as coming from an individual with a unique code, such as a banding number. As expected in supermatrix approaches, the majority of our alignment was missing data (85.72% in the mitochondrial portion, and even more when nuclear data were included), and most samples were represented by a single gene. Nevertheless, a majority of species were represented by several samples with differing sets of sequenced genes. Therefore, when necessary, we combined samples from multiple individuals of the same species, such that each species was represented by a single (sometimes composite/chimeric) sequence that included as much data as possible for that taxon (Fig. 1).

For species represented in our NGS dataset, we preferentially used legacy data assembled from the same NGS sample, with one exception. For [*Accipiter*] *bicolor* (Vieillot, 1816), we used data obtained from a different NGS sample (LSUMZ 24224), from which we assembled fewer UCEs but more legacy markers in comparison to FMNH 260973, which was in our NGS dataset. In a few cases, the NGS sample had unsequenced regions and, when possible, we filled these areas with sequence data from GenBank samples. It is important to note that, when gene tree analysis revealed that a species was not monophyletic, we created a composite sequence from only one monophyletic lineage or clade (e.g. from a single subspecies or group of closely related subspecies, respectively). The resulting alignment (hereafter called the '237 species alignment') contained 33.59% of missing data. The Supporting Information (Table S1) lists the accession numbers of all samples in this final alignment.

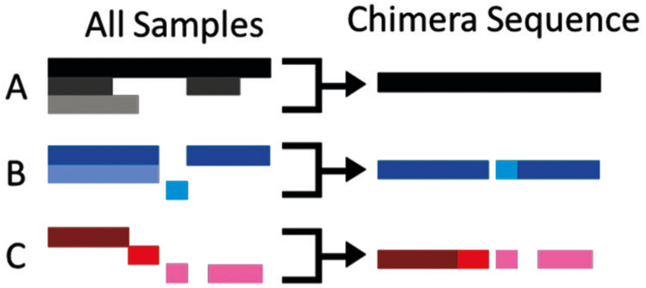

Figure 1. Schematic diagram showing three methods for assembling composite (chimeric) sequences. In each case (A–C), samples from different individuals of the same species (denoted by different shades of the same colour) were combined to create a single composite sequence containing the most complete set of sequence data possible. In scenario A, a full mitochondrial genome was available (black bar) and therefore chosen to represent the species in the final alignment (i.e. no composite was necessary). In scenario B, because the middle sample was of identical length to the corresponding fragment in the top sample, which had additional fragments available, the top sample was retained in the composite sequence; the lowest sample did not overlap with any sequenced portions of the top sample and was therefore also retained in the composite. In scenario C, the three sequenced individuals did not share any overlapping sequenced regions, hence all samples were combined to form the chimeric sequence.

Phylogenetic inference

To estimate a UCE phylogeny, we concatenated the 2360 UCE alignments into a single partitioned file using CATFASTA2PHYML (https://github.com/nylander/catfasta2phyml). We performed tree inference in IQ-TREE v.1.6 (Nguyen *et al.* 2015) using CIPRES (Miller *et al.* 2010) and assigned a GTR+G substitution model to each UCE (Abadi *et al.* 2019). We also performed 1000 ultrafast bootstraps (Hoang *et al.* 2018) to assess statistical support for each node. Hereafter, we refer to this phylogeny (provided in Supporting Information, Fig. S1) as the 'UCE backbone phylogeny'.

Although legacy data might be useful for determining relationships among recently diverged groups, in most phylogenies of Accipitriformes published to date, they have been insufficient to resolve deeper (older) relationships between clades (e.g. Lerner and Mindell 2005, Starikov and Wink 2020). Our legacy dataset was no exception. Preliminary analysis of commonly used nuclear and mitochondrial genes, using IQ-TREE v.1.6 (Nguyen *et al.* 2015) for model selection and tree inference, produced phylogenies with no statistical support for many key nodes. These topologies were also impacted by the non-random distribution of missing data. Therefore, to determine the placement of the 103 species represented only by legacy markers, relative to the well-supported 134 species UCE phylogeny, we used the UCE tree as a 'backbone' by using the –tree-constraint command in RAxML-NG v.1.1.0 (Kozlov *et al.* 2019) as implemented on CIPRES (Miller *et al.* 2010). We then selected a GTR+G model for each legacy gene and performed a (constrained) phylogenetic analysis on the 237 species alignment, which produced a phylogeny that matched the topology of the UCE backbone phylogeny, while allowing the legacy data to determine the placement of the taxa lacking NGS data.

In our first attempt, three species were unexpectedly placed in the resulting phylogeny (i.e. placed in clades not found in any gene tree). One species, *Accipiter madagascariensis* Verreaux, 1833, was represented by a miniscule amount of data (298 bp of *COI*). Likewise, *A. poliogaster* (Temminck, 1824) and *A. ovampensis* Gurney, 1875 were represented by a small fragment of *COI* (298–652 bp) and a fragment of *myc* (1074 bp). In the *COI* gene tree, these species were clustered unambiguously in a clade that also included *A. nisus* (Linnaeus, 1758), *A. rufiventris* Smith, 1830, and *A. striatus* Vieillot, 1808, whereas in the *myc* gene tree, *A. ovampensis* was included in the *A. nisus* clade and the placement of *A. poliogaster* was equivocal (although within '*Accipiter*' *s.l.*). Therefore, we reanalysed the 237 species alignment with an additional topological constraint, requiring *A. madagascariensis*, *A. ovampensis*, and *A. poliogaster* to be placed within the clade containing *A. nisus*, *A. rufiventris*, and *A. striatus*, but did not assign them to any particular position within that clade. Finally, because we used multiple topological constraints, we did not calculate support values for nodes in the resulting phylogeny.

Divergence time estimation

We performed divergence time estimation on the 237 species phylogeny with BEAST v.1.7.5, by restricting our dataset to the most commonly sequenced genes (*COI*, *ND1*, *ND2*, *ND6*, *cytb*, *RAG1*, and *myc*) and holding the topology constant. For each gene, we unlinked substitution rates and clock rates, assigned a GTR+G substitution model, and estimated divergence times with a strict clock. We calibrated the molecular clock with two fossils: (i) *Circaetus rhodopensis* (Boev, 2012), which is informative of the split between the *Circaetus* + *Dryotriorchis* clade and *Terathopius ecaudatus* (Daudin, 1800), implemented using a lognormal prior with a mean (±SD) of 7.5 ± 0.25 Mya and an offset of 7.25; and (i) *Aegypius varswaterensis* (Manegold,Pavia & Haarhoff, 2014), which is informative of the split between *Aegypius* and *Torgos*, implemented using a lognormal prior with a mean of 5.0 ± 0.25 Mya and an offset of 3.6. We also placed a normal prior on the root of the tree, with a mean of 60.34 ± 1.61 Mya (Knapp *et al.* 2019). We then performed 10 million Markov chain Monte Carlo steps, sampling every 1000 generations, and used TreeAnnotator to annotate the maximum clade credibility tree after discarding 25% of the trees as burn-in.

RESULTS

Phylogenetic hypotheses

The UCE backbone phylogeny of 134 species (Fig. 2; for detailed divergence estimates, see Supporting Information, Fig. S2) was fully supported at virtually every node (bootstrap values = 100). Only five nodes had less than perfect support, and four of those represented splits between closely related species or groups of species (two within *Buteo*, one within *Geranoaetus*, and one within *Gyps*). The fifth node with less than perfect support represented the split between two closely related 'kites', *Helicolestes hamatus* (Temminck, 1821) and *Rostrhamus sociabilis* (Vieillot, 1817). Of the 20 genera for which multiple species were sampled in the UCE backbone phylogeny, all but *Accipiter* and *Circaetus* were monophyletic. The non-monophyly of *Accipiter* was caused primarily by the embedded placement of *Circus*, *Erythrotriorchis*, and *Megatriorchis*. Additionally, *Dryotriorchus* was embedded in the genus *Circaetus*, rendering *Circaetus* not monophyletic.

The order Cathartiformes formed a clade that was sister to Accipitriformes. Within Accipitriformes, the family Sagitariidae was sister to the rest of Accipitriformes, and the family Pandionidae was sister to the rest of Accipitridae. Several large clades within Accipitridae corresponded roughly (except as noted) to the subfamilies recognized by Mindell *et al.* (2018) and Lerner and Mindell (2005). Hereafter, for convenience, the genera included in the UCE backbone phylogeny are shown in boldface.

