REVISED EVOLUTIONARY AND TAXONOMIC SYNTHESIS FOR PARROTS (ORDER: PSITTACIFORMES) GUIDED BY PHYLOGENOMIC ANALYSIS

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CONTENTS

FRONTISPIECE. Double-eyed Fig Parrots (*Cyclopsitta diophthalma*) in Cairns, Queensland, Australia. In this work, genera in fig parrots have been revised to better reflect their phylogenetic relationships. Photo by Daniel J. Field.

ABSTRACT

Parrots (Order: Psittaciformes) are a diverse clade that is easily distinguishable from other birds. Despite the clear characters that define Psittaciformes (hooked bills, zygodactylous feet, and plumage that is often predominantly green or red), relative morphological uniformity among parrots has made taxonomic classification a fraught endeavor for over a century. Parrot systematics were propelled forward when DNA sequencing data shed insights into higher- and species-level relationships. However, despite these significant advances, major gaps in taxon sampling and uncertainty in relationships remained due to inferring phylogenetic relationships with short fragments of DNA. Recent work using genome-wide molecular markers with nearly complete parrot species-level sampling has brought clarity to many of the remaining outstanding questions on taxonomic relationships. Here, we build on this work by including four additional species to present a taxonomic revision of Psittaciformes better aligned with its evolutionary tree. We infer maximum likelihood and time-calibrated phylogenies for parrots, present accounts for 106 genera, compare how our findings relate to previous work, and highlight future areas of research. The family-group nomenclature we propose reflects deep evolutionary divergences with diagnosable synapomorphies that are commensurate across comparable ranks in psittaciform clades. We erect three new family-group names at the rank of tribe (Brotogerini Smith, Thom, and Joseph, 2024; Neophemini Schodde, Mason, Smith, Thom, and Joseph, 2024; Bolbopsittacini Smith, Thom, and Joseph, 2024). We elevate one tribe to subfamily rank for the cacatuid genus *Probosciger* and we restrict usage of the recently introduced tribe Touitini to its type genus *Touit*. At shallower taxonomic scales, recognition of more rather than fewer genera addresses issues of paraphyly or high discordance in morphological and genomic characters at those levels. We support many reinstatements of older generic names advocated in recent decades, and we further reinstate five valid, available generic names not widely used in recent literature if at all (*Licmetis*, *Gymnopsittacus*, *Clarkona*, *Suavipsitta*, *Cardeos*). We advocate the retention of *Vini* Lesson, 1833, over *Coriphilus* Wagler, 1832, based on preliminary examination showing substantially more frequent usage of the former. We redraw generic limits in some other cases (e.g., *Bolborhynchus* parrotlets and allies) and this includes recognizing fewer genera than recently proposed for the *Psittacula* sensu lato ringneck parakeets. Our revised classification of parrots addresses many longstanding taxonomic questions including those that have arisen through the acquisition of genetic data. It provides context for the temporal origins of psittaciform clades and the taxonomic and phenotypic diversification throughout their evolutionary history. We hope that it will be a benchmark guiding further taxonomic study as well as for downstream analyses in many other fields.

INTRODUCTION

> There has been little doubt about which birds are, and which birds are not, parrots.
>
> —Sibley and Ahlquist (1990)

> The overall morphological sameness which makes the order so distinct also makes further subdivision difficult."
>
> —Smith (1975)

> However, despite [their] superficial variation, [parrots] are really a very homogeneous group and [...] this presents problems to systematists.
>
> —Forshaw (1989)

These three quotes illustrate the challenge that parrots have posed to systematists since the 1750s. Any bird is easily seen to be a parrot or not based on their hooked bills, which may more accurately be described as "short, blunt bill with a down-curved upper mandible [maxilla] fitting neatly over a broad, upturned lower mandible" (Forshaw and Knight, 2010). Among less readily visible traits, which were reviewed thoroughly by Sibley and Ahlquist (1990), only parrots have feather pigments known as psittacofulvins. Krukenberg (1882) identified that red to yellow colors in parrots are due to these unique biochrome pigments that he named psittacofulvins. This sets parrots apart from other birds, which use diet-derived carotenoids to produce pigment-based red. Moreover, the green plumage of many parrots is also unique, an interaction between feather structure and pigments such as psittacofulvins (reviewed in Berg and Bennett, 2010). Recognition of the nearly 400 species of parrots, which occur on all continents except Antarctica, as comprising the Order Psittaciformes is unquestioned. Determining relationships within and among subordinal groupings of parrots and how those groupings should be ranked taxonomically remains debated and unsettled, however. Several detailed reviews of the history of parrot classification have appeared (Holyoak, 1973; Smith, 1975; Sibley and Ahlquist, 1990; Forshaw and Knight, 2010). These works laid important foundations, but they were based mostly on a key criterion of similarity. Without any kind of cladistic or indeed phylogenetic framework, synapomorphies could not be distinguished from shared ancestral plesiomorphies let alone recognized as such. Accordingly, many outstanding questions of relationships had not been resolved, or indeed could not have been resolved, until well after the advent of molecular phylogenetic techniques. Here we briefly review major trends noting that this history itself mirrors that of avian higher-level systematics generally.

Brief History of Psittaciform Systematics

Initial attempts to discern relationships within and among the parrots themselves and to other birds were rooted in gross external morphology and anatomy (extensive reviews in Smith, 1975; Sibley and Ahlquist, 1972, 1990). Interpretation of this massive body of work was, as just noted, based on similarity and difference. That continued throughout the 20th century (Holyoak, 1973) and even into the 21st (Smith, 1975; Sibley and Ahlquist, 1990, Forshaw and Knight, 2010). In hindsight, we see that the challenge in implementing this approach is the general sparsity of morphological synapomorphies that can be reliably placed in a phylogenetic framework. Consequently, signals of convergent trait evolution were often not disentangled from those informing evolutionary relationships. Two examples follow. One involves the early hypotheses based on bill morphology proposing a close relationship between parrots and diurnal raptors, all of which have similarly "hooked" bills. Study of the evolution of bill morphology in all birds, not just parrots, has been reinvigorated in recent years in the contexts of elaboration, innovation, and microevolutionary and megaevolutionary trends across the avian phylogeny generally (Cooney et al., 2017; Bright et al., 2019; Guillerme et al., 2023). Second is where the sparsity of morphological synapomorphies led to the recognition of groups now seen as non-monophyletic (e.g., Loricoloriinae; Mayr, 2008).

Systematic surveys of Psittaciformes have supported contrasting intraorder configurations ranging from 1–8 families and up to nine subfamilies (Salvadori, 1891; Reichenow, 1913; Peters, 1937; Glenny, 1957; Verheyen, 1956; Brereton, 1963). Frequently, the lories and lorikeets (Loriidae), which have a highly derived phenotype, were assigned to their own family, as were the cockatoos (Cacatuidae). The vast diversity of the remaining parrots, while often recognized as distinct subfamilies, were considered by some authors to comprise a single family, Psittacidae. Clarity with respect to higher-level relationships in Psittaciformes was not resolved until the maturation of molecular phylogenetics much later (Joseph et al., 2012). Molecular systematic studies have unambiguously resolved natural groupings, although their taxonomic ranks might be debated, and highlighted the limitations of previously assessed morphological characters for classifying major parrot groups.

In the latter part of the 20th century, other methodologies appeared. Some were very short-lived, such as behavioral studies (e.g., whether head-scratching with the bird's foot was over or under the wing; Brereton and Immelmann, 2008) and taxonomy of ectoparasitic lice living in the feathers of parrots as a potential source of information about relationships among their hosts (summarized in Forshaw, 1973; see also Johnson and Doña, 2024). Early methodologies exploring the genome, whether indirectly through gene products or directly through DNA, have had vast impact.

Indirect, biochemical methods of studying relationships commenced with egg-white protein electrophoresis wherein data were analyzed using qualitative "eyeballing" of similarity and difference on electrophoretic gels within given pH ranges. An example was Sibley and Ahlquist's (1972) survey of nonpasserine birds, which concluded that parrots and pigeons were closely related, an older hypothesis long since rejected. Next was allozyme electrophoresis, which flourished for a few years in the late 1970s and early 1980s, addressing relationships within major clades of birds (Sibley, 1974; Avise and Aquadro, 1982), and within and among clades of parrots too, affirming hypotheses based in morphology, e.g., that *Nymphicus* is a cockatoo (Adams et al., 1984), or favoring others since rejected, e.g., that *Psittacella* is part of the platycercine or broad-tailed parrot assemblage (Christidis et al., 1991). These methods were replaced by more direct assays of the genome through banding patterns of chromosomes and karyology and DNA-DNA hybridization, all of which were similarity- or distance-based methods applied broadly in systematics (Sibley and Ahlquist, 1985; Christidis, 1986, 1990; Sibley and Ahlquist, 1990; Kirsch et al., 2008; O'Connor et al., 2024). Eventually, more direct DNA sequence-based methods arose. Restriction-fragment analysis of mitochondrial DNA was first and then direct sequencing of up to several hundred base pairs of mitochondrial and nuclear DNA became available. The latter sometimes even focused on one gene such as *spindlin* to assess major divisions with parrots (de Koet and de Kloet, 2005) and the first recognition of parrots as sister to passerine birds (Hackett et al., 2008; Suh et al., 2011). These evolved into longer read methodologies and, ultimately, today's various methodologies of modern genomics, which would be used to provide far greater clarity to parrot systematics.

As reviewed in more detail in Provost et al. (2018) and Olah et al. (2021), the proliferation of molecular phylogenetic studies using mitochondrial and nuclear DNA markers over the past two decades resulted in the most comprehensive progress in understanding relationships within the Psittaciformes. Higher-level studies (Tavares et al., 2006; Wright et al., 2008; Schirtzinger et al., 2012; Rheindt et al., 2014), while less numerous, have clarified a number of outstanding questions related to clade membership and the temporal origins of parrots (e.g., Selvatti et al., 2022). Arguably more common, however, have been studies at the generic level that examined generic limits and composition, including *Amazona* (Russello and Amato, 2004; Eberhard and Bermingham, 2004; Ribas et al., 2007b; Urantówka et al., 2014a), *Aratinga* (Ribas and Miyaki, 2004), *Barnardius* (Joseph and Wilke, 2006), *Forpus* (Smith et al., 2013), *Pyrrhura* (Ribas et al., 2006), *Pionus* (Ribas et al., 2007a), *Pyrilia* (Ribas et al., 2005, Eberhard and Bermingham, 2005), *Platycercus* (Joseph et al., 2008; Shipham et al., 2015), *Psittacella* and *Pezoporus* (Joseph et al., 2011), *Prioniturus* (Schweizer et al., 2012), and *Psittacula* (Braun et al., 2019; Groombridge et al., 2004; Kundu et al., 2012; Jackson et al., 2015; Podsiadlowski et al., 2017). Notably, these included resolving the placement of extinct species such as Carolina Parakeet (Kirchman et al., 2012); Cuban Macaw (Johansson et al., 2018); and Mascarene Parakeet (Podsiadlowski et al., 2017), the last-named having been briefly sidetracked by earlier misinterpretation of data (Kundu et al., 2012). Collectively, these studies have yielded a stable backbone of major groups and resolved several contentious groups. Similarly, at shallower taxonomic scales, species-level relationships have been resolved for numerous groups and many of the papers just cited included this level of taxonomic resolution. However, a substantial number of species have remained unsampled, leaving the monophyly of some groups and thus generic limits in question. Further, the limited size and nucleotide sampling of molecular datasets has left some relationships uncertain and unstable (e.g., Androglossini). The most recent studies have taken advantage of DNA sequencing technology that allows for sampling of genome-wide markers (Shipham et al., 2019; Smith et al., 2020; Ewart et al., 2020; Huynh et al., 2023) and so provide increased accuracy in estimating evolutionary parameters and relationships.

Revising Psittaciform Systematics Using Phylogenomics

Our aim here is to review the taxonomy of the entire Order Psittaciformes, especially at the level of genus and above, and so provide a solid benchmark taxonomic foundation for downstream analyses in fields such as ecology and biogeography as well as conservation and management, given how endangered many parrots have become through illegal trade (Pires et al., 2021; Nandika et al., 2021; Tella et al., 2022, and papers therein). We build on the scalability made possible through genomic approaches, which enabled the sampling of nearly all parrot species in a single study (Smith et al., 2023) and allowed sampling of >1 million sites across the genome. We have added four additional species into analyses that were not included in Smith et al. (2023), thus filling nearly all remaining gaps in species-level sampling. The sampling included DNA from historical museum specimens of extinct and endangered taxa and of taxa now difficult to sample afresh.

We generated a time-calibrated phylogeny representing 96% of species-level diversity to inform our discussion on revising the systematics and taxonomy of Psittaciformes. We discuss each clade in the tree, the relationships within it, and how the topology differs from previous studies. The main goal of our taxonomic revision was to align the taxonomy of parrots, again emphasizing the levels of genus and above, with the comprehensive phylogenomic analysis of Smith et al. (2023). Following Joseph et al. (2020), we adopt the rationale articulated by Provost et al. (2018) to justify taxonomic changes that reflect the underlying phylogenetic signal.

Ultimately, a taxonomic classification should reflect phylogenetic pattern without necessarily putting forth an explanation of the evolutionary processes that generated those patterns. This presents a conundrum. Using some data types, such as molecular data from neutral or near-neutral loci, diagnosis of a clade and phenotypic characters may well be concordant. In contrast, nonconcordance of molecular and phenotypic markers can arise because phenotypic characters, especially morphological ones, are subject to natural and sexual selection. These distinctions are best reflected in how each of these types of data are modeled in evolutionary analyses. DNA substitutions, under neutrality, which are reflected in branch lengths, occur at the rate at which mutations occur (Bromham and Penny, 2003). In contrast, morphological evolution in comparative phylogenetic analysis is frequently modeled as a stochastic process (e.g., Brownian motion; Blomberg et al., 2020). This discrepancy can result in rapid and convergent evolution and a decoupling between morphological disparity and time. The extent of phenotypic change, therefore, is not easily predictable.

Consequently, morphological data will often be discordant with respect to phylogenetic patterns defined by neutral and nearly neutral molecular markers. This poses serious challenges for classification at various taxonomic ranks. Synapomorphies corresponding with cladogenetic events may not always be apparent. For example, consider the speciose but phenotypically coherent parrot genus *Pyrrhura*, comprising ~23 species, each of which is easily assignable to *Pyrrhura*. It is a monophyletic assemblage originating some seven million years ago (Mya). Recognition of membership of all its species in *Pyrrhura* is unquestioned, to our knowledge, owing to the relative homogeneity of its member species in morphology and plumage. In contrast, another Neotropical clade of parrots contains five monotypic and, with respect to each other, phenotypically diverse genera (*Diopsittaca*, *Ognorhynchus*, *Leptosittaca*, *Guaruba*, and *Thectocercus*). Collectively, its crown age was six Mya. Rates of evolution appear different in these two clades given the asymmetry in recognized genera. Of course, it is well accepted that morphological disparity varies among clades. Yet the disparity between these two clades highlights that the outcomes of evolution have been very different for these groups, which, in turn, impacts the comparability of taxa at the same rank. In this paper we have encountered this problem frequently.

Where external synapomorphies have not been identified, we have pursued an approach of recognizing more rather than fewer genera and tribes. The reason is that they can be anchored in and thus reflect our phylogenomic framework, which we stress includes temporal depths of nodes. Equally, though, our decisions have been informed by morphological, ecological, and behavioral dissimilarity among those groups in light of phylogenetic relationships.

We make two further points about how we have taxonomically interpreted relationships in our tree: First is that support values are often high in phylogenomic studies because there are so many characters (Minh et al., 2020a). These high support values can indicate that there is strong genome-wide support for a relationship or that a small number of genes or sites are driving a given relationship. In the latter case, the robustness of a relationship determined by nodal support may be overturned with data from different genomic regions. In our descriptions of phylogenetic relationships there is reference to ultrafast bootstraps (Minh et al., 2013; Hoang et al., 2018), which were performed to account for the large size of the phylogenomic dataset. Importantly, ultrafast bootstraps (UFBS) have a more stringent level for accepting a node as supported (≥95%), as do local posterior probabilities (LPP) for the species trees we discuss in the text.

Second is the reliance on historical DNA from museum specimens of species for which there are no modern genetic samples. Historical DNA tends to be heavily degraded and yields more missing data than modern samples. This poses challenges in accurately estimating branch lengths and relationships (Smith et al., 2020). We do not repeat the analyses of Smith et al. (2023), whose rigorous interrogation of data signals in the parrot phylogenomic alignment was a primary focus. Instead, we highlight areas where uncertainty may linger due to data quality. Data completeness is particularly relevant in interpreting topological differences between the concatenated and species tree phylogenies. Although concatenated trees can produce erroneous relationships by not accounting for gene tree discordance, summary species tree methods like the one included by Smith et al. (2023) are particularly sensitive to gene tree estimation error due to samples with lower phylogenetic signal. For simplicity, we present the findings of only the concatenated phylogenomic tree but point out major differences against the species tree when relevant. When the text refers to a species tree, we are referring to the species tree estimated using ASTRAL-III (Zhang et al., 2018) presented in Smith et al. (2023), which summarizes gene trees assuming a coalescent framework. Collectively, through these ways of interpreting phylogenomic signal and conflict, we have provided a detailed overview of the phylogenetic relationships and taxonomy of Psittaciformes.

Genus- and Family-level Taxonomy

We agree that genera "should ideally make sense to someone not familiar with the constituent species" (Ford, 2006). Conversely, genera should represent monophyletic groups, yet evolution does not always result in phenotypically coherent groups that are monophyletic and vice versa. Aside from understanding the direction and polarity of character evolution, the task of delimiting genera can become one of deciding where to draw the line or how much phenotypic diversity a genus should or should not include while still consistent with monophyly. Countering the difficulties of delimiting genera are the multiple hierarchical levels that the Linnaean system offers in family-group names. Together, genera and the levels of family-group taxonomic ranks offer mechanisms for taxonomically translating much of the evolutionary complexity that a group as diverse as Psittaciformes shows geographically, evolutionarily, genetically, and even phenotypically. Reflecting these complexities, phylogenetic and phylogenomic analyses of birds have consistently driven the recognition of more rather than fewer genera in birds. This can be seen not only in parrots (reviewed in Provost et al., 2018) but in other groups as well, such as the radiations of Neotropical thamnophilid antbirds (Isler et al., 2006, 2013) and thraupid tanagers and tanager-finches (Burns et al., 2016), the Indo-West Pacific columbid fruit-pigeons (Cibois et al., 2014) and meliphagid honeyeaters (Joseph et al., 2014; McCullough et al., 2019), and African hirundinids (de Silva et al., 2018), Afro-Asian timaliid babblers (Moyle et al., 2012) and phalacrocoracid microcormorants (Kennedy et al., 2023). To the criticism that this trend generates a high number of unfamiliar genera, we reply that the number of genera per se or indeed their familiarity have little or nothing to do either with the science underpinning a classification or the merit of a classification in reflecting that science. Clearly, such critiques are of no concern to other branches of zoology, such as entomology, that also deals with highly diverse and speciose groups. Nonetheless, a way of reducing genera while recognizing phylogenetic structure is to employ subgenera within genera. We have debated the use of subgenera extensively in preparing this paper. Earlier (Provost et al., 2018), we with a colleague refrained from subdividing some genera as a concession to maintaining familiarity (e.g., retaining four species in *Psephotellus*) or minimizing change to others (changing *Pseudeos* from monotypic to ditypic not to two monotypic genera). Here we have reconsidered many such decisions based on data now available. We have considered temporal and geographical criteria with which to recognize genera especially when the estimated divergence times are greater than ~2 million years. We now see more merit in recognizing genera rather than subgenera to reflect phylogenetic structure. The reason is that in ornithology subgenera are rarely used and where they have been used (e.g., Schodde and Mason, 1999; Shipham et al., 2015), we are aware of little or no uptake.