The most basal split within Accipitridae separated the monophyletic subfamily Elaninae (composed of ***Elanus***, *Gampsonyx*, and *Chelictinia*) from the rest of the taxa. Within the sister group of Elaninae, a clade containing all genera traditionally placed in Gypaetinae (***Polyboroides***, *Gypohierax*, *Neophron*, and *Gypaetus*) and Perninae (*Eutriorchis*, ***Leptodon***, *Chondrohierax*, ***Elanoides***, ***Pernis***, ***Aviceda***, ***Hamirostra***, *Lophoictinia*, and ***Henicopernis***) formed the sister group of the remainder of Accipitridae. However, the African harrier-hawk, *Polyboroides typus* Smith, 1829, was placed as sister to the rest of the Gypaetinae + Perninae clade, which rendered Gypaetinae non-monophyletic.

Within the sister group of Elaninae + Gypaetinae + Pe rninae, a clade containing all members of the subfamilies Circaetinae (***Spilornis***, *Pithecophaga*, *Terathopius*, ***Circaetus***, and ***Dryotriorchis***) and Aegypiinae (*Sarcogyps*, *Trigonoceps*, *Torgos*, ***Aegypius***, *Necrosyrtes*, and ***Gyps***), which were reciprocally monophyletic, formed the sister group to the rest of Accipitridae. *Dryotriorchis spectabilis* (Schlegel, 1863) was embedded within the genus ***Circaetus***, rendering it paraphyletic. Within the sister group of Elaninae + Gypaetinae + Perninae + Circaetinae + Aegypiinae, a clade containing the subfamily Aquilinae (*Stephanoaetus*, ***Nisaetus***, ***Spizaetus***, *Lophotriorchis*, *Polemaetus*, ***Lophaetus***, *Ictinaetus*, ***Clanga***, ***Hieraaetus***, and ***Aquila***) formed the sister group to the rest of Accipitridae.

Within the sister group of Elaninae + Gypaetinae + Pern inae + Circaetinae + Aegypiinae + Aquilinae, a clade composed of genera traditionally placed in the subfamily Harpiinae (***Macheiramphus***, ***Harpyopsis***, *Morphnus*, and *Harpia*) was the sister group of the rest of Accipitridae. Within the sister group of Elaninae + Gypaetinae + Perninae + Circaetinae + Aegypiina e + Aquilinae + Harpiinae, the monotypic [*Accipiter*] *trivirgatus* was the sister group to the rest of Accipitridae, which was divided into three major clades. The first of these was the '*Accipiter*' complex (***Kaupifalco***, ***Micronisus***, ***Melierax***, *Urotriorchis*, ***Erythrotriorchis***, ***Megatriorchis***, ***Circus***, and ***Accipiter***), which included taxa traditionally placed in three subfamilies (Melieracini, Circinae, and Accipitrinae). The final two major clades were reciprocally monophyletic. One contained the genus ***Harpagus*** and two '*Accipiter*' species that were recently reclassified in ***Microspizias*** (i.e. [*Accipiter*] *superciliosus* and [*A.*] *collaris*; see Sangster *et al.* 2021), and the other clade corresponded to the subfamily Buteoninae, which has occasionally been divided into two tribes, Milvini (***Milvus***, ***Haliastur***, and ***Haliaeetus***) and Buteonini (***Butastur***, ***Ictinia***, ***Busarellus***, ***Rostrhamus***, ***Helicolestes***, ***Geranospiza***, ***Cryptoleucopteryx***, ***Buteogallus***, ***Morphnarchus***, *Rupornis*, ***Parabuteo***, ***Geranoaetus***, ***Pseudastur***, ***Leucopternis***, and ***Buteo***), which were reciprocally monophyletic in our phylogeny.

Divergence timing

The orders Cathartiformes and Accipitriformes were estimated to have diverged at 61.3 Mya. The common ancestor of extant taxa within Cathartidae was estimated at 16.2 Mya. The family Sagittariidae diverged from the rest of Accipitriformes at 60.9 Mya, and the family Pandionidae diverged from Accipitridae at 50.8 Mya. The clades corresponding to subfamilies within Accipitridae diverged between 25.1 and 33 Mya, except for Elaninae, which split from the rest of Accipitridae at 45.3 Mya. The majority of genus-level splits occurred ≥5 Mya, although in some cases several million years passed between the inferred origin of the genus (i.e. the node uniting it with its sister group)

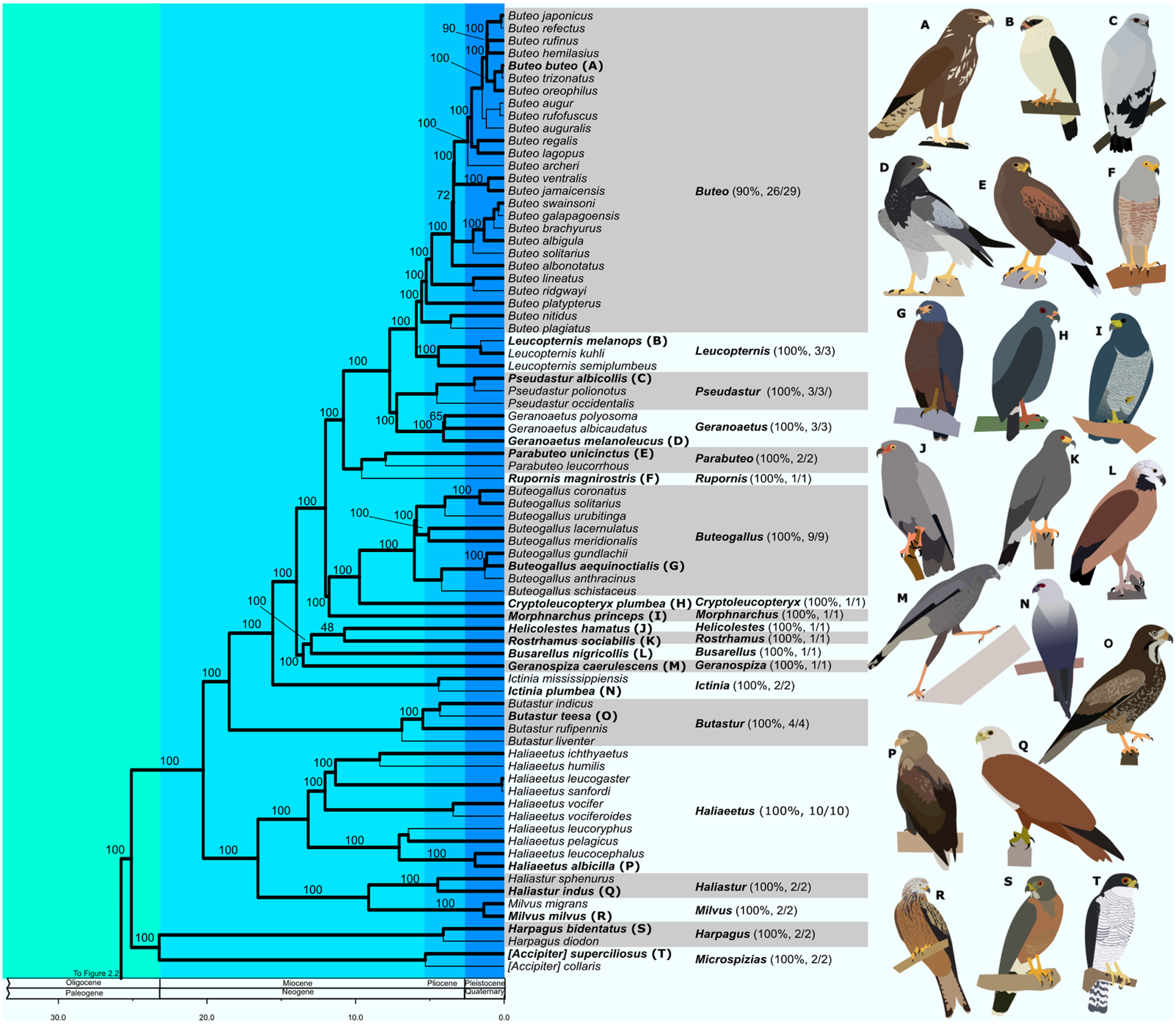

Figure 2. Phylogeny of the Accipitridae, with outgroup sequences of Pandionidae, Sagittariidae, and Cathartiformes. Thick lines show the topology of the 134 species ultraconserved element (UCE) 'backbone' phylogeny. Thin lines show the placement of taxa represented only by legacy markers (see Materials and methods). The UCE bootstrap values are shown above each node. Support values were not calculated for nodes connecting taxa represented only by legacy data. Colours represent geological epochs. Grey and white shaded areas denote monophyletic groups that are classified at the rank of genus in our taxonomic revision. For each group, the genus name that holds taxonomic priority is used, and the type species is shown in boldface. Illustrations (not to scale) of each type species are by T. A. Catanach.

and the most recent common ancestor of its extant (or recently extinct) members.

DISCUSSION

Our phylogeny was similar topologically to previously published studies of Accipitridae and included the non-monophyly of *Accipiter*. By including several enigmatic species, we removed most of the uncertainty that prevented former authors from reconciling the genus-rank nomenclature with phylogenetic data. Our dense sampling framework included 90% of extant Accipitridae species (226 of 249, following Clements *et al.* 2021), plus two extinct species, all of which were represented by at least one gene. Approximately half of these species were included in the UCE backbone phylogeny, which enabled us to test the monophyly criterion with greater confidence. These data are sufficient to recommend a conservative revision of the generic classification, which divides the non-monophyletic *Accipiter* into multiple genera that reflect evolutionary relationships. Hereafter, we discuss our results and taxonomic proposals within the context of each major clade.

Cathartiformes

Our analysis, which included UCE data from all five extant genera and legacy data from all currently recognized extant species, recovered Cathartiformes as the sister group of Accipitriformes. This finding is supported by multiple morphological synapomorphies (e.g. Griffiths 1994). Within Cathartiformes, we

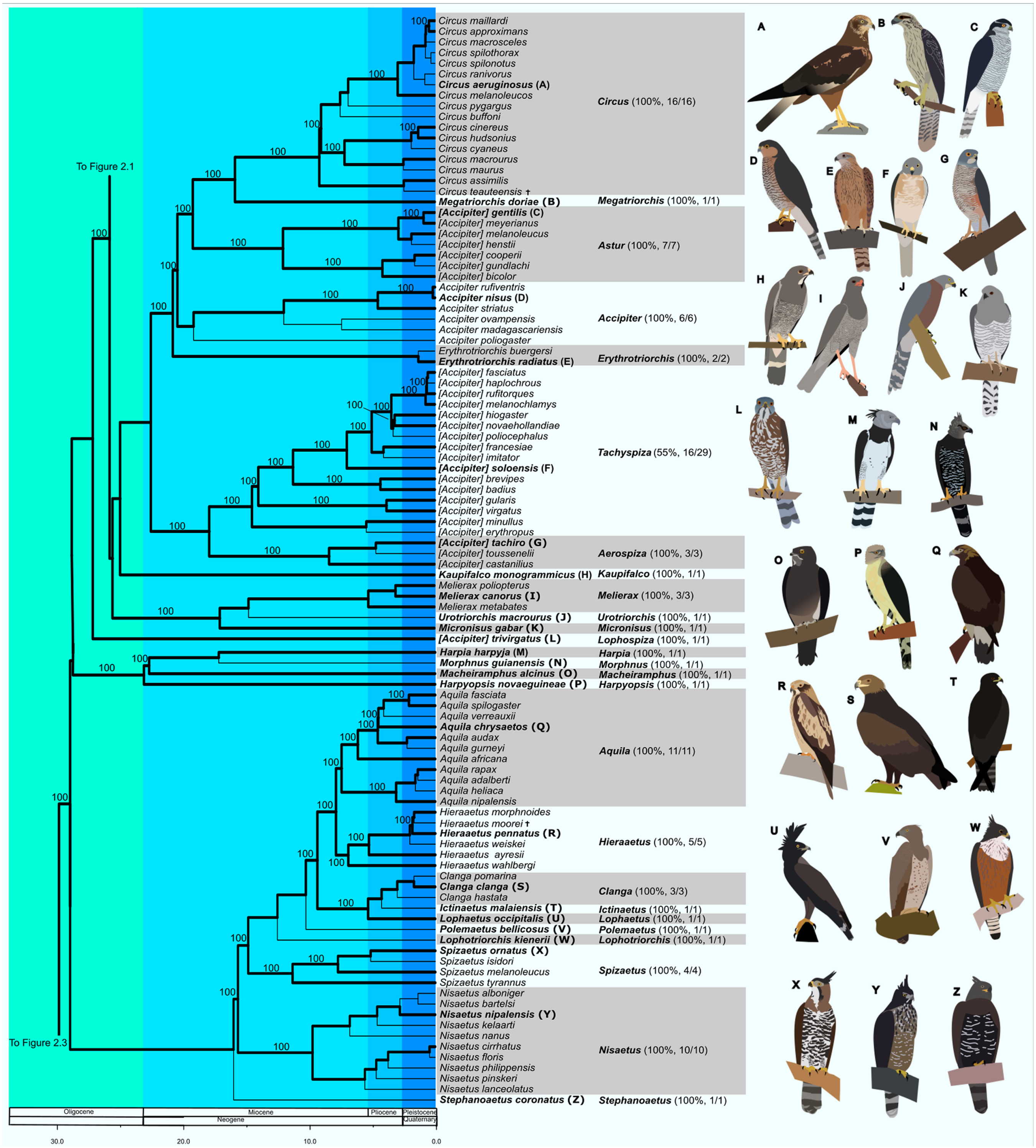

Figure 2. Continued

found that the black vulture, *Coragyps atratus* (Bechstein, 1793), was sister to *Cathartes*, and the *Coragyps* + *Cathartes* clade was sister to a clade containing the remaining New World vultures (i.e. *Gymnogyps* + *Vultur* + *Sarcoramphus*). This hypothesis was proposed previously by Johnson *et al.* (2016). We also found strong evidence (bootstrap value = 100) that *Gymnogyps* was sister to *Vultur* + *Sarcoramphus*, corroborating one of the poorly supported topologies recovered by Johnson *et al.* (2016). Our estimated divergence time for the split between the two main clades of Cathartiformes (16.2 Mya) was similar to the estimate by Johnson *et al.* (2016), but they estimated an older date for the divergence of Cathartiformes and Accipitriformes (~69 Mya), whereas our estimate (61.3 Mya) was more similar to those by Jarvis *et al.* (2014) and Knapp *et al.* (2019).