SPECIES-LEVEL TAXONOMY

Notably, recent years have seen many subspecies previously known from little more than a few specimens elevated to species rank. This has followed a surge in fieldwork and increased familiarity with their natural populations. It has also arisen from application of criteria such as those of Tobias et al. (2010), whose method of species delimitation has been widely criticized (e.g., Remsen, 2016; Rheindt and Ng, 2021). While subspecies suffer from empirical and philosophical limitations (Burbrink et al., 2022), our study was designed to sample recognized species with a preference for recently collected material from wild birds. Our rationale was to optimize data quality and thereby increase the resolution of phylogenetic relationships. As stated earlier, DNA sourced from historical museum specimens is often highly fragmented and more likely to be subject to gene tree estimation error. A potential consequence of our sampling design was that we did not preferentially sample the nominotypical subspecies in polytypic species. In cases where species are later found not to be monophyletic, the inferred relationships in our phylogeny may be incorrect for some species complexes (see *Forpus* as an example; Smith et al., 2013). To standardize our selection of species, which began in 2015, we used the International Ornithological Congress (IOC) World Bird List (e.g., Gill et al., 2024), which provided classification for all parrots globally. During data generation of this project, a number of new species resulting from split complexes were recognized by the IOC, and we did not make an attempt to include all these taxa. We further acknowledge that for some of these new species, there is considerable disagreement about their taxonomic rank among classification committees. Our taxon sampling, which is still far from complete for many polytypic species, does not inform some current species-level taxonomic proposals in the literature. We take the opportunity, however, to discuss recent decisions and pinpoint further work needed.

Where possible, we have cited names of genera (whether in full or by initial letter abbreviation) and species, e.g., *B. barnardi* as shorthand for *Barnardius barnardi*. When the topic under discussion is the appropriate taxonomic rank for a species-group epithet, i.e., species or subspecies, or to which genus such an epithet should be assigned, we have used only the species-group epithet.

MATERIALS AND METHODS

Sampling, Wet-lab Protocols, and Bioinformatic Processing

We used genome-wide markers known as ultraconserved elements (UCEs; Faircloth et al. 2012) from published studies and generated sequence data from four additional taxa to fill sampling gaps. Our final data matrix included 323 species across Psittaciformes from Smith et al. (2023), 58 species within the Loriini (Smith et al., 2020), *Conuropsis carolinensis* (Smith et al., 2021), sequence data from a published genome of *Amazona vittata* (Oleksyk et al., 2012) and three outgroup taxa (*Caracara cheriway*, *Calyptomena viridis*, *Icterus cucullatus*; Oliveros et al., 2019). The unsampled species include both extinct (*Nestor productus*, *Cyanoramphus ulietanus*, *C. zealandicus*, *Psittacula wardi*, *P. exsul*, *Mascarinus mascarin*, *Vini diadema*, and *Ara tricolor*) and extant (*Tanygnathus gramineus*, *Loriculus camiguinensis*, *L. flosculus*, *Pyrrhura pfrimeri*, and *Poicephalus crassus*) species. Of the four new samples, three came from historical museum specimens (*Psittacara wagleri* AMNH 111438; *Pionus menstruus* AMNH 170946; and *Psephotellus chrysopterygius* AMNH 623349) and one from a modern tissue sample (*Aratinga maculata* YPM 137433). Other extinct species are represented only in literature e.g., extinct Indian Ocean island parrots (Hume, 2007).

We followed the same wet-lab protocol as Smith et al. (2023). Extraction of DNA from modern tissue samples used the DNeasy tissue extraction kit (Qiagen, Valencia, CA). DNA from historical samples that came from the toe pads of museum specimens were extracted using a modified protocol because the DNA in these samples is highly fragmented. To compensate for this level of DNA degradation, we replaced the DNeasy filter columns with ones from the QIAquick PCR kit to size-select for smaller DNA fragments. DNA extraction from historical samples was done in a dedicated lab for working on degraded samples to reduce contamination risk. We quantified DNA extracts using a Qubit 2.0 Fluorometer (Thermo Fisher Scientific). Library preparation of UCEs, enrichment, and Illumina sequencing were performed by RAPiD Genomics (Gainesville, FL). The Tetrapod UCE 5K probe set was used to enrich 5060 UCE loci (Faircloth et al., 2012). Sequencing was done on an HiSeq X Ten. FASTQ files are available on the Short Read Archive (SRA numbers are available in supplementary table S1; available on Dryad at doi.org/10.5061/dryad.h70rxwdrx).

We followed the same variant calling pipeline as in Smith et al. (2023) that is briefly described here. Low-quality bases and adaptor sequences were trimmed from demultiplexed FASTQ files in Illumiprocessor v1 (Faircloth, 2013; Bolger et al., 2014). Contigs were mapped to UCE probes, and an index for a genus-specific reference sequence was generated, and reads were mapped to references using BWA v0.7.13-r1126 (Li and Durbin, 2009). SAM files were converted to BAM files and sorted with SAMtools v. 1.10 (Li et al., 2009). A VCF file was produced using the mpileup function in SAMtools v. 1.10 (-C 30; -Q 20). bcftools v. 1.12 (Danecek et al., 2021) and vcfutils were used to call and filter variant sites with <5× coverage per SNP and a quality score <20. seqtk was used to convert FASTQ files to FASTA. After retaining loci that were a minimum of 100 base pairs (bp) with heterozygous sites converted to IUPAC ambiguity codes, MAFFT v. 7.455 (Katoh and Standley, 2013) was used to align loci. The concatenated alignment and the final UCE alignments for which 75% of the samples were present in each locus were produced using default settings in PHYLUCE (Faircloth, 2016).

Phylogenetic Inference and Molecular Dating

We followed the methodology of Smith et al. (2023) to infer a concatenated topology and to time calibrate the phylogeny, which is repeated here. We used IQ-TREE2 v. 2.1.3 (Minh et al., 2020b) to produce a concatenated maximum likelihood phylogeny and 1000 ultrafast bootstraps (Hoang et al., 2018). The best-fit substitution model for each gene partition was estimated on ModelFinder (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017). Bootstrap trees were rooted on the outgroup, *Caracara cheriway*, using Phyx (Brown et al., 2017). We conducted an additional analysis on just *Cacatua* using the mixture across sites and trees (MAST) model in IQTREE v.2.2.2.6 (Minh et al., 2020b; Wong et al., 2024), to calculate the tree weights for the concatenated and species tree topologies using an alignment with stringent filtering where species with >1.31 deviation in parsimony informative sites were excluded (see Smith et al., 2023).

Next, we estimated a time-calibrated tree for the phylogenomic tree of Psittaciformes using a penalized likelihood method to estimate divergence dates to accommodate the large number of species and characters in our dataset. We dated the rooted bootstrap trees using treePL (Smith and O'Meara, 2012) from 100 ultrafast bootstrap trees, and calibrated nodes with the fossil ages of four taxa and specifying the root age using an external calibration from Jarvis et al. (2014) for the split between Falconiformes and Psittacopasserae (minimum age 57 Mya, maximum age 62 Mya). Kimball et al. (2019) and Oliveros et al. (2019) provide justifications for the fossil calibrations, except *Cacatua*, which was not used in those studies and whose age was reported in Boles (1993). The four taxa used to calibrate nodes are: (1) *Eozygodactylus americanus* (Weidig, 2010) [minimum age 51.81 Mya, maximum age 66.5 Mya for calibrating the split within Psittacopasserae (Psittaciformes and Passeriformes)]; (2) *Nelepsittacus minimus* (Worthy et al., 2011) [minimum age 15.9 Mya, maximum age 66.5 Mya for the split between *Strigops* and *Nestor*]; (3) an unidentified member of Cacatuinae (Boles, 1993) [minimum age 11.608 Mya, maximum age 23.03 Mya for the split between *Eolophus* and *Callocephalon*]; and (4) Suboscines indet. (Mayr and Manegold, 2006) [minimum age 27.25 Mya, maximum age 56.0 Mya for the split between oscine and suboscine passerines]. We estimated the optimal parameter settings using the prime and thorough options and randomly sampled during the cross-validation over a range of smoothing parameters (1×10^{-7}–1×10^{4}) for 10 iterations over the 100 ultrafast bootstrapped trees. We summarized the 100 treePL trees in TreeAnnotator v.1.10.4 (Suchard et al., 2018) by setting the burnin to 0 and specifying the target tree type as Maximum Clade Credibility and node heights as Common ancestor height.

The taxon-sampling table, DNA sequence alignment, and time-calibrated phylogeny are available on Dryad (doi: 10.5061/dryad.h70rxwdrx).

RESULTS AND DISCUSSION

We inferred a time-calibrated phylogeny from a maximum likelihood tree estimated from a 1,142,292 bp alignment, constituting 3040 ultraconserved element loci. Support values are reported from the maximum likelihood tree. We present and discuss our results in the order provided by the frameworks of figure 1 and table 1.

STRIGOPOIDEA

Strigopidae (*Strigops*)

Nestoridae (*Nestor*)

These two genera are of large to massive parrots of New Zealand. *Strigops* is nocturnal and flightless and extraordinarily convergent with Australia's *Pezoporus* parrots in its green plumage mottled black and yellow. Species of *Nestor* are long-billed, predominantly brownish or bronze-green parrots with red underwings or reddish underparts.

Aside from the extinct Miocene *Nelepsittacus* (see Worthy et al., 2011), the low-diversity superfamily Strigopoidea consists of three extant and two recently extinct, large-bodied

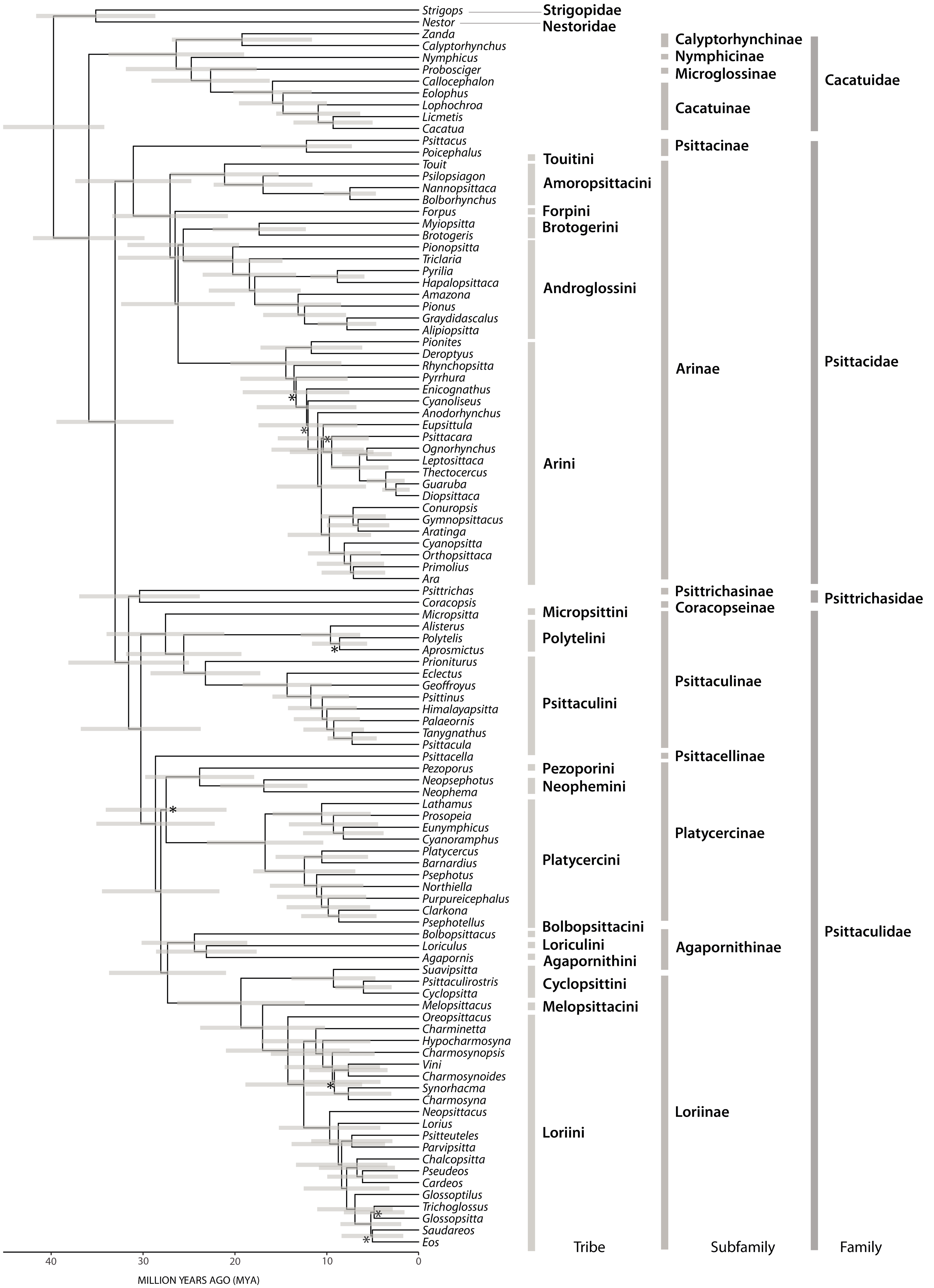


FIGURE 1. Generic-level phylogeny of Psittaciformes. Left to right: tribes, subfamilies, families. * = unsupported nodes; all other nodes have ultrafast bootstrap values ≥ 95%. Main text discusses nomenclature of family-group names Microglossinae, Touitini, Amoropsittacini, and Androglossini. Brotogerini tr. nov., Neophemini tr. nov., and Bolbopsittacini tr. nov. are described herein.

parrots that are endemic to New Zealand and surrounding islands. It was sister to the rest of the entire parrot radiation. One species, *Strigops habroptilus* (Family: Strigopidae; see Savage and Digby, 2023, for orthography of the epithet *habroptilus*), is monotypic and flightless, and two extant species, *Nestor notabilis* and *N. meridionalis* (Family: Nestoridae), are diurnal and volant. The three species' positions are stable and well resolved in our phylogenomic tree (fig. 1). This is in agreement with previous work. The ages of Strigopoidea and the families Strigopidae and Nestoridae have varied across studies, but a consensus has emerged in more recent work. Using a calibration of the splitting of New Zealand from Gondwana to date the split between Strigopoidea and all other parrots, Wright et al. (2008) dated the crown age of Strigopoidea to 81.91 Mya and 49.84 Mya for the split of Strigopidae and Nestoridae. We stress, however, that later work (e.g., reviewed in Worthy et al., 2017) has cautioned use of the 82 Mya split of New Zealand. The opportunity probably existed until about 55 Mya for taxa to join the Zealandian terrestrial biota by overland dispersal. Subsequent studies using fossil calibrations beyond Psittaciformes or secondary calibrations have found progressively younger ages for dates within the clade. Schweizer et al. (2011) estimated that Strigopoidea, which was represented in their taxon sampling by *Nestor*, diverged from other parrots 58.6 Mya (95% highest posterior density [HPD]): 44.9–72). Rheindt et al. (2014) estimated that this same divergence time had a mean of 49 or 42 Ma, depending on the type of calibration. Within the Strigopoidea, the divergence of Strigopidae and Nestoridae was dated to 28–29 Mya (95% HPD: 18–38 Mya) by Rheindt et al. (2014). We found that the stem and crown splits for Strigopoidea occurred at 40 and 35 Mya (figs. 1, 2), dates that are similar to the conclusions of another phylogenomic study using a reduced number of taxa (Huang et al., 2022).

Divergences within *Nestor* range from the late Miocene to early Pleistocene. We estimated the divergence of *N. notabilis* and *N. meridionalis* at 2.6 Mya (fig. 2), similar to the age determined by Rheindt et al. (2014), whereas Wood et al. (2014) dated the split to ~5 Mya. An extinct species, *Nestor productus* from Norfolk Island, is known from only 16 museum specimens and went extinct in the 1840s (Holdaway et al., 2001). It has yet to be placed in a molecular phylogeny. Also extinct, the Chatham Island Kaka (*Nestor chathamensis*) was found to be sister to *N. meridionalis* and molecular dating based on 571 bp of mtDNA estimated the split between the two taxa at 1.74 Mya (Wood et al., 2014).

Although not directly related to systematics, recent efforts to produce genomic resources for the three species in Strigopoidea have served both applied and basic science purposes. For example, extensive species management of the critically endangered *Strigops habroptilus* has led to whole genome sequencing of all individuals in the population (N = 169), an unprecedented resource for mitigating genetic associations with disease risk and low reproductive output (Guhlin et al., 2023). Genomic data for *Nestor* has indicated that *N. notabilis*, which occurs in the alpine zone of New Zealand, exhibits the same adaptive signatures of high-elevation habitation as the forest-adapted *N. meridionalis* (Martini et al., 2021).

CACATUOIDEA

CACATUIDAE

Cacatuoidea has its highest diversity in Australia, but it also occurs in New Guinea, Indonesia, Solomon Islands, and the Philippines. The phylogenomic time-calibrated tree shows Cacatuoidea splitting from Psittacoidea 35.9 Mya and that the clade has a crown age of 26.4 Mya (fig. 2). Our phylogeny further supports four subfamilies, in addition to the three now conventional: (1) Calyptorhynchinae—the large black-cockatoos with distinctively colored tail panels; (2) Nymphicinae—the small-bodied, monotypic *Nymphicus hollandicus*; (3)

TABLE 1

Taxonomic and nomenclatural summary of the classification of Psittaciformes, parrots, recommended in the present study for family-group and genus-group names.

See the text for discussion in current literature about use of the following names and alternatives: Microglossinae, Forpini, Amoropsittacini, Androglossini.