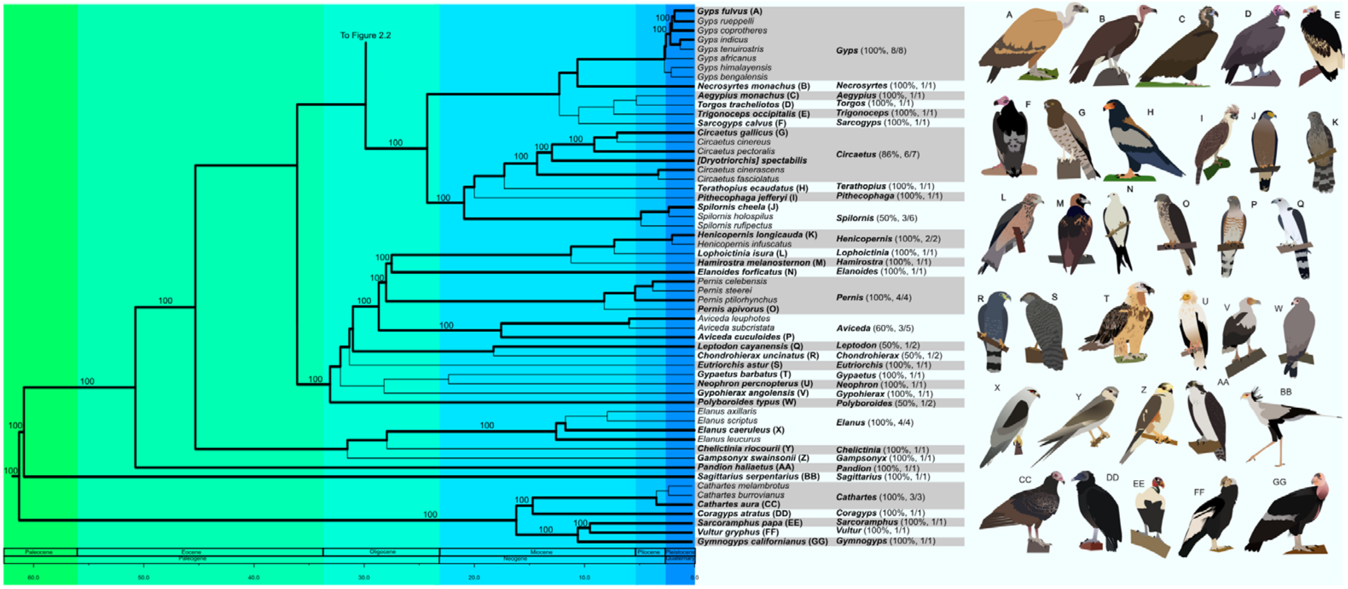

Figure 2. Continued

Sagitariidae and Pandionidae

The phylogenetic placement of these monotypic families was identical to previous studies. We estimated that Sagittariidae diverged from the Pandionidae + Accipitridae clade ~60.9 Mya, shortly after the split between Accipitriformes and Cathartiformes, and that Pandionidae diverged from Accipitridae ~50.8 Mya. These estimates were similar to those inferred by Johnson *et al.* (2016) and Knapp *et al.* (2019), but considerably older than those of Mindell *et al.* (2018) (~45 and ~38 Mya, respectively) and Prum *et al.* (2015) (~40 and ~28 Mya, respectively). These discrepancies probably resulted from different calibration methods. In our study, following Johnson *et al.* (2016) and Knapp *et al.* (2019), we placed a prior on the split between Cathartiformes and Accipitriformes, whereas Mindell *et al.* (2018) and Prum *et al.* (2015) did not. Johnson *et al.* (2016) also used several fossil calibrations to inform the divergence estimates. Interestingly, although we used different priors and fossils from those used by Johnson *et al.* (2016), we arrived at nearly identical divergence estimates for these two splits.

Elaninae

Within the Elaninae, the monotypic scissor-tailed kite, *Chelictinia riocourii* (Temminck, 1821), was sister to the monophyletic genus *Elanus*, which is composed of four species; and the pearl kite, *Gampsonyx swainsonii* Vigors, 1825, was sister to the *Chelictinia* + *Elanus* clade. An identical arrangement was proposed by Starikov and Wink (2020), based on analysis of one nuclear and two mitochondrial genes, although they lacked data from the letter-winged kite, *Elanus scriptus* Gould, 1842. Our results were also similar to those of Mindell *et al.* (2018), who lacked data from *Chelictinia riocourii* and the black-shouldered kite, *Elanus axillaris* (Latham, 1802). Divergence estimates published by these authors differed from each other and our own. Our estimate for the divergence of Elaninae from the rest of Accipitridae (45.3 Mya) was roughly twice as old as that by Starikov and Wink (2020), and the estimate made by Mindell *et al.* (2018) was intermediate. Conversely, our estimate for the divergence of *Elanus* and *Chelictinia* was about twice as old as that by Mindell *et al.* (2018), whereas Starikov and Wink (2020) provided an intermediate estimate. These discrepancies are not surprising, given that each study used different calibration methods.

Gypaetinae, Perninae, and Polyboroidinae

Within the clade containing most species typically placed in the subfamilies Gypaetinae, Perninae, and Polyboroidinae (e.g. Brown and Amadon 1968, Lerner and Mindell 2005), we found that the African harrier-hawk (*Polyboroides typus*) was sister to a clade containing the rest of the species. This relationship was recovered by Lerner and Mindell (2005) using three legacy markers, although Mindell *et al.* (2018) later found evidence that *P. typus* was sister to the palm-nut vulture (*Gypohierax angolensis*), supporting a monophyletic Gypaetinae (i.e. *Polyboroides* + *Gypohierax* + *Neophron* + *Gypaetus*). Our results support a monophyletic Gypaetinae only if *Polyboroides* is excluded, although we think additional sampling is needed to be confident about this result. Three members of the 'true' Gypaetinae were represented in our analysis by six or more legacy genes, but we lacked UCE data for this group and therefore hesitate to recognize a monotypic subfamily for *P. typus* (Polyboroidinae) at this time, as some authors have done (e.g. Brown and Amadon 1968). Nevertheless, we acknowledge that these three monotypic genera are highly divergent from each other, both morphologically and ecologically (e.g. van Lawick-Goodall and van Lawick 1966, Stoyanova *et al.* 2010). Within the 'Gypaetinae' clade (i.e. minus *Polyboroides*), we recovered a sister relationship between the bearded vulture, *Gypaetus barbatus* (Linnaeus, 1758), and Egyptian vulture, *Neophron percnopterus* (Linnaeus, 1758), and found that this clade was sister to the palm-nut vulture (*G. angolensis*).

We found no support for the inclusion of the Madagascar serpent-eagle (*Eutriorchis astur*) in the Circaetinae (*contra* Brown and Amadon 1968) or in the Gypaetinae (*contra* Lerner and Mindell 2005), nor nested within the Perninae, as sister to a clade containing the grey-headed kite, *Leptodon cayanensis*(Latham, 1790), and hook-billed kite, *Chondrohierax uncinatus* (Temminck, 1822), as proposed by Mindell *et al.* (2018). Instead, we recovered *E. astur* as the sister group of a monophyletic Perninae containing the genera *Henicopernis*, *Lophoictinia*, *Hamirostra*, *Elanoides*, *Pernis*, *Aviceda*, *Leptodon*, and *Chondrohierax*. Because *E. astur* was represented only by legacy data, we were unable to resolve its placement conclusively. Within the remaining clade of Perninae (i.e. sister to *E. astur* in our phylogeny), we found similar (but not identical) relationships among species to Lerner and Mindell (2005) and Mindell *et al.* (2018), albeit with denser taxon sampling. One notable difference was our placement of the swallow-tailed kite, *Elanoides forficatus* (Linnaeus, 1758), as sister to a clade containing *Hamirostra*, *Lophoictinia*, and *Henicopernis*, whereas Mindell *et al.* (2018) found *E. forficatus* to be sister to the rest of Perninae, and Lerner and Mindell (2005) did not include *Henicopernis*. Furthermore, we found that all three sampled members of *Aviceda* formed a clade, including the Pacific baza, *Aviceda subcristata* (Gould, 1838), and African cuckoo-hawk, *A. cuculoides* Swainson, 1837 (i.e. the genus *Aviceda* was monophyletic), whereas Mindell *et al.* (2018) placed *A. subcristata* as sister to the *Henicopernis* + *Lophoictinia* + *Hamirostra* clade, and Lerner and Mindell (2005) did not include any *Aviceda* samples in their analysis. This situation highlights the risk of relying on a sparsely populated supermatrix, which might produce erroneous topologies. Notably, in the dataset used by Mindell *et al.* (2018), there was no gene overlap between the two included *Aviceda* species. Our approach of mining legacy markers from NGS data allowed us to fill in these gaps, resulting in a phylogeny that confidently placed *A. cuculoides* within this clade, although it was represented only by legacy data.

Circaetinae

Within a clade containing most of the genera formerly placed in the subfamily Circaetinae (excluding *Eutriorchis*, *contra* Lerner and Mindell 2005), samples from three species in the genus *Spilornis*, which is composed primarily of Southeast Asian island endemics, formed a clade that was sister to a clade containing samples from the genera *Pithecophaga*, *Terathopius*, *Circaetus*, and *Dryotriorchis*. A sample of the Congo serpent eagle (*Dryotriorchis spectabilis*), which had been classified in *Circaetus* before the work by Mindell *et al.* (2018), was nested within a clade of *Circaetus* samples. A sample of the Bateleur eagle (*Terathopius ecaudatus*) was sister to *Circaetus* (*s.l.*, including [*Dryotriorchis*] *spectabilis*), and a sample of the Philippine eagle, *Pithecophaga jefferyi* Ogilvie-Grant, 1896, was sister to the *Circaetus* + *Terathopius* clade. These results agreed with previous phylogenies in the placement of *Pithecophaga* as sister to a clade containing *Terathopius* and *Circaetus* (Lerner and Mindell 2005, Mindell *et al.* 2018), but not with respect to the arrangement of the other species. Lerner and Mindell (2005) did not sample [*D.*] *spectabilis*, whereas Mindell *et al.* (2018) found that it was sister to the *Terathopius* + *Circaetus* clade. Our dataset included UCE data from [*D.*] *spectabilis* and several *Circaetus* species, including data from both clades created by the inclusion of [*D.*] *spectabilis*. Therefore, we think it is appropriate to restore [*D.*] *spectabilis* to *Circaetus*, according to tradition. Our divergence estimate for the crown age of Circaetinae was 20.9 Mya, which is substantially older than the date of ~14 Mya estimated by Mindell *et al.* (2018). We used the same fossil calibration as Mindell *et al.* (2018) for the split between *Circaetus* + *Terathopius*, but our tree topologies were in conflict for this node.

Aegypiinae

A clade containing the six genera traditionally placed in the subfamily Aegypiinae (*Trigonoceps*, *Gyps*, *Necrosyrtes*, *Aegypius*, *Torgos*, and *Sarcogyps*) contained two subclades, one containing the (reciprocally monophyletic) sister genera *Gyps* and *Necrosyrtes* and the other containing the genera *Aegypius*, *Torgos*, *Trigonoceps*, and *Sarcogyps*, arranged in a nested pattern. This topology agreed with the studies by Arshad *et al.* (2009) and Mindell *et al.* (2018), which is unsurprising because in our phylogeny many genera were primarily represented by legacy data generated by Arshad *et al.* (2009) and used by Mindell *et al.* (2018). Notwithstanding, our estimated divergence times were different from those of Mindell *et al.* (2018); for example, we estimated the split between the two main clades of Aegypiinae at 12.3 Mya (vs. 8 Mya) and the split between *Gyps* and *Necrosyrtes* at 10.6 Mya (vs. 6 Mya). Lastly, we estimated that the most recent common ancestor of *Gyps* occurred at 2.7 Mya (vs. 1.5 Mya; Mindell *et al.* 2018). Arshad *et al.* (2009), who performed multiple divergence estimates using different molecular clock calibrations, arrived at an estimate between 3.7 and 1.1 Mya.

Aquilinae

We recovered a clade containing 10 lineages corresponding to genera traditionally classified in the subfamily Aquilinae {*Stephanoaetus*, *Nisaetus*, *Lophotriorchis*, *Polemaetus*, *Spizaetus* [including *Spizaetus isidori* (Des Murs, 1845), formerly in the monotypic genus *Oroaetus*; see Haring *et al.* 2007], *Ictinaetus*, *Lophaetus*, *Clanga*, *Aquila* [including *Aquila africanus* (Cassin, 1865), formerly in *Spizaetus*; see, Haring *et al.* 2007], and *Hieraaetus*}, although generic relationships were different in our phylogeny compared with former studies.

Represented only by legacy data, our phylogeny placed the sub-Saharan species the crowned eagle, *Stephanoaetus coronatus* (Linnaeus, 1766), as sister to the rest of Aquilinae. Previously published phylogenies have been inconclusive about the placement of this taxon. Helbig *et al.* (2005) found it to be sister to *Nisaetus* (Asian hawk-eagles), and this clade was sister to the rest of Aquilinae; Haring *et al.* (2007) found *S. coronatus* to be sister to the rest of Aquilinae, excluding the long-crested eagle, *Lophaetus occipitalis* (Daudin, 1800); Lerner *et al.* (2017) were unable to determine the placement of *S. coronatus* consistently; and Mindell *et al.* (2018) found *S. coronatus* to be sister to the rest of Aquilinae (including *Lophaetus occipitalis*). The phylogenetic position of *S. coronatus* remains unresolved because we lacked UCE data.

In our analysis, the Neotropical genus *Spizaetus* was sister to a clade containing all Aquilinae taxa except *Stephanoaetus coronatus* and *Nisaetus*, corroborating several previous studies (Helbig *et al.* 2005, Lerner *et al.* 2017, Mindell *et al.* 2018) but differing from the study by Knapp *et al.* (2019), who relied solely on mitochondrial DNA and recovered *Spizaetus* as sister to *Nisaetus*.

In our 134 species UCE backbone phylogeny, which included samples from species representing both major clades of *Aquila* and several *Hieraaetus* species, the reciprocal monophyly of *Aquila* and *Hieraaetus* was fully supported (bootstrap value = 100), similar to the study by Helbig *et al.* (2005). This differed from the work of Haring *et al.* (2007), Lerner *et al.* (2017), and Mindell *et al.* (2018), who found that *Aquila* was not monophyletic with respect to *Hieraaetus*. Notably, several legacy markers, particularly from the mitochondrial genome, produced topologies that conflicted with the one generated from UCE data, pointing to possible mito-nuclear discord. This could explain why existing Aquilinae phylogenies are in conflict. More sequence data are needed to refine our understanding of the relationships within this clade. It is difficult to compare our estimates of divergence timing with former studies using different topologies. Our estimate for the common ancestor of modern Aquilinae (16 Mya) was similar to that by Knapp *et al.* (2019; ~17 Mya), but much older than the estimate by Mindell *et al.* (2018; ~10 Mya).

Harpiinae

The four genera traditionally placed in the subfamily Harpiinae (*Harpia*, *Macheiramphus*, *Morphnus*, and *Harpyopsis*) formed a clade, but the branching order differed from the phylogenies of Griffiths *et al.* (2007) and Mindell *et al.* (2018). We found *Harpyopsis* to be the earliest diverging taxon, followed by *Macheiramphus*. However, like those studies, we recovered *Morphnus* and *Harpia* as sister species. Additionally, the placement of Harpiinae in our phylogeny, with respect to its sister group, differed from the studies by Griffiths *et al.* (2007) and Mindell *et al.* (2018). We found this clade to be sister to the Buteoninae + Accipitrinae clade, whereas former studies placed it as sister to Aquilinae (Mindell *et al.* 2018) or a clade containing Aquilinae + Buteoninae + Accipitrinae *s.l.* (Lerner *et al.* 2017). In our UCE backbone phylogeny, we found full support (bootstrap value = 100) for the placement of the bat hawk, *Macheiramphus alcinus* Bonaparte, 1850, in the Harpiinae, a relationship previously suggested by several authors based on analysis of a single nuclear gene (*RAG1*), but with no statistical support (Griffiths *et al.* 2007, Barrowclough *et al.* 2014, Mindell *et al.* 2018). Our divergence estimates for the split between *Harpyopsis* and the rest of Harpiinae, and between the crested eagle, *Morphnus guianensis* (Daudin, 1800) and Harpy eagle, *Harpia harpyja* (Linnaeus, 1758), at 23.1 and 17.2 Mya, respectively, were older than the estimates of ~15 and ~11 Mya, respectively, made by Mindell *et al.* (2018).

Accipitrinae, Circinae, and Melieracini

In our 237 species phylogeny, we recovered a clade containing most taxa that were placed within these subfamilies by Lerner and Mindell (2005). In particular, the subfamily Accipitrinae, which included taxa in the genera *Accipiter*, *Erythrotriorchis*, *Megatriorchis*, and *Microspizias*, was rendered polyphyletic by the embedded placement of *Circus* (subfamily Circinae), and several species currently placed within *Accipiter* were not recovered as part of this larger clade. For example, our analysis placed the crested goshawk, *Accipiter trivirgatus* (Temminck, 1824), as sister to a large clade containing the Accipitrinae (*s.l.*) and Buteoninae (bootstrap value = 100). This relationship was also recovered, without statistical support, by Mindell *et al.* (2018). Therefore, we join Sangster *et al.* (2021) in applying the generic name *Lophospiza* to [*A.*] *trivirgatus* and the Sulawesi goshawk, [*A.*] *griseiceps* (Kaup, 1848), which lacks molecular data but is thought to be closely related based on morphology (Mayr 1949, Wattel 1973). We also recommend recognizing these two species in their own subfamily (Lophospizinae), which we formally describe below in the 'Taxonomic Implications' section.

We recovered a sister relationship between the genera *Harpagus* and *Microspizias*, which was erected by Sangster *et al.* (2021) to accommodate the phylogenetic placement of [*Accipiter*] *superciliosus* and [*A.*] *collaris*. Mindell *et al.* (2018) found a similar relationship, but placed the lizard buzzard, *Kaupifalco monogrammicus* (Temminck, 1824), within this group. Like Oatley *et al.* (2015), we found the *Microspizias* + *Harpagus* clade to be sister to Buteoninae, whereas Mindell *et al.* (2018) found it to be sister to a clade containing Buteoninae and the rest of Accipitrinae (*s.l.*). Based on these results, we recognize the genera *Microspizias* and *Harpagus* as members of the subfamily Harpaginae.

Within the clade containing the genera *Melierax*, *Micronisus*, and *Urotriorchis* (all monophyletic), which we classify in the subfamily Melieracini, we found that the Gabar goshawk, *Micronisus gabar* (Daudin, 1800), was sister to a clade containing *Melierax* + *Urotriorchis*, confirming a relationship suggested by Mindell *et al.* (2018). However, Mindell *et al.* (2018) inferred Melieracini to be sister to a clade containing Accipitrinae + Ci rcinae + Buteoninae, whereas we found it to be sister only to Accipitrinae + Circinae, an arrangement also proposed by Lerner *et al.* (2008).