Superfamily	**Family**	**Subfamily**	**Tribe**	**Genus/genera**
Strigopoidea Bonaparte, 1849	Strigopidae			*Strigops* G.R. Gray, 1845
	Nestoridae Bonaparte, 1849			*Nestor* Lesson, 1830; †*Nelepsittacus* Worthy, Tennyson, and Scofield, 2011
Cacatuoidea G.R. Gray, 1840	Cacatuidae	Calyptorhynchinae Bonaparte, 1853		*Calyptorhynchus* Desmarest, 1826; *Zanda* Mathews, 1913
		Nymphicinae Bonaparte, 1857		*Nymphicus* Wagler, 1832
		Microglossinae Hogg, 1846		*Probosciger* Kuhl, 1820
		Cacatuinae		*Callocephalon* Lesson, 1837; *Eolophus* Bonaparte, 1854; *Lophochroa* Bonaparte, 1857; *Cacatua* Vieillot, 1817; *Licmetis* Wagler, 1832
Psittacoidea Rafinesque-Schmaltz, 1815	Psittacidae	Psittacinae		*Psittacus* Linnaeus, 1758; *Poicephalus* Swainson, 1837
		Arinae G.R. Gray, 1840 (1825)	Forpini Brereton, 1963	*Forpus* Boie, 1858
			Amoropsittacini Brereton, 1963	*Bolborhynchus* Bonaparte, 1857; *Psilopsiagon* Ridgway, 1912; *Nannopsittaca* Ridgway, 1912
			Touitini Sangster, Gregory, and Dickinson, 2023	Touit G.R. Gray, 1855
			Brotogerini Smith, Thom, and Joseph, 2024	*Brotogeris* Vigors, 1825; *Myiopsitta* Bonaparte, 1854
			Androglossini Sundevall, 1872	*Pionopsitta* Bonaparte, 1854; *Triclaria* Wagler, 1832, *Hapalopsittaca* Ridgway, 1912; Pyrilia Bonaparte, 1856; *Amazona* Lesson, 1830; *Pionus* Wagler, 1832; *Graydidascalus* Bonaparte, 1854; *Alipiopsitta* Caparroz and Pacheco, 2006
			Arini	*Pionites* Heine, 1890; *Deroptyus* Wagler, 1832; *Rhynchopsitta* Bonaparte, 1854; *Pyrrhura* Bonaparte, 1856; *Enicognathus* G.R. Gray, 1840; *Cyanoliseus* Bonaparte, 1854; *Anodorhynchus* Spix, 1824; *Eupsittula* Bonaparte, 1853; *Psittacara* Vigors, 1825; *Leptosittaca* Berlepsch and Stolzmann, 1894; *Ognorhynchus* Bonaparte, 1857; *Thectocercus* Ridgway, 1912; *Diopsittaca* Ridgway, 1912; *Guaruba* Lesson, 1830; *Conuropsis* Salvadori, 1891; *Aratinga* Spix, 1824; *Gymnopsittacus* Miranda-Ribeiro, 1920; *Cyanopsitta* Bonaparte, 1854; *Orthopsittaca* Ridgway, 1912; *Primolius* Bonaparte, 1857; *Ara* Lacépède, 1799

TABLE 1 *continued*

Superfamily	Family	Subfamily	Tribe	Genus/genera
	Psittrichasidae Boetticher, 1859 (1854)	Psittrichasinae		*Psittrichas* Lesson, 1831
		Coracopseinae Joseph, Toon, Schirtzinger, Wright and Schodde, 2012		*Coracopsis* Wagler, 1832
	Psittaculidae Vigors, 1825	Psittaculinae	Micropsittini Reichenow, 1881	*Micropsitta* Lesson, 1831
			Polytelini Mathews, 1916	*Alisterus* Mathews, 1911; *Aprosmictus* Gould, 1842; *Polytelis* Wagler, 1832
			Psittaculini	*Prioniturus* Wagler, 1832; *Eclectus* Wagler, 1832; *Geoffroyus* Bonaparte, 1850; *Psittinus* Blyth, 1842; *Psittacula* Cuvier, 1800; *Himalayapsitta* Braun, 2019; *Palaeornis* Vigors, 1825; *Tanygnathus* Wagler, 1832
		Psittacellinae Joseph, Toon, Schirtzinger, Wright & Schodde, 2012		*Psittacella* Schlegel, 1871
		Platycercinae Selby, 1836	Pezoporini Bonaparte, 1837	*Pezoporus* Illiger, 1811
			Neophemini Schodde, Mason, Smith, Thom, and Joseph, 2024	*Neophema* Salvadori, 1891; *Neopsephotus* Mathews, 1912
			Platycercini	*Lathamus* Lesson, 1830; *Prosopeia* Bonaparte, 1854; *Eunymphicus* Peters, 1937; *Cyanoramphus* Bonaparte, 1854; *Platycercus* Vigors, 1825; *Barnardius* Bonaparte, 1854; *Psephotus* Gould, 1845; *Northiella* Mathews, 1912; *Purpureicephalus* Bonaparte, 1854; *Psephotellus* Mathews, 1913; *Clarkona* Mathews, 1917
		Agapornithinae Salvin, 1882	Bolbopsittacini Smith, Thom & Joseph, 2024	*Bolbopsittacus* Salvadori, 1891
			Loriculini Verheyen, 1956	*Loriculus* Blyth, 1849
			Agapornithini	*Agapornis* Selby, 1836
		Loriinae Selby, 1836	Melopsittacini Bonaparte, 1857	*Melopsittacus* Gould, 1840
			Cyclopsittini Salvadori, 1891	*Cyclopsitta* Reichenbach, 1850; *Psittaculirostris* J.E. and G.R. Gray, 1859; *Suavipsitta* Mathews, 1917
			Loriini	*Oreopsittacus* Salvadori, 1877; *Charminetta* Iredale, 1956; *Hypocharmosyna* Salvadori, 1891; *Charmosynopsis* Salvadori, 1877; *Vini* Lesson, 1833; *Charmosynoides* Joseph, Merwin, and Smith, 2020; *Synorhacma* Joseph, Merwin, and Smith, 2020; *Charmosyna* Wagler, 1832; *Neopsittacus* Salvadori, 1875; *Lorius* Vigors, 1825; *Psitteuteles* Bonaparte, 1854; *Parvipsitta* Mathews, 1916; *Pseudeos* Peters, 1935; *Cardeos* Verheyen, 1956; *Glossoptilus* Hartert, 1896; *Chalcopsitta* Bonaparte, 1850; *Glossopsitta* Bonaparte, 1854; *Trichoglossus* Stephens, 1826; *Saudareos* Joseph, Merwin, and Smith, 2020; *Eos* Wagler, 1832

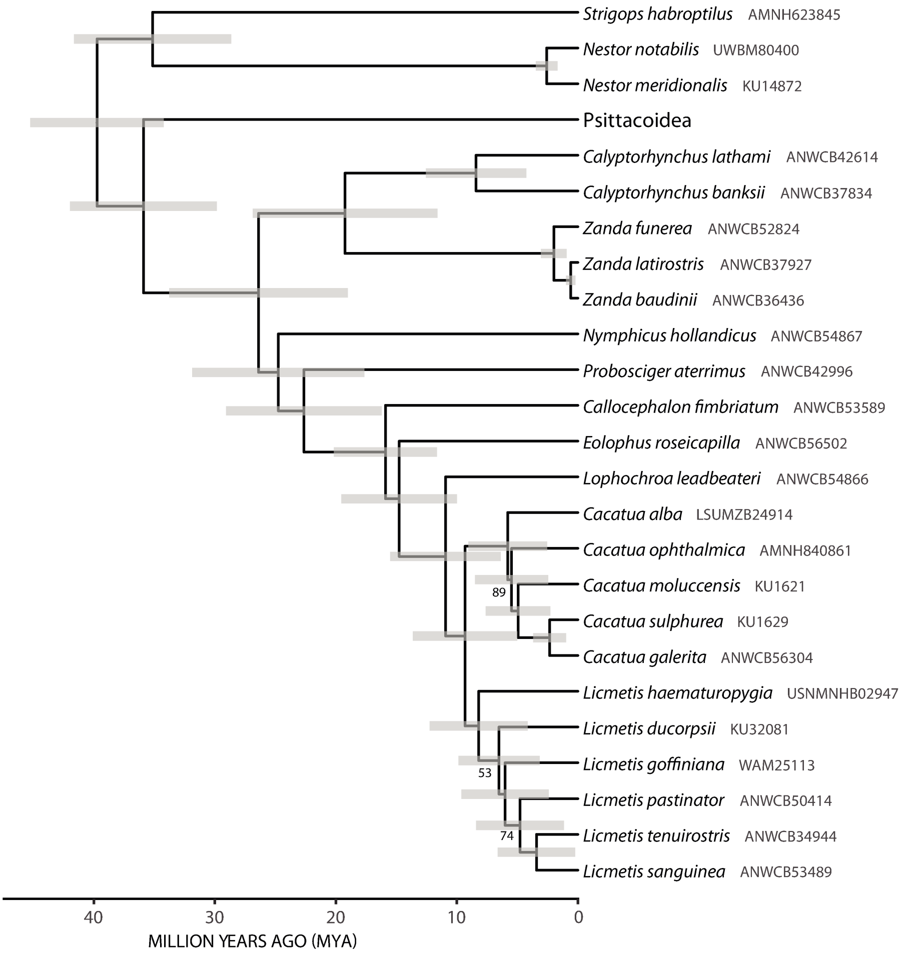


FIGURE 2. Species-level topology of Strigopoidea and Cacatuoidea. Support values come from the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted.

Microglossinae (sometimes Proboscigerinae (see below)—the massive, large-bodied slaty black monotypic *Probosciger*; and (4) Cacatuinae—mid- to large-sized cockatoos that are primarily white, gray, or pink. In advocating placement of *Probosciger* in its own subfamily (or, alternatively, as a monotypic tribe within Cacatuinae), we acknowledge current literature (Gregory and Sangster, 2023) on whether Microgloss- or Probosciger- is the correct stem for the family-group name to which this genus should be assigned. A counter argument to Gregory and Sangster (2023) was made by Schodde (accepted) to retain Microglossinae. The issue turns on debate over a small number of usages of these names by an even smaller number of authors. Until this is settled, we use Microglossinae. Among the main complications in comparing our temporal estimates of divergence in Cacatuidae with previous ages was the placement of Nymphicinae in the phylogenomic tree. We found *Nymphicus* to be sister to Cacatuinae whereas previous phylogenies placed it as sister to the clade comprising Calyptorhynchinae and Cacatuinae (Wright et al., 2008; White et al., 2011).

CALYPTORHYNCHINAE

Calyptorhynchus and *Zanda*

Calyptorhynchus and *Zanda* are large predominantly black cockatoos with distinctively colored, broad subterminal tail panels, predominantly red or orange-yellow in *Calyptorhynchus* and yellow to creamy white in *Zanda*. Bill color is often sexually dimorphic (less prominently so in *C. lathami*) and *Zanda* also have sexually dimorphic ear-covert patches broadly concolorous with the subterminal tail band. Vocalizations are distinctive, typically being an oddly "funereal" cry in *Zanda* and higher pitched somewhat wheezy cries in *Calyptorhynchus*.

In the Calyptorhynchinae, relationships among the five conventionally recognized species are stable and well supported across phylogenomic trees and a previously inferred species tree (White et al., 2011). We support the generic placement of the species *funerea*, *baudinii*, and *latirostris* in *Zanda* Mathews, 1913. *Zanda* was in synonymy with *Calyptorhynchus* for most of the 20th century, but its reinstatement began with Schodde's (1997) recognition of it at subgeneric rank within *Calyptorhynchus*. Following White et al.'s (2011) molecular study, its elevation to genus level has become conventional (Gill et al., 2023; Dickinson and Remsen, 2013). Saunders and Pickup (2023a) have revisited and reinforced support for the recognition of *Zanda* based on morphological and vocalization data. Divergence between *Zanda* and *Calyptorhynchus* dates to 19.2 Mya and divergences within each genus date to 0.6–2 Mya and 8.4 Mya, respectively (fig. 2).

Turning to species-level systematics, we note that an analysis of genome-wide single nucleotide polymorphisms (SNPs) (Ewart et al., 2020) found that the Red-tailed Black Cockatoo (*Calyptorhynchus banksii*) comprises five evolutionarily significant units, the corresponding species-group epithets of which are *banskii*, *graptogyne*, *naso*, *escondidus*, and *samueli*. Unsurprisingly, some uncertainties remain in relationships among these five taxa, given their shallow divergence times. Ewart et al. (2020), however, made two taxonomic recommendations: (1) synonymy of *banksii* and *macrorhynchus* in nominotypical *banksii* and (2) that *samueli*, the three isolated populations of which did not form a single monophyletic group, should be broken into eastern and central populations, *samueli*, which did form a single monophyletic group, and western population, *escondidus*, which was sister to *naso* and which they newly described at subspecies rank.

Saunders and Pickup (2023a) elevated the five subspecies to species rank. Key elements of their decision were morphometric analyses, the time of divergence (latter half of the Pleistocene; Ewart et al., 2020), and their allopatry. Present-day geographic interactions and gene flow between *banksii* and *samueli* in eastern Australia seem highly probable, however, and warrant further study regardless of their taxonomic status (see maps in Saunders and Pickup, 2023a). Similarly, but perhaps with a lower probability, *escondidus* and *banksii* may be in geographic and genetic contact in northwestern Australia. One species with five subspecies or five monotypic species are among equally plausible arrangements in light of the data available: five geographical units appear monophyletic, but their divergences are shallow relative to many other species and there is no extensive sympatry to affirm species status by that criterion.

The shallow divergence between *Z. latirostris* and *Z. baudinii* warrants discussion. This pair is among the most notable examples in ornithology of cryptically differentiated sibling species (White et al., 2014). Saunders (1974, 1979) elegantly showed on morphological grounds that the two taxa are distinct, primarily in bill morphology. This work led to the removal of *latirostris* from synonymy of *baudinii* and recognition of the two taxa at species rank. Next, White et al. (2011) presented a multilocus phylogenetic analysis arguing that radiation within *Zanda* into three species happened relatively recently, within the last 1.3 million years. White et al. (2014) pursued genetic differentiation between *Z. latirostris* and *Z. baudinii* with microsatellite data. They suggested that the differentiation between the two taxa started during anthropogenic land clearing in the 20th century. They also remarked that some gene flow is still occurring between the two but estimated that fewer than 10 individuals per generation are moving between regions separated by an anthropogenically generated barrier of unsuitable habitat.

Saunders and Pickup (2023a) presented an updated synthesis of all data concerning this pair. They disputed White et al.'s (2014) claim of differentiation within the past ~100 years, a finding that was corroborated with our phylogenomic data that dates the split at 0.6 Mya (0.2–1) (fig. 2). Further, they found no morphological indication of hybridization and stressed the overlapping breeding ranges of the two taxa, surely here a gold standard for species-level recognition. On adding our data to these syntheses, we conclude that while population-level sampling of Z. *latirostris* and *Z. baudinii* with genomic methods now available is likely to be highly rewarding, the optimal taxonomic conclusion at this point is that they indeed represent two species.

Taxonomic subdivision of *Z. funerea*, in contrast, has become far more contentious since Saunders and Pickup (2023a, 2003b) proposed that the three taxa at best tentatively recognized as subspecies within it by earlier treatments (Schodde and Mason, 1997; Forshaw and Cooper, 2002) should be elevated to species rank. Our sampling has not addressed variation within *Z. funerea*. We are highly skeptical of Saunders and Pickup's (2023a, 2023b) proposal to elevate three questionably recognizable subspecies within *Z. funerea* to species rank but will address this in more detail elsewhere.

NYMPHICINAE

Nymphicus

Nymphicus is predominantly a small midsized gray parrot with yellow and red facial markings, white wing patches conspicuous in flight and a forward-curving crest. It is one of the world's most popular aviary birds.

Although monotypic *Nymphicus* has unquestionably been recognized for decades as within the Cacatuoidea and essentially a diminutive cockatoo (see Adams et al., 1984, and Schodde and Mason, 1997, for brief reviews of morphological, karyological, behavioral, and allozyme data), its precise relationships have remained unclear. Adams et al. (1984) in an allozyme study found its position ambiguous depending on the analysis, either aligning it with the *Calyptorhynchus* black cockatoos or the *Cacatua* sensu lato white cockatoos. Brown and Toft's (1999) results based on mitochondrially encoded *12S* sequence data and reanalysis of allozyme data were similarly ambiguous. A consensus of their results was that it aligned with *Calyptorhynchus* as one of the "more basal cockatoo species." A multilocus analysis led White et al. (2011) to place it as the sister group to the rest of the Cacatuoidea.

Our phylogenomic data strongly place *Nymphicus* as the sister to all non-calyptorhynchine cockatoos, and not as the sister to all cockatoos or indeed to the calyptorhynchines, diverging 24.8 Mya (16.2–30.4; fig. 2). We argue that all lines of data fully support retention of *Nymphicus* in a monogeneric subfamily, Nymphicinae, which was sister to the Cacatuinae. Similarly, it is usually treated as a monotypic species given its almost continentwide range and high vagility.

MICROGLOSSINAE

Probosciger

Probosciger is a massive, large-bodied slaty black cockatoo, which is phylogenetically as well as phenotypically distinctive in its permanently open bill, rose-red colored facial skin, colored tongue, slaty black plumage with some fine orange-red ventral barring in young birds and finely plumed erectile but uncolored crest, whistled vocalizations, and drumming behavior in males (Schodde and Mason, 1997; Heinsohn et al., 2017, 2023).

We have discussed above why we favor placing *Probosciger* in its own subfamily rather than tribe and we acknowledge ongoing debate about the correct stem for the family-group name to be assigned to this subfamily.

Within *Probosciger aterrimus*, 3.3% divergence in the control region of the mitochondrial genome corresponds to a geographical split between populations on the Bird's Head Peninsula at the western end of New Guinea and those in the rest of New Guinea and Australia (Murphy et al., 2007). A subsequent study using SNP data and the mtDNA gene *ND2* found evidence of shallow genetic structuring between Australia and New Guinea (Keighley et al., 2019).

CACATUINAE

Callocephalon, Eolophus, Lophochroa, Cacatua, and *Licmetis*

Callocephalon is a monotypic genus of medium-sized cockatoo, predominantly gray in plumage and having a distinctive, forward-curving crest of filamentous feathers. It is sexually dimorphic in its head plumage, red in males, gray in females. It is endemic to wetter forests and woodlands in southeastern Australia. *Eolophus* is also a monotypic, medium-sized cockatoo with three recognized subspecies. It is distinctively gray dorsally and pink ventrally with a backward-curving pink to whitish crest having a "split" appearance in some populations. It has bare, carunculated periophthalmic skin varying subspecifically from white to shades of pink. It is one of the most familiar of all Australian birds occurring across the continent in all but the wettest forests and woodlands. *Lophochroa* comprises one species with two currently recognized subspecies. Resembling in overall morphology the large *Cacatua galerita*, it differs in having salmon-pink underparts and a similarly pink and yellow crest, and a pale bill. It primarily inhabits arid- and semiarid woodlands. All three of these genera have distinctive vocalizations.

We discuss the taxonomic implications of the phylogenomic data in light of the two phenotypically distinct groups within *Cacatua* sensu lato that the data in turn mostly affirm. The first of these is *Cacatua* sensu stricto having mostly forward-curving, yellow or white to orange crests, broad wings, naked white to bluish ocular skin, usually concentric with the eye itself, black bills, and characteristically as well as extraordinarily harsh shrieks. The second is *Licmetis*, the corellas, having vestigial, backward-curving crests, slender wings, milky to leaden blue ocular skin extending below the eye in an oval shape, white bills and a distinctive yodel or crying vocalizations (see Forshaw, 1973; Schodde et al., 1979; Schodde and Mason, 1997; Forshaw and Knight, 2010).

Relationships within Cacatuinae are the most unstable and taxonomically challenging within Cacatuoidea. This is largely due to lower-quality samples for some taxa (e.g., *Cacatua ophthalmica*) and gene tree–species tree discordance reported in Smith et al. (2023). Phylogenetic patterns within Cacatuinae are represented by a series of well-supported and consecutive nodes, then nodes leading to each of the three monotypic genera *Callocephalon*, *Eolophus*, and *Lophochroa*, and a final node subtending a clade comprising white cockatoos long treated within the genus *Cacatua* (fig. 2). Previous multilocus work found weak evidence of *Callocephalon fimbriatum* and *Eolophus roseicapilla* as sister taxa (White et al., 2011), but we found them diverging on successive branches with 100% bootstrap support. They are each phenotypically unique, and this includes their vocalizations as well as plumage patterns. Generic-level divergences span 9.3–22.6 Mya (fig. 2). We first examine genus-level divergences before discussing species-level issues.