In our analysis, *Kaupifalco monogrammicus* was recovered (bootstrap value = 100) as sister to a clade containing the remainder of '*Accipiter*' (i.e. excluding [*A.*] *trivirgatus* and [*A.*] *griseiceps*, now in *Lophospiza*, and [*A.*] *superciliosus* and [*A.*] *collaris*, now in *Microspizias*) + *Erythrotriorchis* + *Circus* + *Mega triorchis*. This placement conflicted with Griffiths *et al.* (2007) and Mindell *et al.* (2018), who placed *K. monogrammicus* outside the Accipitrinae (*s.l.*) + Buteoninae clade, and with Lerner *et al.* (2008), who placed it as sister to Melieracini. Our result was based on UCE data, whereas these former studies used Sanger datasets and found low statistical support for the placement of *K. monogrammicus*.

Even after the removal of the species now placed in *Lophospiza* or *Microspizias*, the remaining members of *Accipiter* (*s.s.*) still do not form a monophyletic group because *Circus*, *Erythrotriorchis*, and *Megatriorchis* are embedded within the '*Accipiter*' clade. To resolve this issue, we could either (i) synonymize *Circus*, *Erythrotriorchis*, and *Megatriorchis* with *Accipiter*, which would result in the fewest nomenclatural changes; or (ii) split *Accipiter* into four genera while retaining *Circus*, *Kaupifalco*, *Erythrotriorchis*, and *Megatriorchis*. In our opinion, the distinct morphological and ecological characteristics of *Circus* necessitate the retention of this genus, despite its nested position within '*Accipiter*'. Additionally, each of these lineages diverged between 15 and 25 Mya, a similar time scale to, or even older than, clades currently treated as genera in other subfamilies. Therefore, we opt for the second approach and propose splitting the remnants of *Accipiter* into multiple genera. This will bring *Accipiter* (*s.s.*), which in the work of Clements *et al.* (2021) contained 47 species and was the 11th most species-rich genus in the class Aves, more in line with levels of species-level diversity exhibited by other Accipitridae genera. We provide details about these suggested nomenclatural changes in the following paragraphs.

Within the sister group of *Kaupifalco*, we recovered a clade of '*Accipiter*' species that was sister to a large clade containing the remainder of '*Accipiter*' + *Megatriorchis* + *Circus*. This '*Accipiter*' clade was itself composed of two subclades, which we recognize as sister genera, applying the oldest available generic names for each. One subclade, restricted to sub-Saharan Africa, contained [*Accipiter*] *tachiro* (Daudin, 1800), type species of the genus *Aerospiza* Roberts, 1922, in which we place the following species (with new combinations): *Aerospiza tachiro*, *Aerospiza castanilius* (Bonaparte, 1853) comb. nov., and *Aerospiza toussenelii* (Verreaux, Verreaux & Des Murs, 1855) comb. nov. The genus *Aerospiza* was erected by Roberts (1922) to include *A. tachiro* and other medium-sized '*Accipiter*' species in Africa, based on the presence of five emarginate primaries, that the fifth primary is longest, that primary 10 is shorter than the secondaries, and that the tail is three-quarters of the length of the wing. Wattel (1973) also noted that these species have a long tarsometatarsus and bill and a short middle toe and hallux, relative to other '*Accipiter*' species.

The other subclade of '*Accipiter*' species, which formed part of the sister group of '*Accipiter*' + *Megatriorchis* + *Circus*, included [*Accipiter*] *soloensis* (Horsfield, 1821), type species of the genus *Tachyspiza* Kaup, 1844, which we recognize on the basis of priority, and 26 other species formerly placed in *Accipiter*. Kaup (1844) described two genera, *Tachyspiza* and *Leucospiza* {type species = [*Accipiter*] *novaehollandiae* (Gmelin, J.F., 1788); see Sangster *et al.* 2021: 424}, of which the type species were placed within this species-rich clade. Here, acting as first reviser, we elect to use the name *Tachyspiza*, which is more broadly descriptive of this group of species than *Leucospiza* (i.e. very few members have substantial amounts of white plumage). The genus *Tachyspiza*, as recognized here, is morphologically variable, although members tend to have relatively short toes and talons, especially when compared with *Accipiter* (*s.s.*). These two clades (*Aerospiza* and *Tachyspiza*, as denoted here) have been recovered in several previous studies, although the make-up and topology of *Tachyspiza* has varied among studies (Breman *et al.* 2013, Oatley *et al.* 2015, Mindell *et al.* 2018). Our 237 species phylogeny included all three members of *Aerospiza* (two represented by UCEs) and 16 of 27 species now placed in *Tachyspiza* (12 represented by UCEs). We estimated that the common ancestor of *Aerospiza* and *Tachyspiza* diverged at 17.9 Mya, whereas Mindell *et al.* (2018) gave an estimate of ~10 Mya.

Next, within the sister group of *Erythrotriorchis*, we recovered a clade that included *Accipiter nisus*, type species of *Accipiter*, and several other small, primarily bird-catching species traditionally placed in *Accipiter*. Hereafter, we restrict the generic name *Accipiter* to this clade, of which all six species were included in our 237 species phylogeny (three represented by UCE data). Our topology of *Accipiter* (*s.s.*) generally matched that of Mindell *et al.* (2018), although we found that *Accipiter poliogaster* was a member of this clade rather than sister to *Megatriorchis doriae* Salvadori & D'Albertis, 1876. Although this finding is not supported by morphology (Wattel 1973), we tentatively place [*A.*] *poliogaster* in *Accipiter* until additional data are available. Likewise, our analysis placed *A. madagascariensis* and *A. ovampensis*, which were represented only by legacy data, within the *Accipiter* (*s.s.*) clade, unlike Breman *et al.* (2013), who found them to be sister to a clade containing [*Accipiter*] *gentilis* (without statistical support). In this case, our phylogenetic placement of *A. madagascariensis* and *A. ovampensis* is also supported by morphology, because these two species share the primary characters of *Accipiter* (*s.s.*), which are the long, thin tarsometatarsi and toes, relatively small bills and halluces, and small body size.

Within the sister group of *Accipiter* (*s.s.*), we recovered a clade of '*Accipiter*' species that was sister to *Megatriorchis* + *Circus*. This topology matched those of Breman *et al.* (2013) and Mindell *et al.* (2018), but had more complete species sampling (seven species, five represented by UCEs). For this clade, we apply the generic name *Astur* Lacépède, 1799 (type = *Astur gentilis*; see Sangster *et al.* 2021: 424) on the basis of priority. As defined, species in *Astur* are characterized morphologically by their relatively large bills and long halluces. Syringeal characters formerly assumed to be synapomorphic to a clade containing the northern goshawk (*Astur gentilis*) and sharp-shinned hawk (*Accipiter striatus*) are now homoplastic (Griffiths 1994: 794). Within *Astur*, we found two sister clades. The first clade, which contained *Astur gentilis* and its relatives, has a worldwide distribution; the second clade, which contained *Astur cooperii* and relatives, is restricted to the Americas. Relative to the '*cooperii* clade', species in the '*gentilis* clade' are generally distinguished by their larger body size, shorter tarsometatarsi, and shorter middle toes. Although these two clades are genetically and morphologically distinct, we prefer to classify them in one genus because the age of the split (12 Mya) is considerably younger than the other genus-level splits in the '*Accipiter*' complex and younger than most genus-level splits in the family Accipitridae. Should additional research support treatment of these clades in different genera, the name *Cooperastur* Bonaparte, 1854 is available for the clade containing *Astur cooperii* (see Sangster *et al.* 2021: 424).

We found support (bootstrap value = 100) for a monophyletic clade consisting of all samples in the genus *Circus* deLacépède, 1799, with comprehensive sampling of extant species and one extinct species. All *Circus* species are associated with open grasslands and/or wetlands and are united morphologically by the presence of a facial disc and, possibly, by cranial asymmetry (Pecsics *et al.* 2021). Corroborating Knapp *et al.* (2019), our data indicate that the extinct Eyles's harrier, *C. teauteensis* Forbes, 1892, known only from New Zealand, was the sister of the spotted harrier, *C. assimilis* Jardine & Selby, 1828, which occurs in Australia and some islands. In general, our topology agreed with previous studies (Oatley *et al.* 2015, Mindell *et al.* 2018, Knapp *et al.* 2019), except for the placement of *C. assimilis* (and therefore *C. teauteensis*), which we recovered as sister to the rest of *Circus*, rather than sister to one of two main clades within *Circus*. We attribute this difference to more comprehensive sampling of genetic loci in our study. Our estimates for the divergence between *Circus* and *Megatriorchis* (15.9 Mya), and for the common ancestor of *Circus* (9.1 Mya), were slightly younger than the estimates by Knapp *et al.* (2019; ~17.5 and ~10 Mya, respectively), but older than those by Mindell *et al.* (2018; ~10 and ~5 Mya, respectively) and Oatley *et al.* (2015), who tried several different calibration methods.