We fully support the retention of *Callocephalon*, *Eolophus*, and *Lophochroa* as monotypic genera. Notably, *Lophochroa* was sister to a clade comprising *Cacatua* sensu stricto and the *Licmetis* corellas, not just the former with which it has long been placed in *Cacatua* and with some species of which it shares the phenotypic trait of a forward-curving crest. We favor the retention of *Lophochroa* at generic rank because of its phylogenomic separation from *Cacatua* and this includes the age of its lineage coupled with its utterly distinct phenotypic traits including bicolored crest and unique vocalizations.

There was topological discordance between the concatenated and species tree topologies for *Cacatua*. The bulk of the discordance was within the two main clades corresponding to *Cacatua* sensu stricto and *Licmetis*, and often involved lower-quality historical samples and nodes with low support, but there are also likely cases of phylogenetic conflict. We find it puzzling that these two groups have for so long been unquestioningly placed in one genus, *Cacatua* Vieillot, 1817. This treatment has prevailed in Australian literature at least since RAOU (1926); it is difficult to determine why it was introduced and why it has prevailed despite the obvious phenotypic differences just outlined. Further, it has prevailed despite several demonstrations of substantial genetic divergences (Adams et al., 1984; Brown and Toft, 1999). We now address in more detail the merit of breaking of *Cacatua* sensu lato into these two genera. For ease of discussion, we anticipate our recognition of *Licmetis* at rank of genus.

One source of uncertainty in our analysis is the generic placement of *haematuropygia*. It is either sister to the remaining *Licmetis* (concatenated tree) or the clade composed of *Cacatua/Licmetis* (species tree). Morphologically, *haematuropygia* would appear to belong in *Licmetis* in that it is similar in size, shape, and bill color to *L. goffiniana*, a taxon firmly nested within the corellas (but we note its white ocular skin concentric with the eye). From our additional MAST analysis on *Cacatua* we found that the concatenated phylogeny, which has a monophyletic *Licmetis*, was the predominant topology (tree weight: 0.87) across the alignment versus the topology with *L. haematuropygia* as sister to all other *Licmetis* and *Cacatua* as the minor tree (tree weight: 0.13). These results confirm the analyses of this clade by Smith et al. (2023), where there was more signal for the concatenated topology. Given *haematuropygia*'s morphological affinities with *Licmetis* and the overriding phylogenomic signature that indicates it is sister to the other corellas, the best evidence supports the recognition of *Cacatua* and *Licmetis*. We do not advocate a new genus for *L. haematuropygia*.

There were also several cases of gene tree–species tree discordance within both groups. Relationships among the corellas (*L. sanguinea*, *L. tenuirostris*, *L. pastinator*, and *L. goffiniana*) varied among the phylogenomic trees. Similarly, there was such discordance in *Cacatua* sensu stricto (*C. sulphurea*, *C. moluccensis*, *and C. ophthalmica)*. Divergence times within *Cacatua* and *Licmetis* ranged from 2.3 to 5.8 Mya and 3.4 to 8.2, respectively (fig. 2).

We are confident that the combined weight of our genomic data, uncertainties within the two strongly supported clades notwithstanding, and the phenotypic differentiation in body and wing morphologies generally, crest morphology in particular and vocalizations, all combine to provide strong support for the breakup of *Cacatua* sensu lato and the reinstatement of *Licmetis* Wagler, 1832, for the corellas. Indeed, we argue that this situation strongly parallels the basis for recognition of *Calyptorhynchus* and *Zanda*, the separation of which is now accepted and entrenched such that treating them as congeneric is considered little more than bad taxonomic habit. A similarly prevalent generic separation of sister clades is that of *Platycercus* and *Barnardius*. We acknowledge the call made by Adams et al. (1984) for detailed comparative study of any social function of crests and bare facial skin in these cockatoos to test whether contrasting combinations of these traits may have arisen through character displacement.

Phylogeographic work in Cacatuinae has been limited to a few species. Engelhard et al. (2015) found that phylogeographic structure in *Eolophus roseicapilla* broadly corresponds with eastern, western, and northern subspecies recognized by morphological traits. Future work should examine phylogeographic variation in *Callocephalon*, *Cacatua*, and *Licmetis.* In the widely distributed Australian endemic *Lophochroa leadbeateri*, SNP data identified contains 2–3 genetic groups corresponding with a break across the Eyrean Barrier and in central Queensland (Ewart et al., 2021). This break corresponds to the subspecies *L. l. leadbeateri* and *L. l. mollis*, but interestingly, the genetic structuring among these groups was not observed in mtDNA. *Cacatua galerita* and the *Licmetis sanguinea* complex are both of particular interest given their uncertain subspecific taxonomy and their widespread distributions.

PSITTACOIDEA

The majority of parrot diversity is within the superfamily Psittacoidea. It is distributed on multiple continents, and the majority of species are either in the family Psittaculidae or the subfamily Arinae. Higher-level relationships are generally stable across phylogenomic trees and previous phylogenies with a few exceptions discussed below. Psittacidae (Psittacinae: African parrots; Arinae: Neotropical parrots) was sister to Psittrichasidae/Psittaculidae. Psittrichasidae (Coracopseinae) of Madagascar and the Seychelles-Comoros archipelago in the southwestern Indian Ocean; Psittrichasinae of New Guinea) was sister to Psittaculidae. The families in Psittacoidea (Psittacidae, Psittrichasidae, and Psittaculidae) have estimated ages that indicate diversification within these lineages began in the early Oligocene (30.2–31.1 Mya; fig. 1). In comparison with previous time-calibrated phylogenies for Psittaciformes inferred from a small number of molecular markers (Wright et al., 2008; Rheindt et al., 2014), our time-calibrated tree found younger ages for common nodes.

PSITTACIDAE

Psittacinae

The Psittacinae is a low-diversity radiation endemic to Africa comprising two genera, *Psittacus* and *Poicephalus*. The Psittacinae split from their sister clade, the Arinae in the early Oligocene (~30 Mya; fig. 1) well after the proposed split between Africa and South America in the Middle Cretaceous age, about 115–125 Mya (Valencio and Vilas, 1969).

Psittacus

Psittacus are predominantly gray-plumaged parrots with red tails and prominent bare white facial skin. Along with Australian *Nymphicus* and *Melopsittacus*, they are among the world's most familiar parrots, and are among the parrots most heavily harvested for the captive bird trade (Mulliken, 1995). Their ethology has been intensely studied (e.g., Giret et al., 2009, Pepperberg et al., 2013). *Psittacus* was long treated as monotypic, but two species are now conventionally recognized, *P. erithacus* and *P. timneh*. In the phylogenomic tree, the sister relationship between the two was stable and dated to the early Pleistocene (1.9 Mya; fig. 3). Relationships within and among populations of the two species have also been addressed through mitochondrial DNA sequences by Melo and O'Ryan (2007).

Poicephalus

The *Poicephalus* parrots are a small radiation endemic to Africa. They are midsized stocky parrots, predominantly green with dark upperparts but with species-specific bands of color often on the abdominal (belly) plumage, underwings and rump. We note below (see *Psephotellus* of Australia) a possible case of convergent plumage evolution involving several species of *Poicephalus*.

Pioneering molecular work on *Poicephalus* (Massa et al., 2000) was based on random amplified polymorphic DNA (RAPD). While one of its findings, a sister-group relationship between *P. cryptoxanthus* and *P. meyeri*, may have reflected plesiomorphy or homoplasy, many of their results are supported broadly here.

The radiation of *Poicephalus* had a crown age of 7.5 Mya and the majority of the species had divergences in the Pliocene (fig. 3). The topology within *Poicephalus* was less robust due to low-quality samples and nodes with low support. The issues likely stemmed from the *P. flavifrons* and *P.*

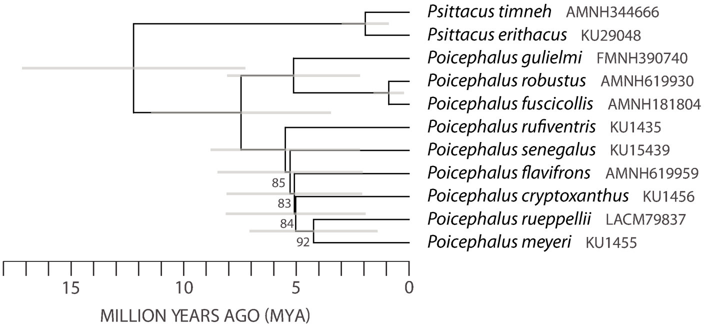


FIGURE 3. Species-level topology of Psittacinae. Support values come from the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted.

rueppellii samples coming from historical samples that produced limited data, making them harder to place in the tree. *Poicephalus fuscicollis* also had lower-quality data and did not meet more stringent filters of quality control of Smith et al. (2023); it was, however, sister to *P. robustus* in the phylogenomic trees. This result was consistent with previous phylogenetic work based on mtDNA but inconsistent with a phylogeny inferred from concatenated nuclear and mtDNA, which found *P. robustus* to be more closely related to *P. gulielmi* (Coetzer et al., 2015). *Poicephalus crassus* is known from few museum specimens and has not been sequenced. Given the close similarity in plumage in *P. crassus* and *P. cryptoxanthus*, they are likely closely related. The positions of *P. rufiventris* and *P. senegalus* varied between estimated trees, but the species tree had a better phylogenetic resolution. Recent work describes an unrecognized subspecies in *P. rueppellii* that differs in size and plumage color across populations in Angola (Hubers et al., 2023).

Arinae

Subfamily Arinae is highly diverse in species richness and morphological variation, yet it is a cohesive monophyletic assemblage occurring in the Neotropical region. Revisionary work has delimited four tribes within Arinae that are all supported by our phylogenomic trees (Schodde et al., 2013). The Arinae has a crown age of 27.1 Mya and the tribes (Arini, Androglossini, Amoropsittacini, and Forpini) began diverging within a few million years (fig. 1). The crown ages of tribes were widely variable. The diverse Arini, the long/attenuate-tailed macaws and allies, had a crown age of only 14.5 Mya, whereas the largely short/round-tailed amazons and allies of Androglossini had a crown age of 25.6 Mya (fig. 1). Amoropsittacini also had a deep divergence of 21.1 Mya separating *Touit* and *Bolborhynchus*/*Psilopsiagon*/*Nannopsittaca* (fig. 1). The Forpini diverged from the clade containing Arini/Androglossini 26.5 Mya and were estimated to have begun diversifying at around 5 Mya (figs. 1, 4). The position of the Forpini in relation to the other tribes in Arinae has varied across phylogenetic studies. In the phylogenomic tree, Forpini was separated from Arini/Androglossini by a short internode, consistent with the instability observed in this part of the tree.

For discussion of the often contentious topic of extinct parrots in the Caribbean region, in particular species of the genera *Ara* and *Amazona*, we refer the reader to Williams and Steadman (2001), Olson and López (2008), Gala and Lenoble (2015), Forshaw and Knight (2017), and Oswald et al. (2023).

Forpini

Forpus

Brereton (1963) first published Forpini and Amoropsittacini diagnosed in symbols and let-

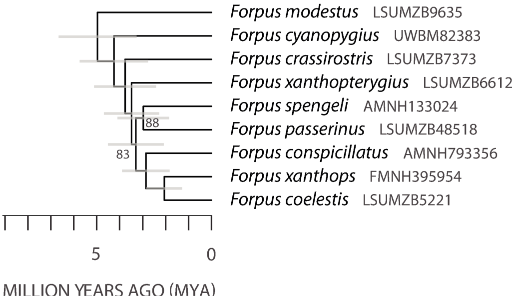


FIGURE 4. Time-calibrated phylogeny of Forpini. Support values come from the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted.

ters in a table with an accompanying legend explaining the meaning of the symbols and letters in words. Schodde et al. (2013) accepted this as validating the names. Sangster et al. (2023) nevertheless disputed it, claiming that Brereton's descriptions did not conform to the requirements of the current edition of the International Code of Zoological Nomenclature (ICZN, 1999), and replaced Brereton's names with their own. Schodde et al. (submitted) have since applied to the International Commission on Zoological Nomenclature to conserve Forpini and Amoropsittacini as published by Brereton (1963). The details of these nomenclatural arguments are to be explained fully in that paper but hinge on due and fully appropriate detail having been given by Brereton (1963). Until this is settled, we consider Forpini and Amoropsittacini as valid family-group names.

The Forpini contains nine small, stocky-bodied, sexually dimorphic, and largely green species in the genus *Forpus*. *Forpus* is currently distributed from Mexico to Argentina, but the fossil record suggests that it occurred in the Bahamas up until at least the Late Pleistocene (Steadman and Franklin, 2020). Recent molecular (Smith et al., 2013) and morphological (Bocalini and Silveira, 2015) data were used to elevate *F. spengeli* of northwest Colombia and *F. crassirostris* of western Amazonia to species rank. Bocalini and Silveria (2015) assessed phenotypic variation within *F. xanthopterygius* and synonymized the remaining taxa (*crassirostris*, *flavissimus*, *flavescens*, and *olallae*) within monotypic *F. xanthopterygius* due to high morphological variation among localities and because plumage patterns did not conform to described subspecies limits. This finding has important implications for species limits in the genus and highlights the limits of using morphological data to assign taxonomic ranks. As recovered in previous work (Smith et al., 2013), our phylogenomic tree had *F. crassirostris* as sister to a clade containing all other *Forpus* except *F. modestus* and *F. cyanopygius*. The timing of this divergence (approximately 3.8 Mya; fig 4) was similar to the age estimated using a small number of mtDNA and nuclear DNA loci (Smith et al., 2013). This deep intraspecific divergence, which was not reflected in the high number of specimens examined by Bocalini and Silveria (2015), indicates that morphological evolution is not tracking population history and is thus not a reliable data source for species delimitation.

The opposite is true for *F. passerinus*. *Forpus spengeli* was originally treated at species rank until at least Cory (1918). To the best of our knowledge, it was then placed in *F. passerinus* by Peters (1937), without comment. At a later date, it was transferred to *F. xanthopterygius* (Forshaw, 1973). Smith et al. (2013) found that *spengeli* was nested within *passerinus* differing by only a few base pairs in mtDNA, whereas Bocalini and Silveria (2015) found *spengeli* to be distinct given its clearly diagnostic turquoise rump on males. They restored the taxon to species rank as *F. spengeli*. Bocalini and Silveria (2015) included *F.*

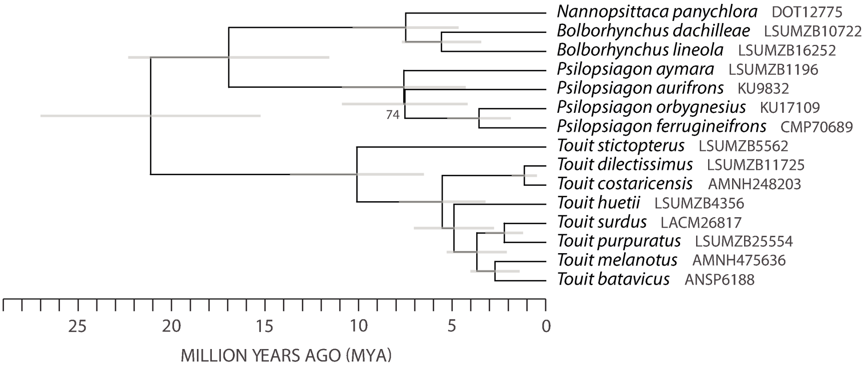


FIGURE 5. Time-calibrated phylogeny of Amoropsittacini and Touitini. Support values come from the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted.

passerinus in their study, but did not consider that *F. spengeli* could be a geographical variant within *F. passerinus* or, alternatively, its mtDNA may have been introgressed and/or captured by the nearest population of *F. passerinus*, i.e., *F. passerinus cyanophanes*. *Forpus passerinus*, which exhibits a wide variation in rump color in males, ranging from blue to green even with excluding *F. spengeli*. The molecular changes that result in a shift from a green to turquoise feather patch may be simple, as observed in captive *Melopsittacus undulatus*, in which a single base-pair change expresses tryptophan, blocking expression of yellow pigment, and so changes green feathers to blue (Cooke et al., 2017). The identical mutation was also found to produce blue feathers in captive *Agapornis* (Ke et al., 2024), suggesting there may be a single genetic mechanism underlying the green to blue color shift in parrots. While the phylogenomic tree here strongly shows a deep divergence between *F. passerinus* and *F. spengeli* (fig. 4), caution is warranted when interpreting this divergence in light of previously characterized shallow mtDNA divergence. The phylogenomic tree is either reflecting discordance between nuclear and mtDNA, possibly due to mitochondrial introgression, or the branch length is artificially long due to the high number of singletons in phylogenomic data. Population-level sampling is necessary to distinguish these scenarios.

Amoropsittacini/Touitini

We acknowledge the recent introduction of Touitini by Sangster et al. (2023) to encompass the genera *Touit*, *Bolborhynchus*, *Psilopsiagon*, and *Nannopsittaca*, and thereby replacing Amoropsittacini Brereton, 1963. As noted above, we similarly acknowledge concomitant preparation of a counterargument by Schodde et al. (submitted) to conserve the family-group name Amoropsittacidae Brereton, 1963. If accepted, the latter still allows retention of Touitini for recognition as a monotypic tribe i.e., containing only *Touit*. Until this is resolved, we use Touitini for *Touit* and Amoropsittacini for the other three genera for reasons we now outline.

There was a deep divergence that dates to 21.1 Mya (13.7–25.5) between *Touit* and the clade containing *Bolborhynchus*, *Psilopsiagon*, and *Nannospsittaca*, which in turn exhibits a basal divergence dating to 16.9 Mya (10.3–21; fig. 5). Based on these deep divergences, we advocate recognition of two tribes, one for *Touit* and one for *Bolborhynchus*, *Psilopsiagon*, and *Nannopsittaca*, this decision being driven largely by the molecular data.

Touit, Bolborhynchus, Nannopsittaca, and *Psilopsiagon*

The four genera in this group (*Touit*, *Bolborhynchus*, *Nannopsittaca*, and *Psilopsiagon*, whether in Amoropsittacini or Touitini as discussed above) comprise small-bodied and largely green-plumaged species occasionally broken up with traits such as black barring, small areas of other colors about the head and face, differently colored underwing coverts, or, as in one species, a crown demarcated from the upperparts and underparts. Tails vary from long and attenuate to short and blunt. Touitini is generally more morphologically uniform than Amoropsittacini. Species in *Touit* have small, stocky bodies with round tails, whereas Amoropsittacini shows greater variation in gross morphology, tail morphology and body size. Sexual dimorphism is also much more pronounced.

Turning to species-level relationships, we first report the relationships inferred from the concatenated tree. *Touit stictopterus* of central Colombia to northern Peru diverged from the remaining *Touit* at 10.1 Mya (5.9–13.1; fig. 5). The next divergence represents a mostly east-west break across the Andes. The clade comprising sister species *T. dilectissimus* and *T. costaricensis* diverged across the Andes at 5.5 Mya (3.1–7.6) from the other clade entirely east of the Andes (*T. surdus*, *T. purpuratus*, *T. batavicus*, *T. melanotus*, and *T. huetii*; fig. 5). The divergence across the Isthmus of Panama between *T. dilectissimus* and *T. costaricensis* occurred 1.1 Mya. This timeframe aligns with other humid forest birds that colonized North America (Smith et al., 2012). The first divergence in the clade east of the Andes was between *T. huetii* and the other taxa (fig. 5). *Touit huetii* is widespread across Amazonia in relatively small allopatric populations. *Touit melanonotus* of southern Brazil and *T. batavicus* of northern Colombia, Venezuela, Suriname, the Guianas, and northern Brazil are highly disjunct with respect to each other, separated by the Amazon Basin and the South American dry diagonal, including the Caatinga and Cerrado Biomes. That disjunction dates to the late Pliocene–early Pleistocene. A second large disjunction is between sister species *T. purpuratus* of northern Amazonian and *T. surdus* of southeastern Brazil. In contrast, the species tree found notable differences in relationships. However, some taxa (*T. costaricensis*, *T. melanonotus*, and *T. surdus*) with lower-quality samples could not be accurately placed in the species tree. The most notable difference was the placement of *T. huetii*, which was sister to *T. purpuratus* in the species tree.

The species in the other three genera occur primarily in montane regions, except *Nannopsittaca dachilleae* of lowland western Amazonia. The traditionally recognized genera *Bolborhynchus* and *Nannopsittaca*, however, are not monophyletic. That is, two of three nominal species within *Bolborhynchus* (*B. ferrugineifrons* and *B. orbygnesius*) and the two species of *Psilopsiagon* (*P. aymara* and *P. aurifrons*) comprise a clade that represents a radiation across the high Andes, with its species-level divergences ranging from 3.6–7.6 Mya (fig. 5). The concatenated and species trees represented here are mostly concordant. *Bolborhynchus ferrugineifrons* was accurately placed in the same clade in both phylogenomic trees but had a significant amount of missing data at parsimony informative sites. The order of *P. aymara* and *P. aurifrons* also differed in the species tree, but they were still paraphyletic with respect to each other, a result that we note with much caution. Although *B. lineola* and the two species in *Nannopsittaca* form a clade, they are biogeographically less cohesive. *Nannopsittaca panychlora* occurs disjunctly in small, restricted parts of Venezuela in the tepui region from 750 to 1850 m (Forshaw and Knight, 2010). *Bolborhynchus lineola* is widely distributed in montane regions from Mexico to Peru. *Nannopsittaca panychlora* was sister of *N. dachilleae* and *B. lineola*, and so *Nannopsittaca* was paraphyletic.

We consider five alternative taxonomic scenarios for addressing the paraphyly within *Bolborhynchus*, *Nannopsittaca*, and potentially *Psilopsiagon* (see fig. 5). They are:

1. Most expediently, all species could be placed in the oldest of the three generic names, *Bolborhynchus* Bonaparte, 1857.

Previous authors have indeed treated *Psilopsiagon aymara* and *P. aurifrons* within *Bolborhynchus* (De Schauensee and Eisenmann, 1966, Forshaw and Knight, 2010). This would produce a genus with high interspecies morphological disparity reflected temporally in the clade dating to the mid-Miocene. Conversely, there is no precedent elsewhere within Psittaciformes for a genus having a crown age as deep as 16.9 Mya, which reflects a timespan encompassing substantial evolutionary divergence. Recalling Ford's (2006) suggestion that a genus should make sense to someone not familiar with it, we reject this option.

2. Given that *Bolborhynchus lineola* (Cassin, 1853) = *Psittacula lineola* Cassin, 1853, is the type species of *Bolborhynchus* (and, parenthetically, of *Grammopsittaca* Ridgway, 1912), the two species of *Nannopsittaca* Ridgway, 1912, although paraphyletic with respect to each other, could be placed in *Bolborhynchus* with *B. lineola.* This is consistent with O'Neill et al.'s (1991) case that they are congeneric notwithstanding that we here advocate placing them in the same genus as *B. lineola*. Two other species currently in *Bolborhynchus* (*ferrugineifrons*, *orbygnesius*) could then be placed in *Psilopsiagon* with *P. aymara* and *P. aurifrons*. However, this option also produces genera with species that are morphologically disparate albeit less so than the previous option.
3. As option 2 but reinstating monotypic *Amoropsittaca* Richmond, 1915, only for *aymara*.
4. Retention of *N. panychlora* in monotypic *Nannopsittaca*, although counter to O'Neill et al.'s (1991) view that *Nannopsittaca* is ditypic, opens this fourth option. Notwithstanding the superficial similarity in gross morphology of the two species usually placed in *Nannopsittaca* (e.g., fig. 5), we find this a reasonable option for two main reasons: (1) *N. panychlora* diverged from *N. dachilleae*/*B. lineola* at 7.5 Mya (4.2–9.8), a depth of divergence that was similar to deeper intra- and intergeneric splits within Psittaciformes, and (2) it was the only Neotropical parrot endemic to the Pantepui region of northern South America (e.g., Mayr and Phelps, 1967). By this option, *B. ferrugineifrons* and *B. orbygnesius* and *aymara* and *aurifrons* could be placed in *Psilopsiagon* as already suggested, and *N. dachilleae* would be moved to *Bolborhynchus* because it was sister to the type species of that genus, *B. lineola*. *Bolborhynchus lineola* and *N. dachilleae* are strongly associated with bamboo albeit of different genera, i.e., *Chusquea* spp. and *Guadua* spp., respectively (O'Neill et al., 1991; del Hoyo et al., 1997; Harvey et al., 2014).
5. As option 4 but with *aymara* in *Amoropsittaca*.

Choosing among these options inevitably becomes subjective. We favor option 4, arguing that retention of *aymara* in *Psilopsiagon* is prudent until its position relative to the other species in that genus is clarified. Similarly, the position of *aurifrons* was poorly supported (UFBS = 74%). This is consistent with our generic decisions made elsewhere to convey as accurately as possible well-supported phylogenomic diversity (e.g., *Licmetis* vs. *Cacatua*; *Zanda* vs. *Calyptorhynchus*; *Psephotellus* vs. *Clarkona*; *Aratinga* vs. *Nandayus*), regardless of the patterns of phenotypic diversity among the various species. Further, it retains all three recognized genera albeit with some inevitable but minimal disruption to their usage, and it presents no conflict between classification and phylogeny. Although it places in the same genera species that are somewhat different in gross morphology, e.g., relative tail length and shape, this is common to either of the arrangements we discussed (see fig. 6). The difficulty of discerning phenotypic traits in diagnosing the three genera as so circumscribed

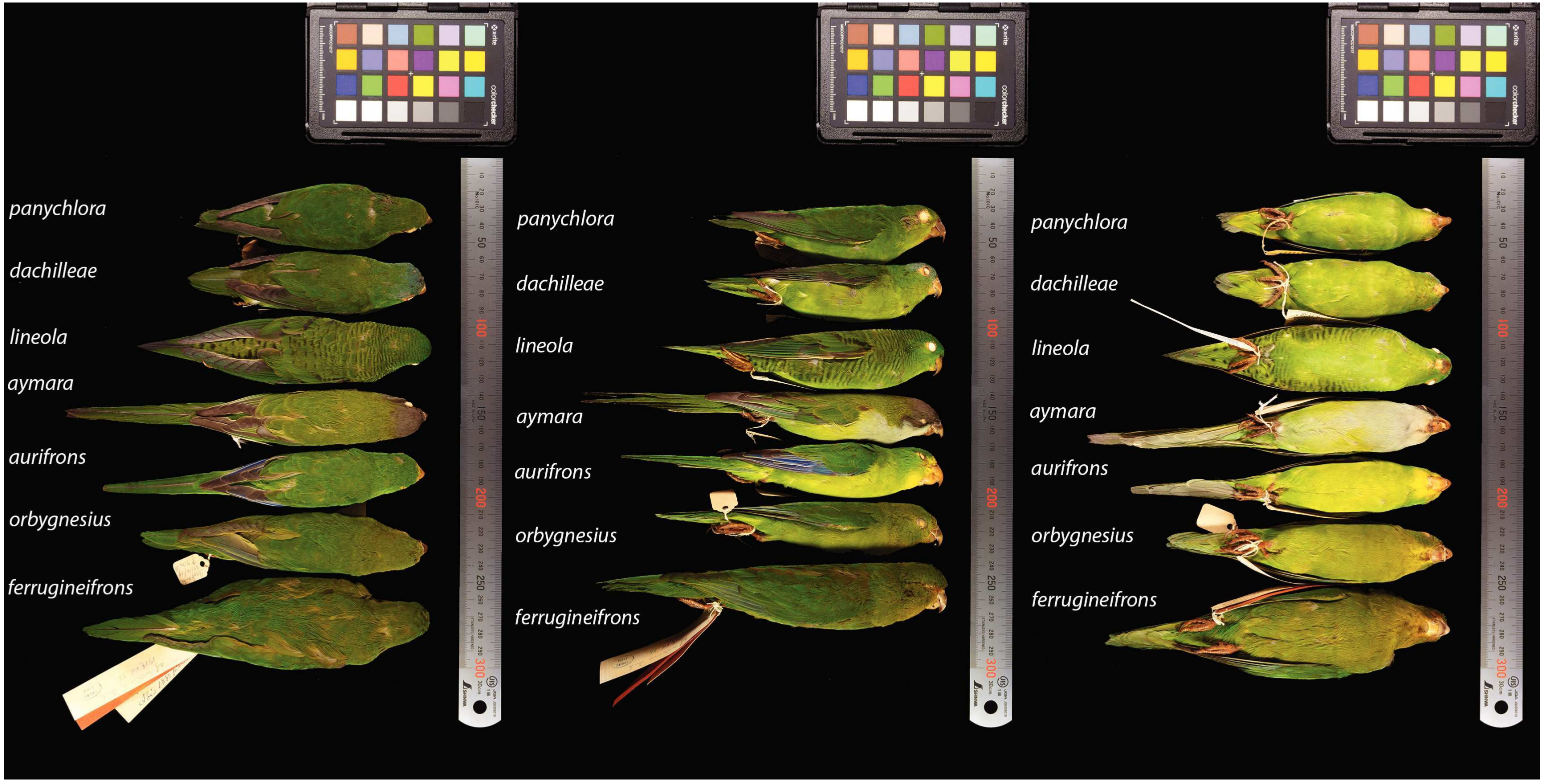


FIGURE 6. Specimens from the American Museum of Natural History (AMNH) and Louisiana State University Museum of Natural Science (LSUMNS) showing proposed groupings for (left to right): *Nannopsittaca panychlora* AMNH 324136, *Bolborhynchus* (*dachilleae* LSUMNS 156199; *lineola* AMNH 820295), and *Psilopsiagon* (*aymara* AMNH 136906; *aurifrons* AMNH 151238; *orbygnesius* AMNH 168922; and *ferrugineifrons* AMNH 44744). Photographs: Sahid Robles Bello.

warrants brief comment. We suggest that this likely arises from very strong selective pressures on these species for cryptic, largely green plumage (see fig. 6). This could feasibly apply to either species inhabiting and primarily foraging in lowland or upland rainforest canopies, such as *dachilleae* and *panychlora*, respectively, or to those foraging in other montane habitats such as lower, scrubby hillside vegetation and terrestrial bogs, as in most of the other species.

We stress that the need for recognition of these three genera and their circumscriptions as we have suggested have arisen largely from our concerns with reflecting the phylogenomic data and structure among them. In summary, we advocate the following taxonomy with phenotypic notes (fig. 6):

- *Psilopsiagon* Ridgway, 1912: *P. ferrugineifrons*, *P. orbygnesius*, *P. aurifrons*, *P. aymara*. Predominantly green plumage with patterning that does not involve barring and moderate to long tails. Species membership in *Psilopsiagon* is tentative pending clearer resolution of phylogenetic relationships. *Amoropsittaca* Richmond, 1915 is available for *aymara* if warranted.
- *Nannopsittaca* Ridgway, 1912: *N. panychlora*. Short-tailed, green plumage with little or no blue particularly in the crown but with a distinctive "broken" ring of yellow periophthalmic feathering. Orbital region mostly feathered (Ridgway, 1916). Bill and cere generally dark gray.
- *Bolborhynchus* Bonaparte, 1857: *B. lineola*, *B. dachilleae.* Diagnostic phenotypic traits shared by the two species are difficult to discern beyond both being short-tailed green parrotlets. *Bolborhynchus lineola* has barred dorsal plumage, which we postulate to be derived, recalling that of Australian *Pezoporus* and *Melopsittacus* and arising from black feather centers on the ventral surface especially under the tail. *B. dachilleae* has generally plainer green plumage, which we postulate as ancestral, apart from a distinctive blue crown. In *B. dachilleae*, the orbital region's bare skin is whitish and the bill and cere are pinkish buff, not dark gray as in *Nannopsittaca* (O'Neill et al., 1991) whereas the similarly colored bill of *B. lineola* is often distally tipped dark. *Bolborhynchus lineola* and *N. dachilleae* are strongly associated with bamboo (see option 4 above), an ecological preference, to our knowledge that has not been observed in *N. panychlora*.

Androglossini and Brotogerini

The next clade to be discussed is diverse, consisting of the amazons and their allies, and has mostly been termed the Androglossini in recent literature (e.g., Joseph et al., 2012; Schodde et al., 2013). We acknowledge the current literature on the correct family-group name for this tribe. Gregory and Sangster (2023) advocate Amazonini in contrast to Joseph et al.'s (2012) and Schodde et al.'s (2013) arguments for Androglossini. Schodde (accepted) has further contested the use of Amazonini in favor of Androglossini. Until this is settled, we use Androglossini.

More immediately relevant here, then, is that within the Androglossini there was a deep divergence dating to 25.6 Mya (17.7–29.9; fig. 1). The two clades resulting from this divergence are diagnostic with respect to their tail morphology. One clade comprises the genera *Myiopsitta* and *Brotogeris*, which have longer, attenuate or pointed tails that are atypical characteristics of the tribe. The sister clade, comprising *Pionopsitta*, *Triclaria*, *Pyrilia*, *Hapalopsittaca*, *Amazona*, *Pionus*, *Graydidascalus*, and *Alipiopsitta*, has species with mostly round and proportionately short tails. The relationship is supported in the species tree, but support for the node and inclusion of both *Brotogeris* and *Myiopsitta* varied depending on how strictly the sample retention was set. Interestingly, whole genome data from an exemplar from each clade (*Myiopsitta monachus* and *Amazona aestiva*) have diploid numbers of 48 and 70 (Huang et al., 2022). This level of variation, due to the fusion of autosomal and sex chromosomes, is atypical for birds because avian karyotypes and genome sizes are generally conserved; birds usually have diploid numbers with a range of 76–82 (Kapusta and Suh, 2017; Zhang, 2018; Furo et al., 2020). The two species of *Brotogeris* that have been karyotyped exhibit different diploid numbers (*B. sanctithomae* 72 and *B. versicolurus* 82 chromosomes; de Lucca et al., 1991), indicating that extensive chromosome fusion may not be a general characteristic of the clade containing *Brotogeris* and *Myiopsitta*.

We are aware of no prior family-group name to accommodate the genera *Brotogeris* and *Myiopsitta*. In accordance with articles 13.1 and 13.2 of the Code (ICZN, 1999) we therefore introduce a new family-group name at the rank of tribe for these two genera:

Brotogerini, new tribe

Zoobank registration: urn:lsid:zoobank.org:pub:3BFB5FD8-9DDC-4419-9EEF-D41AFBB2E9B1

Diagnosis: In accordance with Article 13.1.1, we note that Brotogerini differs from the members of the Androglossini (in the sense used above) from which it is separated principally in the morphology of the tail, which relative to the body is long and attenuated in *Brotogeris* and *Myiopsitta* rather than short and rounded in all other genera in Androglossini. In accordance with Article 13.1.2, we note that this difference has been well illustrated and described on many occasions in the literature, citing as examples reference works on the world's parrots: e.g., Forshaw and Knight (2010); Juniper and Parr (1998).

Type genus *Brotogeris* Vigors, 1825, *Zoological Journal* 2: 400, by original designation. Type species *Psittacus pyrrhopterus* Latham 1801, Supplementum Indicis Ornithologici, 1801: xxii.

Taxonomic position of tribe: Subfamily Arinae of family Psittacidae.

Component genera: *Brotogeris* Vigors, 1825, and *Myiopsitta* Bonaparte, 1854.

Myiopsitta Bonaparte, 1854. Revue et magasin de zoologie pure et appliquée.(2), 6, 1854: 150. Type, by subsequent designation, *Psittacus monachus* Boddaert (G.R. Gray, *Catalogue of the Genera and Subgenera of Birds Contained in the British Museum* , 1855: 87)

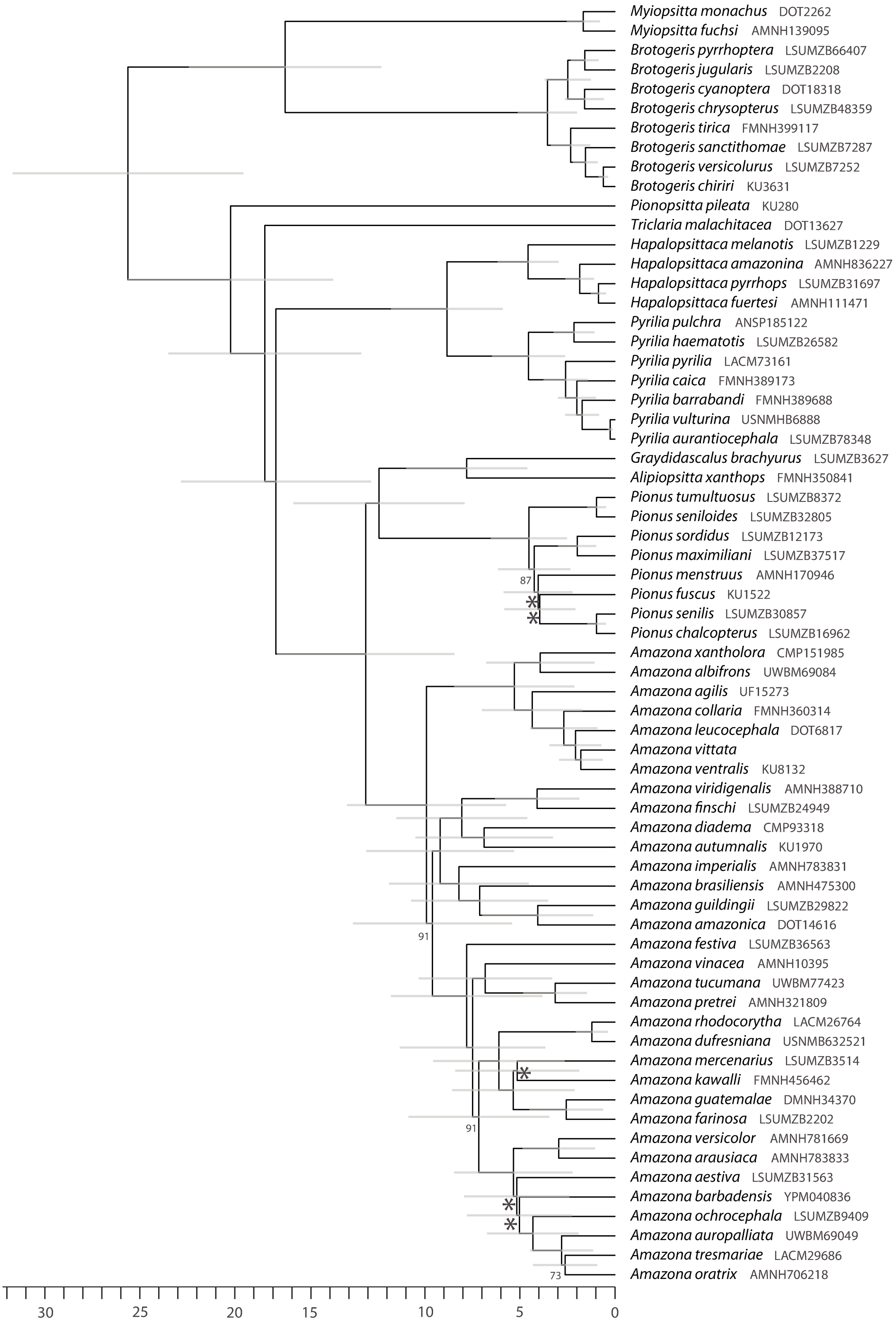
Geographic distribution: Endemic from South America to Mexico.