Finally, we found that both *Erythrotriorchis* (two species) and *Megatriorchis* (monotypic) were embedded within the '*Accipiter*' (*s.l.*) + *Circus* clade, as early-diverging sisters to larger clades. *Erythrotriorchis* was sister to the *Accipiter* (*s.s.*) + *Astur* + *Megatriorchis* + *Circus* clade, which conflicts with the work of Mindell *et al.* (2018), who found *Erythrotriorchis* embedded within *Tachyspiza* (as recognized here; see above), and Barrowclough *et al.* (2014), who reconstructed *Erythrotriorchis* as sister to *Tachyspiza*. Both studies lacked statistical support for these relationships. We found that Doria's goshawk (*Megatriorchis doriae*) was sister to *Circus* (bootstrap value = 100), whereas Mindell *et al.* (2018) placed it as sister to *Accipiter poliogaster*. The placement of *M. doriae* by Mindell *et al.* (2018) was probably an artefact of their supermatrix approach, because these two taxa did not share any sequenced gene regions in their dataset. In contrast, Barrowclough *et al.* (2014) placed *M. doriae* as sister to *Circus* but did not include any representatives of *Astur*. As expected in studies with radically different tree topologies, divergence estimates published here and in these studies are not easily comparable. We found that the split between *Erythrotriorchis* and its sister group occurred at 20.8 Mya, whereas *M. doriae* diverged at 15.9 Mya. Conversely, Mindell *et al.* (2018) dated both splits to have occurred more recently than 3.5 Mya.

Buteoninae

Finally, a clade containing all genera traditionally placed in the subfamily Buteoninae was composed of two major subclades corresponding to the tribes Milvini (*Haliastur*, *Milvus*, and *Haliaeetus*) and Buteonini (*Buteo*, *Leucopternis*, *Geranoaetus*, *Pseudastur*, *Parabuteo*, *Rupornis*, *Cryptoleucopteryx*, *Buteogallus*, *Busarellus*, *Helocolestes*, *Rostrhamus*, *Geranospiza*, *Ictinia*, and *Butastur*). With respect to the two tribes and their constituent members, our phylogeny was in agreement with previous studies (Lerner and Mindell 2005, Amaral *et al.* 2006, 2009, Mindell *et al.* 2018). However, there were some notable differences in the reconstructed relationships within each tribe. For example, the crane hawk, *Geranospiza caerulescens* (Vieillot, 1816), was sister to a clade containing three monotypic genera (*Busarellus*, *Rostrhamus*, and *Helicolestes*) in the UCE backbone phylogeny. In other studies, *G. caerulescens* was sister to *Buteo* (Riesing *et al.* 2003); or to *Rostrhamus* (Lerner and Mindell 2005; other genera not sampled); or to a large clade containing *Busarellus*, *Leucopternis*, *Buteogallus* (*s.l.*, including two species formerly placed in *Harpyhaliaetus*), *Buteo*, and *Parabuteo* (Amaral *et al.* 2006; other genera not sampled); or to *Ictinia*, with the *Geranospiza* + *Ictinia* clade as sister to the rest of Buteonini except *Butastur* (Mindell *et al.* 2018); or embedded in a small clade with *Rostrhamus* and *Busarellus*, which was sister to all Buteonini except *Ictinia* and *Butastur* (Amaral *et al.* 2009). Notably, the genus *Helicolestes* was not sampled in any of these former studies.

The enigmatic barred hawk, *Morphnarchus princeps* (Sclater, 1865), represented by UCE data in our phylogeny, was sister to a clade containing the monotypic *Cryptoleucopteryx* (also represented by UCE data) and the species-rich *Buteogallus* (all nine species represented by legacy data, six by UCEs). This relationship was also recovered by Amaral *et al.* (2006), but with no statistical support. Conversely, Amaral *et al.* (2009) placed *M. princeps* as sister to the large clade containing *Buteo*, *Leucopternis*, *Geranoaetus*, *Pseudastur*, *Parabuteo*, and *Rupornis*, with high statistical support. Mindell *et al.* (2018) found the same relationship, but without statistical support. Lastly, the phylogenetic position of the roadside hawk, *Rupornis magnirostris* (Gmelin, 1788), has been similarly fluid and remains unresolved. We lacked UCE data for this species, but our analysis of legacy data placed it as sister to *Parabuteo*. The same arrangement was proposed by Mindell *et al.* (2018), whereas Amaral *et al.* (2009) placed it as sister to a large clade composed of *Buteo*, *Leucopternis*, *Geranoaetus*, *Pseudastur*, and *Parabuteo*; and Amaral *et al.* (2006) found *Parabuteo* to be sister to *Rupornis* + the other genera already mentioned. Therefore, there is unanimous support for the sister relationship of *Buteo* and *Leucopternis*, but the relationships among *Geranoaetus*, *Pseudastur*, and the other genera have been variable. We found that *Geranoaetus* (three species with UCEs) and *Pseudastur* (one species with UCEs) are sister genera, echoing the statistically unsupported arrangement recovered by Mindell *et al.* (2018). Resolving the relationships of genera in this portion of the phylogeny will require UCE data from *Rupornis*.

Buteoninae include several monotypic genera (*Geranospiza*, *Busarellus*, *Rostrhamus*, *Helicolestes*, *Morphnarchus*, *Cryptoleucopteryx*, and *Rupornis*) and, at this time, we support retaining all of them. Each genus is morphologically, behaviourally, vocally, and ecologically divergent from its closest relatives (del Hoyo *et al.* 1994, Amaral *et al.* 2009). Furthermore, divergence estimates for the nodes separating these genera (9.6–13.5 Mya) are older than most generic splits within the Buteoninae (e.g. several pairs of sister genera diverged between 5.9 and 9.1 Mya). A notable example is provided by the sister taxa the slender-billed kite (*Helicolestes hamatus*) and the snail kite (*Rostrhamus sociabilis*), which are morphologically and ecologically similar, with diets composed almost exclusively of snails. Whether these genera should be retained or lumped under the elder name, *Rostrhamus* Lesson, 1830, has been a perpetual debate among modern systematists. Recent evaluations by the North and South American Checklist Committees have retained them as monotypic genera (Banks *et al.* 2008: NACC proposal 2007-C-2; Remsen *et al.* 2023: SACC proposal 201). Notably, several committee members indicated that they would continue to support the two-genus treatment even if *Helicolestes* and *Rostrhamus* were found to be sister species, unless there was minimal genetic differentiation. Here, with UCE data from both taxa and their closest relatives (i.e. *Busarellus* and *Geranospiza*), we found strong evidence that *Helicolestes* and *Rostrhamus* are sister lineages. Nevertheless, our analysis suggests that they diverged ~10.8 Mya, which is older than some other genus-level splits in Buteoninae (see above). Therefore, although *H. hamatus* and *R. sociabilis* share some morphological and ecological characteristics, the preponderance of evidence supports the retention of two monotypic genera.

TAXONOMIC IMPLICATIONS

We recognize *Lophospiza trivirgatus*, which occupies a long branch that is sister to the diverse Buteoninae + Accipitrinae clade, in a monotypic subfamily (described below). We also advocate expanding the subfamily Accipitrinae to include the genera *Kaupifalco*, *Melierax*, *Urotriorchis*, and *Micronisus*, and we recognize three new tribes to accommodate the following clades: (i) *Melierax* + *Micronisus* + *Urotriorchis*; (ii) *Kaupifalco monogrammicus*; and (iii) *Tachyspiza* + *Aerospiza*. Some taxonomists might prefer to recognize the *Melierax* + *Micronisus* + *Urotriorchis* clade at subfamily level, but this seems unnecessary because that clade does not fall outside of the Buteoninae + Accipitrinae radiation (*contra* Mindell *et al.* 2018, Sangster *et al.* 2021), and the morphologies of *Micronisus*, *Melierax*, and *Urotriorchis* are not exceptionally divergent from the rest of the diverse Acciptrinae (*s.l.*, including *Circus*).

Lophospizinae, new subfamily

Type genus: *Lophospiza* Kaup, 1844.

Diagnosis: Members of Lophospizinae have a well-developed crest (although smaller in *Lophospiza griseiceps*), unlike all species of Accipitrinae and Buteoninae as here defined, a distinct black vertical line crossing a pale throat, and short tarsi and toes (Mayr 1949, Kuroda 1954). This subfamily occurs from Southern China and Taiwan, through the Indian subcontinent, to Southeast Asia including Indonesia.

Included taxa: Crested goshawk, *Lophospiza trivirgatus* (Temminck, 1824), and Sulawesi goshawk, *Lophospiza griseiceps* (Kaup, 1848).

Melieracini, new tribe

Type genus: *Melierax* Gray, 1840.

Diagnosis: Melieracini are restricted to Africa and include species morphologically similar to *Accipiter*, with a well-defined bib contrasting with well-defined barring on the chest and abdomen. The tribe is most similar to *Kaupifalco* but not as stocky, with longer legs, and lacking the pale throat with a thick, well-defined dark vertical line.

Included taxa: *Micronisus gabar* (Daudin, 1800), *Urotriorchis macrourus* (Hartlaub, 1855), *Melierax poliopterus* Cabanis, 1868, *Melierax canorus* (Thunberg, 1799), and *Melierax metabates* Heuglin, 1861.

Kaupifalcini, new tribe

Type genus: *Kaupifalco* Bonaparte, 1854.

Diagnosis: Kaupifalcini are restricted to sub-Saharan Africa and contain a single species identified by its pale throat with a thick, well-defined dark vertical line. It is most similar to *Micronisus gabar* but separated by the throat stripe, stockier build, and presence of a single white bar on a solid black tail.

Included taxa: *Kaupifalco monogrammicus* (Temminck, 1824).

Aerospizini, new tribe

Type genus: *Aerospiza* Roberts, 1922.

Diagnosis: Aerospizini occur in parts of Africa, Asia, Australia, and southern Europe and are differentiated from similar taxa within this range (e.g. *Accipiter s.s.*) by their shorter and thicker toes (particularly the middle toe) and often larger size. Members of the tribe are generally smaller than sympatric members of *Astur*, which lack rufous markings in the adult plumage, whereas, most adult Aerospizini have red markings on the chest, legs, and/or neck.

Included taxa: *Aerospiza toussenelii* (Verreaux, Verreaux & des Murs, 1855), *Aerospiza tachiro* (Daudin, 1800), *Aerospiza castanilius* (Bonaparte, 1853), *Tachyspiza rufitorques* (Peale, 1849), *Tachyspiza haplochrous* (Sclater, 1859), *Tachyspiza fasciatus* (Vigors & Horsfield, 1827), *Tachyspiza melanochlamys* (Salvadori, 1876), *Tachyspiza imitator* (Hartert, 1926), *Tachyspiza novaehollandiae* (Gmelin, 1788), *Tachyspiza hiogaster* (Müller, 1841), *Tachyspiza poliocephalus* (Gray, 1858), *Tachyspiza francesiae* (Smith, 1834), *Tachyspiza soloensis* (Horsfield, 1821), *Tachyspiza badius* (Gmelin, 1788), *Tachyspiza brevipes* (Severtsov, 1850), *Tachyspiza gularis* (Temminck & Schlegel, 1845), *Tachyspiza virgatus* (Temminck, 1822), *Tachyspiza erythropus* (Hartlaub, 1855), and *Tachyspiza minullus* (Daudin, 1800).

CONCLUSION

For more than two centuries, scientists have debated the genus-level taxonomy and evolutionary relationships of genera in the diverse family Accipitridae, with little consensus. Here, we reconstructed a well-supported phylogeny with UCE data from nearly half of the extant species; then, using it as a backbone, we investigated the phylogenetic relationships of taxa for which legacy (Sanger) sequence data, but no NGS data, were available. Thus, we confidently resolved the phylogenetic relationships of 90% of extant species in Accipitridae (225 of 249) and tested the criterion of monophyly for the vast majority of genera. Our UCE sampling also included several enigmatic taxa for which few molecular data were previously available.

The non-monophyly of the diverse genus *Accipiter* has been a particularly thorny problem, unresolved for many years (e.g. Griffiths *et al.* 2007, Hugall and Stuart-Fox 2012, Oatley *et al.* 2015, Mindell *et al.* 2018). Heretofore, because of uncertainty caused by limited sampling of taxa and genetic loci, most researchers have deferred taking nomenclatural action to resolve its apparent polyphyly (but see Sangster *et al.* 2021). We contend that our combined UCE and legacy datasets are sufficient to resolve this issue, to determine generic boundaries, and to restrict genus names to monophyletic groups (clades).

We included sequence data from almost all 237 currently recognized Accipitridae species, but ~40% of species were represented only by Sanger sequence data, and in some cases from a single gene. To maximize the numbers of both taxa and markers per taxon, we adopted a supermatrix approach to combine data generated from Sanger and WGS methods. This approach results in non-random missing data, which might lead to erroneous phylogenetic inference when there is a lack of gene overlap between species. Although our use of a backbone topology inferred using UCEs might have lessened the impacts of these issues, we recommend additional WGS sequencing to help clarify the evolutionary relationships among genera, species, and subspecies in Accipitridae.

The taxa in greatest need of additional sampling include *Accipiter poliogaster*, various monotypic eagle genera, and *Rupornis* *magnirostris*. Although several species within Accipitridae are not monophyletic, for computational reasons we elected to include only a single representative of each species and limit our sampling to the taxonomic limits proposed by Clements *et al.* (2021). This decision meant that we could not test the monophyly or phylogenetic position of several species, including the American goshawk, *Astur atricapillus* (Wilson, 1812), which has recently been split from *A. gentilis*, and which Sanger datasets indicate may not be its phylogenetic sister as widely assumed (Kunz *et al.* 2019). Likewise, detailed revision of species limits within several clades currently treated as polytypic species are sorely needed (e.g. Catanach *et al.* 2021). Divergence time estimates might also be refined further (e.g. by including more fossil calibrations and by identifying datable biogeographical splits).

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

Conflict of interest: None declared.

ACKNOWLEDGEMENTS

We thank Sushma Reddy for providing UCE data from *Helicolestes hamatus* and *Kaupifalco monogrammicus*, and Jason D. Weckstein for providing UCE data from *Astur badius*, *A. bicolor*, *A. gundlachi*, *Tachyspiza gularis*, *Lophospiza trivirgatus*, *Circus assimilis*, and *C. melanoleucos*. We thank the museums and collection staff who provided samples: Academy of Natural Sciences of Drexel University (Nathan H. Rice), Biodiversity Teaching and Research Collection at Texas A&M University (Gary Voelker and Heather L. Prestridge), Burke Museum (Sharon M. Birks), Delaware Museum of Nature & Science (Jean L. Woods), Field Museum of Natural History (Ben D. Marks, John M. Bates, and Shannon J. Hackett), Louisiana State University Museum of Natural Science (Donna L. Dittmann and Steve W. Cardiff), Museum of Southwestern Biology (Christopher C. Witt and Andrew B. Johnson), Museum of Vertebrate Zoology (Jeremiah Trimble, Breda M. Zimkus, and Emily Blank), Natural History Museum of Los Angeles County (Allison J. Shultz and Kimball L. Garrett), University of Kansas Biodiversity Institute (Mark B. Robbins), Western Foundation of Vertebrate Zoology (René Corado), and Yale Peabody Museum (Kristof Zyskowski). We also thank two anonymous reviewers, Harald Fänger, and George Sangster for helpful comments.

FUNDING

Funding was provided by National Science Foundation grant DEB 2203228, awarded to T.A.C.; and Iridian Genomes grant number IRGEN_RG_2021-1345 Genomic Studies of Eukaryotic Taxa, awarded to S.P. T.A.C. was partially supported by National Science Foundation grant DEB 1855812, awarded to Jason D. Weckstein.

DATA AVAILABILITY

All raw reads generated for this project are deposited in the Sequence Read Archive hosted by National Center for Biotechnology Information. A list of all accession numbers representing sequences acquired from publicly available sources (European Nucleotide Archive, GenBank, and Barcode of Life Data) is provided in the Supporting Information (Table S1) within the Legacy_data_samples and UCE_samples_publicly_available tabs. Alignments and tree files are available through Zenodo (10.5281/zenodo.10799082)

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