Brotogeris

Brotogeris are smaller, largely green parrots with pointed, graduated tails varying in relative proportion to body size, however. Relationships among the eight recognized species in the genus are strongly supported and concordant across molecular phylogenies (e.g., Ribas et al., 2009). General tail morphology does not conform neatly to phylogenetic groups. The three longer-tailed species (*B. tirica*, *B. versicolurus*, and *B. chiriri*) are in one clade with shorter-tailed *B. sanctithomae* of the Amazonian floodplain. The other clade contains *B. pyrrhoptera*, *B. jugularis*, *B. cyanoptera*, and *B. chrysoptera*. The majority of the species are distributed east of the Andes in the Amazon Basin. There was a cross-Andes divergence (1.3–3.7 Mya) represented by the split between *B. pyrrhoptera*/*B. jugularis* and *B. cyanoptera*/*B. chrysoptera*. *Brotogeris jugularis* is the only species in Central America, so dispersal out of South America occurred over the Panamanian land bridge. No study to date has sampled across the range of *B. jugularis*, which spans from Mexico to Venezuela, but northward dispersal most likely occurred within the Pleistocene, the time frame after *B. pyrrhoptera* and *B. jugularis* split.

Myiopsitta

Myiopsitta are midsized parrots with pointed, attenuate tails. Uniquely among all parrots it nests not in hollows in trees, cliffs, or rock faces, but in nests of sticks constructed by the birds and placed in trees, cliffs, or in more anthropo-


Myiopsitta monachus DOT2262
Myiopsitta fuchsi AMNH139095
Brotogeris pyrrhoptera LSUMZB66407
Brotogeris jugularis LSUMZB2208
Brotogeris cyanoptera DOT18318
Brotogeris chrysopterus LSUMZB48359
Brotogeris tirica FMNH399117
Brotogeris sanctithomae LSUMZB7287
Brotogeris versicolurus LSUMZB7252
Brotogeris chiriri KU3631
Pionopsitta pileata KU280
Triclaria malachitacea DOT13627
Hapalopsittaca melanotis LSUMZB1229
Hapalopsittaca amazonina AMNH836227
Hapalopsittaca pyrrhops LSUMZB31697
Hapalopsittaca fuertesi AMNH111471
Pyrilia pulchra ANSP185122
Pyrilia haematotis LSUMZB26582
Pyrilia pyrilia LACM73161
Pyrilia caica FMNH389173
Pyrilia barrabandi FMNH389688
Pyrilia vulturina USNMHB6888
Pyrilia aurantiocephala LSUMZB78348
Graydidascalus brachyurus LSUMZB3627
Alipiopsitta xanthops FMNH350841
Pionus tumultuosus LSUMZB8372
Pionus seniloides LSUMZB32805
Pionus sordidus LSUMZB12173
Pionus maximiliani LSUMZB37517
Pionus menstruus AMNH170946
Pionus fuscus KU1522
Pionus senilis LSUMZB30857
Pionus chalcopterus LSUMZB16962
Amazona xantholora CMP151985
Amazona albifrons UWBM69084
Amazona agilis UF15273
Amazona collaria FMNH360314
Amazona leucocephala DOT6817
Amazona vittata
Amazona ventralis KU8132
Amazona viridigenalis AMNH388710
Amazona finschi LSUMZB24949
Amazona diadema CMP93318
Amazona autumnalis KU1970
Amazona imperialis AMNH783831
Amazona brasiliensis AMNH475300
Amazona guildingii LSUMZB29822
Amazona amazonica DOT14616
Amazona festiva LSUMZB36563
Amazona vinacea AMNH10395
Amazona tucumana UWBM77423
Amazona pretrei AMNH321809
Amazona rhodocorytha LACM26764
Amazona dufresniana USNMB632521
Amazona mercenarius LSUMZB3514
Amazona kawalli FMNH456462
Amazona guatemalae DMNH34370
Amazona farinosa LSUMZB2202
Amazona versicolor AMNH781669
Amazona arausiaca AMNH783833
Amazona aestiva LSUMZB31563
Amazona barbadensis YPM040836
Amazona ochrocephala LSUMZB9409
Amazona auropalliata UWBM69049
Amazona tresmariae LACM29686
Amazona oratrix AMNH706218
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genic environments on poles and near buildings (see *Agapornis* below for other parrots that construct smaller nests). They occur in southern South America and have a number of naturalized populations around the globe (Edelaar et al., 2015). *Myiopsitta monachus* occurs in southern Brazil through northern Argentina and Uruguay, and *M. luchsi* is distributed in the Andean valleys of Bolivia. *Myiopsitta luchsi* has long been a subspecies of *M. monachus* and is still treated by some as such (e.g., South American Checklist Committee) whereas others have elevated it to species rank (e.g., IOC). The rationale that has been given for species-rank recognition of *M. luchsi* is in its genetic and phenotypic distinctiveness, ecological divergence in occupying higher elevations, and obligatory cliff-nesting, as opposed to nest construction in trees (Russello et al., 2008). The South American Checklist Committee (proposal 503) rejected these arguments based on the limited mtDNA differentiation of *luchsi* from other taxa, and the lack of both a formal vocal analysis and a published description of how their nesting ecology differs. The phylogenomic molecular dating provides new temporal context for the debate on species limits in *Myiopsitta*, the divergence likely more than a million years (1.7 Mya: 0.8–2.6).

Androglossini

With *Brotogeris* and *Myiopsitta* now separated in Brotogerini, we note that relationships among genera that remain within Androglossini were well resolved. *Pionopsitta pileata* (13.3–24.1 Mya) and then *Triclaria malachitacea* (11.9–22.1 Mya) were deeply split from the remaining taxa in their clade (fig. 7). In the species tree from Smith et al. (2023), *Triclaria malachitacea* was sister to the clade containing *Pyrilia* and *Hapalopsittaca* with varying levels of support across trees with different filtering treatments (LPP = 0.6–0.98). Both of these monotypic genera are endemic to humid, rainforest habitats in Brazil's Atlantic Forest, and they are predominantly in sympatry. Notably, the Atlantic Forest has many other "relict" species, which like these two genera, are on long branches in phylogenetic analyses (e.g., *Pyrrhura cruentata*).

The next major divergence in the core Androglossini was the split between *Pyrilia*/*Hapalopsittaca* and the remaining genera at 11.4–21.4 Mya. The final subclade had *Amazona* sister to *Pionus*/*Graydidascalus*/*Alipiopsitta*. *Graydidascalus* of Amazonian floodplains and *Alipiopsitta* of open cerrado woodlands in central Brazil are also monotypic genera. *Alipiopsitta xanthops* was formerly within *Amazona*, but it has been consistently placed in monotypic *Alipiopsitta* due to its robustly supported placement outside *Amazona* (Tavares et al., 2006; Schirtzinger et al., 2012). The two genera were estimated to have shared a common ancestor 4.1–10.4 Mya and diverged from *Pionus* 6.8–15.8 Mya (fig. 7). In the species tree *Alipiopsitta xanthops* was sister to *Amazona*/*Pionus*/*Graydidascalus*, but the sample was dropped from more stringent alignments due to a high amount of missing data at parsimony informative sites (Smith et al., 2023).

Pionopsitta

The sole species in this genus, *Pionopsitta pileata*, is midsized and mostly green apart from its red coronal and facial plumage. Although it ranges into some drier forest and woodland habitats in Argentina and Paraguay, it is essentially an Atlantic Forest endemic of southeastern Brazil. Our data support the now well-established retention of this species in monotypic *Pionopsitta* of which it is the type species, and the removal of the other species that had been placed in *Pionopsitta* into *Pyrilia* (see Ribas et al., 2005;

←

FIGURE 7. Species-level time-calibrated topology of Androglossini and Brotogerini. Support values come from the maximum likelihood tree. * denotes an unsupported node where the topology of the presented time-calibrated phylogeny differs from that of the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted. Gray bars represent divergence time ranges were estimated from 100 bootstrap trees.

FIGURE 8. Photographs (not to scale) of *Calyptomena hosii* (left photo: Dubi Shapiro) a suboscine passerine of Borneo (Brunei, Indonesia) and *Triclaria malachitacea* (right photo: Marcos Eugênio) of southeastern Brazil showing presumably convergent evolution in ventral coloring. See text for discussion. Photographs reproduced with permission from the photographers.

Eberhard and Bermingham, 2005). The distinctiveness of *Pionopsitta* was further reflected by its deep split from the rest of Androglossini at 20.2 Mya (13.3–24.1).

Triclaria

Triclaria malachitacea is a midsized green parrot in which males have a unique blue abdominal (belly) patch sometimes extending to the lower breast, and with a relatively long tail for Androglossini. It is another Atlantic Forest endemic found in the lower montane forests of southeastern Brazil (Forshaw and Knight, 2010). Apparently, the striking and presumably convergent evolution in the plumage of the underparts of this species and that of a similarly sexually dichromatic suboscine passerine *Calyptomena hosii* of Indonesia has never been noted (fig. 8). Study of the drivers of this convergence would surely be rewarding and presumably may relate to the function of blue in displays of birds inhabiting forests and the forest strata at which the blue is functional in those rainforests (see Endler, 1993).

Pyrilia

Pyrilia are midsized, stocky parrots of humid forest lowlands in Central America through the Amazon Basin. They are predominantly green, but each has a distinctively colored pattern of plumage or skin about the head. Two species remarkable for largely bare heads were formerly placed in *Gypopsitta* Bonaparte, 1856. Banks et al. (2008) demonstrated why *Pyrilia* Bonaparte, 1856, has priority over *Gypopsitta* Bonaparte, 1856, for this assemblage.

The phylogenomic concatenated and species trees differ in the placement of *P. caica* amongst the trees and with previous studies based on mitochondrial DNA and plumage characters (Ribas et al., 2005, Eberhard and Bermingham, 2005). In the phylogeny by Ribas et al. (Ribas et al., 2005), which includes subspecific sampling, *P. caica* was sister to *P. vulturina*/*P. aurantiocephala*. The phylogenomic species tree, however, had *P. caica* as sister to *P. barrabandi*, and they were in turn sister to *P. vulturina*/*P. aurantiocephala*. The phylogenomic concatenated tree had *P. caica* as sister to the clade containing *P. barrabandi*, *P. vulturina*, and *P. aurantiocephala*. These alternative topologies support different biogeographic sequences of divergence. The species tree sister relationship between *P. caica* and *P. barrabandi* supports an initial break across the Rio Negro, whereas the concatenated and prior mtDNA trees support alternative scenarios involving the initial divergence across the Amazon river and Andes. None of the trees support a clade (*P. haematotis*, *P. pulchra*, and *P. pyrilia*) distributed west of the Andes indicating there were multiple crossings over or around the Andes. The time-calibrated phylogenomic tree supported a relatively shallow temporal scale for the diversification of *Pyrilia* (crown age 4.5 Mya [2.6–6.5]).

Hapalopsittaca

Hapalopsittaca is a low-diversity clade comprising four midsized species that occur in allopatry across humid forests of the Andes. Relationships among the species reflect a stepping-stone pattern across the linear distribution of the Andes. The first split, dated to 4.6 Mya (2.8–6), was between a northern clade containing *H. amazonina*, *H. fuertesi*, and *H. pyrrhops* from a southern lineage, *H. melanotis*, which occurs disjunctly along the eastern slopes of the Andes to Huánuco to Cusco, Peru, and La Paz to Cochabamba, Bolivia. The two remaining divergences occurred within the Pleistocene and resulted in the divergence of *H. amazonina* of the Colombian Andes from *H. fuertesi* of the Cordillera Central in western Colombia, and *H. pyrrhops* ranging from southern Ecuador to northern Peru.

Amazona

Amazona is a diverse yet easily recognizable clade of mid- to large-sized stocky birds with relatively short tails, large heads, and barred plumage. Most species are green with colorful patterning on the head but a few Caribbean species have plainer or more elaborate plumage. The concatenated and species trees are largely concordant and indicate at least three independent colonizations of the Caribbean. The main discrepancy between them arises from the relatively high number of lower-quality samples that were not accurately placed in the species tree. Our topology was generally concordant with that of Rusello and Amato (2004) with the exception of the position of two clades (1, 2) that stemmed from short internodes and were placed in our tree with high support: (1) *A. festiva*, *A. pretrei*, *A tucumana*, and *A. vinacea*; and (2) *A. amazonica*, *A. guildingii*, *A. brasiliensis*, and *A. imperialis*. The basal divergence in *Amazona* dated to 9.9 Mya (4.7–13.1; fig. 7). It separates a clade of smaller bodied Caribbean (*A. agilis*, *A. vittata*, *A. ventralis*, *A. leucocephala*, and *A. collaria* and Central American/Mexican (*A. xantholora* and *A. albifrons*) species from all other *Amazona*, a phylogenetic position recovered previously by Russello and Amato (2004). This clade includes dichromatic species (*A. agilis*, *A. xantholora*, and *A. albifrons*), a character state that is generally lacking in *Amazona*. Ancient DNA and archaeological evidence show that *Amazona* in the Greater Antilles, specifically *A. leucocephala* and *A. ventralis*, were translocated across the Caribbean and had natural, more widespread ranges in the past (Oswald et al., 2023). *Amazona leucocephala* was also found to have intraisland divergences throughout the Pleistocene. The next divergence results in two sister clades whose short node now has more support (UFBS = 91% vs. BS = 53%) than that in Russello and Amato (2004). The first clade had a crown age of 9.2 Mya (4.4–12.1) and includes a heterogeneous group of species spanning from Mexico (e.g., *A.*

viridigenalis, *A. finschi*) to Brazil (*A. diadema*, *A. amazonica*; fig. 7). It also represents a colonization of the Caribbean (*A. imperialis* and *A. guildingii*). *Amazon guildingii* is polymorphic, having yellow-brown and green plumage morphs (Forshaw and Knight, 2010). The second of the major sister clades is also geographically widespread and consists of two independent colonizations of Central America. The first was seen in the divergence within what was formerly treated as a single species *A. farinosa*. It supports species rank for its Central American populations now recognized as *A. guatemalae* with two subspecies *A. g. guatemalae* and *A. g. virenticeps*. This accords with Wenner et al.'s (2012) phylogeographic study on the *A. farinosa* complex in which they detected a deep divergence between Central and South American lineages (1.75–2.70 Myr split in mtDNA). Our estimate was comparable but older. Together, the two data sets support divergence that reflects independent evolution of *A. farinosa* and *A. guatemalae* irrespective of a potential contact zone, vocal differences, or morphological distinctiveness. Chesser et al. (2023) did not recognize *A. guatemalae* as a species, arguing that a more thorough population-level study is necessary to better understand species limits. The second divergence across the Isthmus of Panama involves the yellow-headed Amazons and the split of *A. ochrocephala* from *A. oratrix* and *A. auropalliata* of Central America and Mexico, and *A. tresmariae* of the Tres Marias Islands of the Pacific Coast of Mexico. The recognition of these lineages as species (as opposed to subspecies) was in part due to phylogeographic studies that found deep genetic divisions within the yellow-headed Amazon complex (Eberhard and Bermingham, 2004; Ribas et al., 2007b). *Amazona tresmariae*, as with *A. guatemalae*, was not recognized as a species by the North American Checklist Committee for similar reasons of inconclusive data (Chesser et al., 2023). This clade was sister to the third colonization of the Caribbean where *A. barbadensis* of Venezuela and neighboring islands was sister to *A. versicolor* of St. Lucia and *A. arausiaca* of Dominica. The final clade was a group of three species, *A. vinacea*, *A. tucumana*, and *A. pretrei*, that have a southern distribution in Bolivia, Argentina, Brazil, and Paraguay.

Pionus

Pionus comprises a small radiation mostly predominantly either green or bronze-green and blue, midsized parrots with square tails that are distributed from Mexico to Argentina and southern Brazil (Forshaw and Knight, 2010). *Pionus* has a crown age of 4.5 Mya (2.3–6.3), a temporal span that overlaps the estimated ages of Ribas et al. (2007a), but the phylogenomic ages are younger. There was considerable topological disagreement between the phylogenomic trees and a previously published mtDNA tree of *Pionus* (2007a). Immediate sister pairs (*P. senilis*/*P. chalcopterus*; *P. seniloides*/*P. tumultuosus*; and *P. maximiliani*/*P. sordidus*) are consistent across all trees, but most other nodes differ. The widely distributed *Pionus menstruus* was included in the present study but not in Smith et al. (2023), due to a sampling error detected prior to that work's publication. *Pionus fuscus* of the Guianan Shield and adjoining parts of Amazonia is exceptional in the genus in lacking green in its otherwise predominantly brown, blue and red plumage. Both of these species are in unresolved positions in the concatenated tree. *Pionus fuscus* was strongly supported as sister to *P. senilis* and *P. chalcopterus* in the concatenated tree in Smith et al. (2023). However, the inclusion of *P. menstruus* in this study destabilized the position of *P. fuscus*. This may be due in part to our *P. menstruus* coming from a historical museum specimen. The species tree had *P. fuscus* as sister to *P. seniloides* and *P. tumultuosus* (LPP = 1.0). Ribas et al. (2007a) had a third alternative topology, and placed *P. fuscus* as sister to *P. sordidus* and *P. maximiliani*, and *P. menstruus* as sister to *P. chalcopterus* and *P. senilis*. The disparity between the concatenated and species trees presented here was illuminating in that all nodes are supported in the species tree and all internal nodes differ. Another distinction between studies was that Ribas et al. (2007a) included samples of subspecies, which showed deep divergences within species (e.g., *P. sordidus*). Subsequent phylogeographic research on *Pionus senilis* of Mexico and Central America found genetic structure across its range that coalesces to 1.3 Mya (Rivera-Arroyo et al., 2022). Future work with more extensive genome-level sampling will be necessary to resolve the high phylogenetic discordance observed in *Pionus*.

Graydidascalus

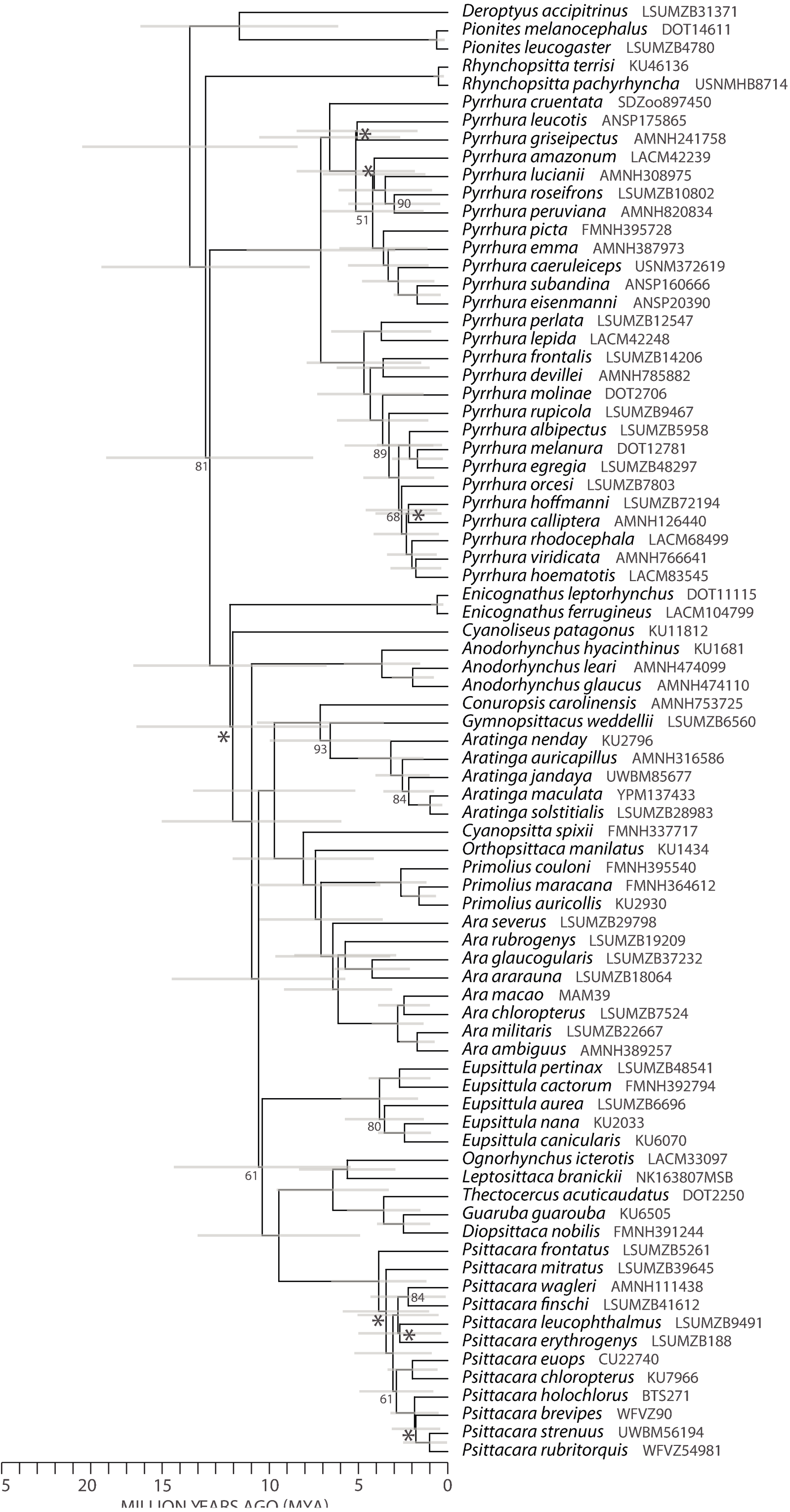
Graydidascalus brachyurus occurs throughout the Amazonian floodplains and is a midsized, predominantly green stocky parrot with black lores, prominent red iris, very short tail, and unusually large bill. As with many other Amazonian birds of floodplains, it is taxonomically monotypic having no described geographic variation (Forshaw, 1973; Remsen and Parker, 1983), yet it may contain uncharacterized genetic structuring along rivers (Thom et al., 2020). *Graydidascalus brachyurus* shares a common ancestor with *Alipiopsitta xanthops* 7.8 Mya (4.1–10.4), reflecting a long period, in both taxa, during which taxonomic or geographic variation did not accumulate.

Alipiopsitta

Alipiopsitta xanthops was formerly placed in *Amazona* due to similarities in size, shape, and general plumage. However, phylogenetic work since the early 1990s shows that *Al. xanthops* was paraphyletic with respect to *Amazona* (Birt et al., 1992), which to our knowledge, has been confirmed by all subsequent molecular studies, including the phylogenomic data presented here. Further, comparisons of karyotypes in Arini showed high similarity between *Al. xanthops*, *Pionus maximiliani*, and *Graydidascalus brachyurus*, and indicated a sister relationship between *Alipiopsitta* and *Graydidascalus* (Caparroz and Duarte, 2004). That sister relationship was supported by DNA sequence data (Russello and Amato, 2004) and our phylogenomic tree. Its continued placement in *Amazona* in some sources (e.g., Forshaw and Knight, 2010), likely an artifact of when the book was published, is unfounded. As noted by Caparroz and Pacheco (2006), Miranda-Ribeiro (1920) erected a new genus *Salvatoria* for *xanthops* to differentiate it from "true" *Amazona*, but this name was preoccupied by *Salvatoria* McIntosh, 1885, a genus of polychaete worms. Accordingly, *Alipiopsitta* was erected (Caparroz and Pacheco, 2006). *Alipiopsitta xanthops* is also polymorphic in that its plumage has green and yellow morphs. Such plumage polymorphism, excluding sexual and age-related dimorphism, is generally rare in parrots, other examples being *Charmosyna stellae*, *Pseudeos fuscata*, *Amazona ochrocephala*, and *A. guildingii*. There is no described geographic variation in *Al. xanthops*. As noted, *Al. xanthops* and *G. brachyurus* shared a common ancestor 7.8 Mya (4.1–10.4).

Arini

Arini exhibits a wide range in body sizes and is a colorful group, including the largest extant parrots, the macaws. It ranges from Mexico (formerly southwestern U.S.) to Argentina. Within Arinae, the Arini is the most speciose clade. Arini also contains a number of other low-diversity genera (2–3 species). *Enicognathus*, *Rhynchopsitta*, and *Pionites*, which, like *Deroptyus* and *Cyanoliseus*, are all on long branches within Arini (fig. 9). The round-tailed *Pionites* and *Deroptyus* shared a common ancestor with the clade that comprises all other Arini at 14.5 Mya (7.1–19.2), which are long-tailed parrots, parakeets, and macaws (fig. 9). Depending on the threshold used to include lower quality samples, the position of *Rhynchopsitta* of Mexico and, formerly, Arizona varied across different phylogenomic trees. The main source of phylogenetic uncertainty for *Rhynchopsitta* was the position of *Pyrrhura*, which was separated from other clades within Arini by a short branch. In the concatenated tree, albeit with more modest ultrafast bootstrap support (81%) and in the most stringent species tree with high support, *Rhynchopsitta* was sister to


Deroptyus accipitrinus LSUMZB31371
Pionites melanocephalus DOT14611
Pionites leucogaster LSUMZB4780
Rhynchopsitta terrisi KU46136
Rhynchopsitta pachyrhyncha USNMHB8714
Pyrrhura cruentata SDZoo897450
Pyrrhura leucotis ANSP175865
Pyrrhura griseipectus AMNH241758
Pyrrhura amazonum LACM42239
Pyrrhura lucianii AMNH308975
Pyrrhura roseifrons LSUMZB10802
Pyrrhura peruviana AMNH820834
Pyrrhura picta FMNH395728
Pyrrhura emma AMNH387973
Pyrrhura caeruleiceps USNM372619
Pyrrhura subandina ANSP160666
Pyrrhura eisenmanni ANSP20390
Pyrrhura perlata LSUMZB12547
Pyrrhura lepida LACM42248
Pyrrhura frontalis LSUMZB14206
Pyrrhura devillei AMNH785882
Pyrrhura molinae DOT2706
Pyrrhura rupicola LSUMZB9467
Pyrrhura albipectus LSUMZB5958
Pyrrhura melanura DOT12781
Pyrrhura egregia LSUMZB48297
Pyrrhura orcesi LSUMZB7803
Pyrrhura hoffmanni LSUMZB72194
Pyrrhura calliptera AMNH126440
Pyrrhura rhodocephala LACM68499
Pyrrhura viridicata AMNH766641
Pyrrhura hoematotis LACM83545
Enicognathus leptorhynchus DOT11115
Enicognathus ferrugineus LACM104799
Cyanoliseus patagonus KU11812
Anodorhynchus hyacinthinus KU1681
Anodorhynchus leari AMNH474099
Anodorhynchus glaucus AMNH474110
Conuropsis carolinensis AMNH753725
Gymnopsittacus weddellii LSUMZB6560
Aratinga nenday KU2796
Aratinga auricapillus AMNH316586
Aratinga jandaya UWBM85677
Aratinga maculata YPM137433
Aratinga solstitialis LSUMZB28983
Cyanopsitta spixii FMNH337717
Orthopsittaca manilatus KU1434
Primolius couloni FMNH395540
Primolius maracana FMNH364612
Primolius auricollis KU2930
Ara severus LSUMZB29798
Ara rubrogenys LSUMZB19209
Ara glaucogularis LSUMZB37232
Ara ararauna LSUMZB18064
Ara macao MAM39
Ara chloropterus LSUMZB7524
Ara militaris LSUMZB22667
Ara ambiguus AMNH389257
Eupsittula pertinax LSUMZB48541
Eupsittula cactorum FMNH392794
Eupsittula aurea LSUMZB6696
Eupsittula nana KU2033
Eupsittula canicularis KU6070
Ognorhynchus icterotis LACM33097
Leptosittaca branickii NK163807MSB
Thectocercus acuticaudatus DOT2250
Guaruba guarouba KU6505
Diopsittaca nobilis FMNH391244
Psittacara frontatus LSUMZB5261
Psittacara mitratus LSUMZB39645
Psittacara wagleri AMNH111438
Psittacara finschi LSUMZB41612
Psittacara leucophthalmus LSUMZB9491
Psittacara erythrogenys LSUMZB188
Psittacara euops CU22740
Psittacara chloropterus KU7966
Psittacara holochlorus BTS271
Psittacara brevipes WFVZ90
Psittacara strenuus UWBM56194
Psittacara rubritorquis WFVZ54981
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all other Arini (except *Pionites* and *Deroptyus*; Smith et al., 2023). Previous work recovered *Rhynchopsitta* as part of a polytomy at the base of Arini or in an unsupported position (Tavares et al., 2006; Wright et al., 2008). *Rhynchopsitta*'s phylogenetic position curiously also reflects one of two large biogeographic disjunctions in Arini. Its distribution in the Mexican highlands can be explained by a single colonization of Central and North America. The occurrences of all other species in Arini in Central America and Mexico are attributable to multiple independent dispersal events. In addition to the colonization of North America and the current large disjunction from South American lineages, *Rhynchopsitta* species are also characterized by a considerable ecological shift. The genus specializes in high-elevation pine forests that occur throughout temperate western North America to Nicaragua, a habitat type that has low psittaciform diversity and one species of which, *R. terrisi*, obligatorily nests in cliff faces.

The remaining taxa in Arini fall into two clades that separated between 6.4–18 Mya (fig. 9). One clade consists of the most speciose genus in Arini, *Pyrrhura*, which began radiating 7.1 Ma (2.2–10.6). The sister clade to *Pyrrhura* contains 15 genera, reflecting the high morphological disparity within this group of Arini. The basal divergence within this sister clade was that of the two temperate South American sister genera (*Enicognathus* and *Cyanoliseus*) from the remaining taxa in Arini. As with previous studies (Wright et al., 2008; Schirtzinger et al., 2012), the phylogenomic tree confirms that neither the large-bodied macaws nor the blue macaws are monophyletic (fig. 9). The large-bodied and large-billed blue macaws in *Anodorhynchus* diverged from the remaining Arini at an early internode. In contrast, the mostly large-bodied and colorful macaws in *Ara* were sister to the genus *Primolius* in a clade that includes all blue *Cyanopsitta* and *Orthopsittaca* (fig. 9). The clade containing *Ara*, *Primolius*, *Cyanopsitta*, and *Orthopsittaca* had a crown age of 8.1 Mya (3.5–11.4; fig. 9). Our results reaffirmed previous findings that *Aratinga* as traditionally recognized is not monophyletic and that instead breaking it up into three genera *Aratinga*, *Eupsittula*, and *Psittacara* is warranted (e.g., Remsen et al., 2013*)*. The position of *Eupsittula* was unresolved in the phylogenomic tree (fig. 9). In the concatenated tree, we found that *Eupsittula* was sister to a clade containing *Psittacara* and *Thectocercus*, *Diopsittaca*, *Guaruba*, *Leptosittaca*, and *Ognorhynchus* with low support (UFBS <70%). In the species tree, *Eupsittula* was sister to *Aratinga*, *Ara*, *Primolius*, *Cyanopsitta*, and *Orthopsittaca*, but also with low support (LPP = 0.79). In both phylogenomic trees, the *Aratinga* sensu stricto species comprise the sister group to *Conuropsis* and in a clade with *Ara*, *Primolius*, *Cyanopsitta*, and *Orthopsittaca* (fig. 9). Also notable within *Aratinga* sensu stricto is that *A. weddellii* of western lowland Amazonia was on a relatively long branch and sister to all other *Aratinga* sensu stricto. It exemplifies a dilemma of whether such species should be separated generically (cf. whether among Australian parrots *Psephotellus varius* should be separated generically or, at least, subgenerically through genus-group name *Clarkona*). A genus-group name is available for *A. weddellii* and we discuss its reintroduction below.

The remaining taxa formerly in *Aratinga* comprise the genus *Psittacara* and are sister to a clade containing five monotypic genera (*Thectocercus*, *Diopsittaca*, *Guaruba*, *Leptosittaca*, and *Ognorhynchus*). These five South American taxa have a crown age of only 6.4 Mya (2.8–9.1), are phenotypically distinct, and span a wide range of ecoregions.

◄

FIGURE 9. Time-calibrated topology of Arini. Support values come from the maximum likelihood tree. * denotes an unsupported node where the topology of the presented time-calibrated phylogeny differs from that of the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted. Gray bars represent divergence time ranges were estimated from 100 bootstrap trees.

Deroptyus

Deroptyus comprises one species, *D. accipitrinus*, whose placement at or near the end of linear taxonomic sequences (e.g., Peters, 1937; Forshaw, 1973; Forshaw and Knight, 2010) reflects either uncertainty as to its relationships or a hypothesized close relationship to *Amazona*. The species' phenotypic uniqueness warrants comment. While dorsally its plumage is unexceptionally mostly green, uniqueness arises from the combination of the following: dark facial plumage streaked white, the yellow eye of adults, the feathers of the underparts and hind neck red or maroon with a terminal blue band, and the erectile feathers of its hind neck, which can be raised into a ruff, perhaps the only parrot to which this term could validly be applied. These combine to give the species its "hawk-headed" appearance. Its two conventionally recognized subspecies, *D. a. accipitrinus* and *D. a. fuscifrons*, occur north and south respectively of the Solimões/Amazon river system.

We have clarified here that *Deroptyus* is part of the earliest divergence in the Arini, as sister to *Pionites* on one of the two branches of that earliest divergence (fig. 9).

Pionites

Pionites has traditionally comprised two species of medium-sized, stocky, short-tailed parrots that largely replace each other on either side of the Amazon river system. Within *Pionites*, del Hoyo and Collar (2014) and Collar et al. (2020) advocate recognition of three species within *Pionites leucogaster* (*P. leucogaster*, *P. xanthurus*, and *P. xanthomerius*) based on plumage and leg and foot colors, including a reported leapfrog pattern in uppertail color (sensu Remsen, 1984). Collar et al. (2020) acknowledge intergradation in these traits at zones of contact between the various forms but cite no primary data. We note clear inconsistencies in at least one of these traits, leg and foot color, as assigned to photographs of wild birds in Collar et al. (2020), i.e., plainly pale colored legs and feet in birds cited by Collar et al. (2020) as *P. xanthomerius*, which is putatively dark legged. Although *P. l. xanthomerius* and *P. melanocephalus palidus* hybridize along the Ucayali River (Haffer, 1977; Moncrieff et al., 2021), the extent of the hybrid zone seems fairly restricted, which might indicate substantial levels of reproductive isolation between these species. Given the scant and inconsistent current evidence for elevating subspecies of *P. leucogaster* to species, we advocate retention of only *P. leucogaster* and *P. melanocephalus* as the two species in *Pionites* until more in-depth genetic and phenotypic research is conducted.

Rhynchopsitta

Rhynchopsitta comprises two predominantly green, massively billed species (*R. pachyrhyncha* and *R. terrisi*) that occur in the high-elevation pine forests of Mexico, and formerly the southwestern United States. The split between *R. terrisi* of the Sierra Madre Oriental and *R. pachyrhyncha* of the Sierra Madre Occidental was dated to 0.5 Mya (0.2–0.8). Despite their relatively recent origin, both taxa are independently evolving. We do not support proposals to treat *terrisi* as a subspecies of *pachyrhyncha* (Urantowka et al., 2014b). This young age could reflect a general pattern identified in temperate North American birds that have shallower origins in comparison with tropical species, presumably due to higher extinction rates (Smith et al., 2017). This scenario is consistent with the long branch *Rhynchopsitta* was placed on. Alternatively, the shallow divergence could reflect a recent colonization of the highland pine forests of Mexico, indicating there has not been enough time to accumulate a deep divergence between the taxa.

Pyrrhura

Pyrrhura are small parakeets easily recognizable by the combination of maroon upper tails, often but not always scalloped or mottled chest plumage, and similarly often differentiated ear coverts and crown and shoulder markings on the wing.

Similar to *Amazona*, *Pyrrhura* is among the most speciose genera of Neotropical parrots. We estimate that its species diversity arose via rapid radiation within 7.1 Mya (2.2–10.6; fig. 9). Relationships within *Pyrrhura*, however, are among the most poorly resolved across the entire parrot phylogeny. This is due to *Pyrrhura*'s rapid radiation, the use of degraded DNA from museum skins for several species and, potentially, extensive introgression and incomplete lineage sorting (see Ribas et al., 2006; Somenzari and Silveira, 2015; Urantowka et al., 2016). Although the most stringently filtered concatenated and species trees yielded a moderately well-resolved topology, there was high discordance in species-level relationships of the trees. Despite most recognized species having been sampled except *P. pfrimeri*, more phylogenetic work is still needed to resolve finer-scale relationships and species limits within the genus.

Our phylogenomic tree (fig. 9) is concordant with the membership of the three main evolutionary lineages identified by Joseph (2000, 2002) and Ribas et al. (2006), but some species-level relationships within these clades vary among phylogenies. Clade 1 comprises only *P. cruentata* of the Atlantic Forest, Brazil. Clade 2 is the *picta-leucotis* complex and clade 3 comprises the remaining species. Forshaw and Knight (2010) described three major groups: species with (1) barring on breast; (2) scalloping on breasts; and (3) neither breast barring nor scalloping. These three groups are not monophyletic in the phylogenomic tree, although some phylogenetic signal is apparent in these traits. Clade 1 (*P. cruentata*) has neither breast barring or scalloping. The difference has been illustrated in Joseph (2000, 2002: see figs. 2, 3 in both papers). Clade 2, which was sister to *P. cruentata* (fig. 9), includes representatives with breast barring or scalloping. For example, clade 2 taxa include *P. leucotis* and *P. griseipectus* of eastern Brazil, which have breast barring, and *P. picta* and *P. amazonum* that have scalloping. Clade 3 also contains the majority of Forshaw and Knight's third group, species without barring or scalloping on breast. The remaining species, without barring or scalloping, do not form a monophyletic group within clade 3. Clade 3 also contains *P. rupicola* of western Amazonia, whose plumage Forshaw and Knight described as a special case of scalloping on the breast, and several species with barring (e.g., *P. frontalis*; *P. devillei*). Despite the presence of some phylogenetic signal in barring, scalloping, or the absence of either, the phylogeny shows this trait should not be used to define taxonomic groups.

Further genomic work to clarify relationships and species limits within *Pyrrhura* ideally would use fresh, wild-collected material of all taxa, many of which remain unsampled. A focus of such effort should be thorough population-level sampling across the geographical ranges of all nominal species but especially for the taxonomically complex and contentious groups, foremost of which is the *P. picta* and *P. leucotis* sensu lato (i.e., sensu Peters, 1937) complex. Here we also note others such as the *P. melanura* complex. Population-level sampling is especially relevant in a radiation as rapid as that of *Pyrrhura*. It is critical to understand how diversity within and among populations, as well as patterns of introgression and gene flow among them, can improve decisions about species limits and relationships. Concerning *P. picta* and *P. leucotis* sensu lato, we note that our data at best provide weak support for the taxa subsumed under the name *P. picta* by Peters (1937) as monophyletic, noting that Peters' (1937) long since entrenched view had no accompanying support. This in turn suggests the merit of earlier suggestions to revisit the breaking up of *P. picta* and *P. leucotis* (Joseph, 2000, 2002; Ribas et al., 2006). Concomitantly, it questions the persistent recognition of *P. picta* as polytypic and inclusion of such divergent taxa as *caeruleiceps* within it at subspecies rank by, for example, Gill et al. (2021) and Remsen et al. (2024). Similarly, and strictly speaking, our data offer ambiguous support for *P. leucotis* as Peters (1937) construed it, i.e., despite being closely related we do not find strong support for *P. leucotis* and *P. griseipectus* as sister taxa. We do nonetheless see strong support for a geographical grouping of western Amazonian taxa (*roseifrons*, *peruviana*) in our data and much weaker support for other geographical groupings such as that of northwestern South America-Central America (*eisenmanni*, *subandina*, *caeruleiceps*) and, potentially, northern South America (*picta*, *emma*) and central Amazonia (*lucianii*, *amazonum).* Determining whether these geographical patterns also correspond to phylogenetic and taxonomic groupings warrants specific attention in future work. Compounding the issue is the recognition of more taxa within the group in recent decades, some of which we have included but many we have not (Delgado, 1985; Ridgely and Gwynne, 1989; Joseph, 2002; Gaban-Lima and Raposo, 2016; Arndt and Wink, 2017).

Enicognathus

Enicognathus comprises two predominantly green species (*Enicognathus leptorhynchus* and *E. ferrugineus*) with dark maroon bellies, the latter presumably a recurrent plesiomorphic trait in Arini. They occur only in temperate forests and woodlands in southernmost South America and primarily along its Pacific seaboard. Interestingly, both *Enicognathus*, and *Rhynchopsitta* of Mexico, which are, respectively, among the most southerly and northerly distributed parrots in the New World, contained shallow divergences among sister species. *Enicognathus leptorhynchus* has an elongate maxilla that may be an adaptation to feed on the seeds of *Araucaria*, a conifer. We find that *Enicognathus* was not closely related to *Pyrrhura*, although it shares with many of them and indeed with *Orthopsittaca manilatus* (fig. 9), a distinctively dark red or maroon abdominal (belly) patch of plumage, presumably a plesiomorphic state within the Arini. *Enicognathus leptorhynchus* and *E. ferrugineus* were of recent origin and shared a common ancestor 0.6 Mya (0.2–0.9). Our data suggest no taxonomic changes to long-standing treatment of two species in both *Enicognathus.*

Cyanoliseus

Cyanoliseus comprises one polytypic species, *C. patagonus*, of southern South America. Its placement in a monotypic genus is absolutely warranted by its phenotypic uniqueness stemming from unusually brownish-olive plumage, orange belly plumage fringed yellow and its large-bodied, long-tailed morphology. Further, it obligatorily rather than opportunistically nests in holes in cliffs, one of just a few parrots to do so. The biology of the species has been extensively studied (e.g., Masello and Quillfeldt, 2004a, 2004b; Masello et al., 2006) and intraspecific genetic diversity has been addressed by Masello et al. (2011, 2015). It continues to challenge accurate phylogenetic placement. We found it to be one of several long branches diverging from very short internodes in the Arini suggesting it as possibly sister to the assemblage of macaws and their allies (e.g., *Aratinga* and their conure-like allies; fig. 9).

Anodorhynchus

Anodorhynchus is a genus of three species of blue macaw each with yellow bare skin about the eye and mandible. One species (*A. hyacinthinus)* is the largest of all extant parrots. Of the two other species, one is extinct and one is endangered and restricted in range to arid zone canyons in eastern Brazil. The extinct *Anodorhynchus glaucus* was sister to *A. leari*, diverging 2 Mya (0.7–3.1), and they in turn are sister to *A. hyacinthinus*, diverging 3.7 Mya (1.4–5.6). This placement of *A. leari* could not be confirmed in the species tree because the sample was of low quality. For a review of morphological specialization and the ecology of *Anodorhynchus*, see Yamashita and Valle (1993). Sick and Teixeira (1983) note the obligatory cliff-nesting of *A. leari.*

Eupsittula

Eupsittula consists of five mostly green small parakeets with long, graduated tails that occur from Mexico to Paraguay. The concatenated and species trees are in agreement and resolved, except for the placement of *E. aurea*. This species ranges from Suriname and northeastern Brazil to northwestern Argentina. The concatenated tree had South American *E. aurea* sister to the two Central American species, *E. nana* and *E. canicularis*, with 80% ultrafast bootstrap support (fig. 9). *Eupsittula aurea* and *E. canicularis* are the only two species in the clade that have orange foreheads. In contrast, the species tree had *E. aurea* as sister to *E. pertinax* and *E. cactorum* in an all South American grouping with a local posterior probability of 1. Provost et al. (2018) had *E. aurea* grouping with *E. nana* and *E. canicularis*, but the position of Central American *E. canicularis* was unresolved. Resolving relationships among these five species is important biogeographically because it will help determine when *Eupsittula* first dispersed into Central America, which seems the most likely direction of dispersal. All the nodes within the clade have mean estimates that fall within the past three million years (fig. 9).

Psittacara

Psittacara comprises medium- to small-sized parakeets with long, attenuated tails and are mostly green. They are remarkable among parrots and indeed all birds for the highly irregular "scattered" distribution of red in their plumage, mostly about the head, tibial feathering (thighs), underwing coverts, and particularly their contour plumage. Some species also have yellow in the underwing. Attempts to delimit species using plumage color (e.g., Arndt, 2006), particularly the extent of red plumage on the head, are now understood to produce paraphyletic species.

Relationships among the species were poorly resolved but nonetheless suggest geographically cohesive clades with varying levels of support. There are three clades of note: (1) *P. mitrata* and *P. frontatus*, species distributed from Peru to Argentina that occur up to 3500 m; (2) *P. wagleri*, *P. finschi*, *P. mitratus*, *P. erythrogenys*, and *P. leucophthalmus*, a widely distributed clade east and west of the Amazon; and (3) *P. chloropterus*, *P. euops*, *P. holochlorus*, *P. brevipes*, *P. rubritorquis*, and *P. strenuus* of the Caribbean, Central America, and Mexico. Given the strong geographic adjacency of species in this clade, it is most likely that the extinct *P. maugei*, formerly of Puerto Rico, was closely related to *P. chloropterus* and *P. euops* of Hispaniola and Cuba, respectively. The whole radiation was dated to have occurred within 0.6–6.7 Mya (fig. 9). This includes multiple colonization events of Central America dated to 2.2 and 3.1 Mya and dispersal into the Caribbean at 1–5.1 Mya (fig. 9).

Given the number of poorly resolved nodes and nonmonophyly of traditionally recognized species, which we discuss in more detail below, *Psittacara* is a high priority for a more detailed study. Peters (1937) considered *P. frontatus* conspecific with *P. wagleri*, and Collar (1997) suggested that *P. wagleri* and *P. mitrata* may be conspecific. Both are inconsistent with the phylogeny (see also Collar et al., 2020). *Psittacara frontatus* was formerly recognized as a subspecies of *P. wagleri* and, based on our analyses, they are not closely related. *Psittacara frontatus* of the Pacific slope and central Andes of Peru and Bolivia and *P. mitratus* of the southern Andes, branch sequentially at the base of the *Psittacara* clade although their relationship had 78% ultrafast bootstrap support (fig. 9). Moreover, all nodes in the clade of South and Central American *Psittacara* (clade 2, above) had low support values.

The resolution of relationships within clade 3 containing taxa in Central America, Mexico, and Cuba/Hispaniola was better, but there were several key nodes that were not also strongly supported (fig. 9). The clade containing the four species of *Psittacara* (*P. holochlorus*, *P. strenuus*, *P. rubritorquis*, and *P. brevipes*) from Mexico and northern Central America had high support. Within this clade, only the placement of *P. brevipes* of Socorro Island was weakly supported as sister to *P. strenuus* of southern Mexico to Guatemala and *P. rubritorquis* of Central America. The clade also included *P. holochlorus* of Mexico (and extreme southeastern Texas where the origin of its populations is unclear; Uehling et al., 2019) as sister to the other three species. However, this relationship could not be confirmed because of low support for the placement of *P. brevipes* (fig. 9). Within clade 3, the *Psittacara* of

Mexico and Central America are sister to the two Caribbean species, *P. chloropterus* of Hispaniola and *P. euops* of Cuba, but this relationship was poorly supported (UFBS = 61%).

Leptosittaca, Ognorhynchus, Thectocercus, Diopsittaca, and *Guaruba*

These five genera are all midsized parrots with long, attenuate tails. All are predominantly green or green and yellow with blue, yellow and red in localized parts of the plumage such as the bend of the wing, head and face, or underparts. They are thus a phenotypically disparate group.

The monotypic genera *Thectocercus*, *Diopsittaca*, *Guaruba*, *Leptosittaca*, and *Ognorhynchus* are recovered as a clade, which was sister to *Psittacara*. Relationships within the clade have biogeographical cohesion. The sister pair of *Ognorhynchus* and *Leptosittaca* are relatively restricted-range species endemic to midmontane parts of the northern to western Andes. Sister to them are the other three genera, which form a subclade, mainly in lowlands east of the Andes. Overall, the latter three are more widespread than *Leptosittaca* and *Ognorhynchus*, notwithstanding *Guaruba* being fragmented and rare. Each is as phenotypically unique as might be expected. We recommend no changes to generic taxonomy and in particular we reject synonymy of *Leptosittaca* within *Aratinga* as is occasionally proposed (e.g., Forshaw and Knight, 2010). Of the five, only *Diopsittaca nobilis* and *Thectocercus acuticaudatus* have described subspecies, but we know of no suggestions to recognize any of these at species rank. Although both species have subspecies with large disjunctions that warrant phylogeographic investigations. Maximum likelihood estimates of node ages in this clade range from 2.5–6.4 Mya (fig. 9).

Conuropsis

Conuropsis is extinct and comprises only one species, *C. carolinensis*, the only parrot known solely from North America since European settlement of the continent. It was predominantly green with a bold yellow neck and head but for its orange crown. We confirm the earlier discovery by Kirchman et al. (2012) that *C. carolinensis* has a close relationship to the *Aratinga solstitialis* complex. However, we placed it as sister to that group (fig. 9), along with what we recognize as *Gymnopsittacus weddellii*, a species not sampled in their study. We further agree with Kirchman et al. (2012) in finding that that clade is itself sister to the macaws. Our phylogenomic data further casts doubt that *Conuropsis fratercula*, a taxon described from a single humerus from a 16 Mya deposit in Nebraska (Wetmore, 1926), was closely related to *C. carolinensis*. *Conuropsis fratercula* is older than the phylogenomic molecular estimate of 7.1 Mya (3–10.1; fig. 9), the divergence of *Conuropsis* from the ancestor of *Gymnopsittacus* and *Aratinga*. This divergence date also encompasses the likely origin of *Conuropsis* in North America, which is well after the age of *C. fratercula*. Demographic modeling using whole genome data (Gelabert et al., 2020) and genome-wide markers of *C. carolinensis* (Smith et al., 2021) indicate that that there were not strong signatures of genetic decline prior to its extinction and that it exhibits the typical genetic signatures of population declines and expansion during the Pleistocene in eastern Nearctic birds.

Aratinga and *Gymnopsittacus*

Aratinga are small to medium-sized parakeets that are mostly green, but several species have extensive yellow and orange plumage. They have long, attenuated tails. We included the first genetic data for *A. maculata*, which was recently separated from the closely related *A. solstitialis* (Silveira et al., 2005; Nemésio et al., 2009). Phylogenomic results confirm previously proposed relationships from mtDNA (Ribas and Miyaki, 2004). That is, *Aratinga auricapillus*, *A. jandaya*, *A. maculata*, and *A. solstitialis*, hereafter the core *A. solstitialis* group, are closely similar in plumage and form a well-supported clade in the concatenated and species tree. As suspected, based on genetic distances in mtDNA within the core

A. solstitialis group, their divergences from one another occurred in the past two million years. We further confirmed a sister species relationship between *A. maculata* and *A. solstitialis*, the two taxa sharing an estimated common ancestor 1 Mya (0.3–1.7; fig. 9).

Also reinforcing Ribas and Miyaki's (2004) mtDNA findings, we recovered a further species, *A. nenday*, as sister to the core *A. solstitialis* group. This species has often been placed in monotypic *Nandayus*, Bonaparte 1856. Its phenotypic distinctiveness is undeniable due to its black head, differently colored and sharply demarcated chest and abdominal plumage, and red confined to the tibial feathers. A close relationship between *A. nenday* and the core *A. solstitialis* group, however, was first proposed by Miranda-Ribeiro (1920) who placed them all in *Nendayus* [sic] Bonaparte, 1856. Most phenotypic similarities of *nenday* to the brightly colored core *A. solstitialis* group, possibly synapomorphic and thus consistent with a sister relationship, are not readily apparent in a typical museum specimen or a perched living individual. However, Silveira et al. (2005) outlined this similarity as follows: "The most remarkable characters shared by the members of the group [i.e., the core *A. solstitialis* group] are found in the wings and tail. Remiges are dorsally green, with middle and distal portions deep blue and black, respectively. They are black ventrally, and the greater wing coverts are mostly deep blue. Upper side of tail is mostly green with deep blue in the tip; underside is mostly black. *Nandayus nenday* (Nanday Parakeet) also shares the characters that otherwise diagnose the *A. solstitialis* group and probably belongs to the same clade" (Silveira et al., 2005). To these we can add a black bill.

The impetus to move *nenday* to *Aratinga* involved a further species, *weddellii*. That is, although *nenday* is sister to the core *A. solstitialis* group (Ribas and Miyaki, 2004; this study), *weddellii* is in turn that larger group's sister (see South American Checklist Committee [SACC] proposal 578). Retaining all these species in *Aratinga* is simple and expedient (e.g., Remsen et al., 2013); it even has biogeographic cohesion in that the group is distributed around the lowland periphery of most of Amazonia. It obviates the need to recognize three genera, which is necessitated if *nenday*, nested within the group, is assigned to monotypic *Nandayus*. However, we do recommend assigning *weddellii* to its own genus (see below), so the issue returns to one of whether to generically recognize the two sister lineages, i.e., *nenday* and the core *A. solstitialis* group. Like so many similar decisions involving sister lineages, this ultimately is arbitrary. How might we resolve it here?

The divergence between *A. nenday* and the core *A. solstitialis* group had a mean estimate of 3.2 Mya (1.1–4.8; fig. 9). This age was younger than the majority of intrageneric divergences in parrots (only the *Diopsittaca* and *Guaruba* split at 2.5 Mya [0.9–3.8] was younger), and it is comparable with that of intraspecific divergences frequently observed within Neotropical birds (Smith et al., 2017). We conclude that relative to the core *A. solstitialis* group, phenotypic differences of *nenday* have evolved rapidly while plumage similarities (Silveira et al., 2005) likely are synapomorphic. We advocate retention of *nenday* in *Aratinga*.

Further research might usefully focus on the evolution of plumage color in the core *A. solstitialis* group complex, which presumably uses blue structural color and psittacofulvins to produce the greens and yellows in plumage of the entire head (reviewed in Berg and Bennett, 2010), whereas *nenday* has a melanin-producing pathway in its dark crown. Mutations in the gene *SLC45A2* in captive color morphs of *Psittacula* sensu lato parakeets were shown to lead to a loss of melanin and produce a yellow phenotype (Roy et al., 2024). Identifying the reverse molecular pathway, a gain in melanin production, would help clarify the taxonomic relevance of the dark crown in *nenday*. Qualitatively, evolution to melanin-producing plumage color was infrequent in parrots, but it has independently evolved multiple times outside of *nenday*.

The final species to be discussed in the genus is *A. weddellii* of western lowland Amazonia. In our analyses, it is strongly supported as sister to all other *Aratinga* and on a relatively long branch (fig. 9), corroborating previous work (Kirchman et al., 2012). The disparity in plumage and skin color and patterning between *A. weddellii* and all other *Aratinga* is striking. It is reflected in the deep split at 6.6 Mya (2.7–9.4; fig. 9), separating these two lineages. The estimated timing of this divergence is largely overlapping with the split of the extinct *Conuropsis carolinensis* from the whole subclade (fig. 9).

The combined phenotypic and phylogenetic distinctiveness of *Aratinga weddellii* strongly suggests the merit of its generic separation (cf. distinctiveness of *Psephotellus varius* relative to other *Psephotellus* spp.). A genus group name, *Gymnopsittacus* Miranda-Ribeiro, 1920, is available for *A. weddellii*. We advocate for and suggest the reintroduction of its status as a monotypic genus.

Miranda-Ribeiro (1920) designated *Aratinga weddellii* (see note below on orthography) as the type species and *Eupsittula cactorum* as what he termed a cotype species. Peters (1937) as first reviser fixed *Conurus weddellii* Deville, 1851, as the type species of *Gymnopsittacus*. Further, Miranda-Ribeiro (1920) included a third taxon, *aeruginosa*, in *Gymnopsittacus* but it has long since been recognized as a subspecies within the polytypic *Eupsittula pertinax* complex. Similarly, *Eupsittula* also holds *E. cactorum*.

It is beneficial to reiterate the diagnostic phenotypic traits of *Gymnopsittacus* as follows: rose-pink (*côr de carne* = color of flesh sensu Miranda-Ribeiro, 1920) colored nares and lateral gular skin along the base of the bill; frequently very pale iris, albeit possibly bicolored; large, broadly circular area of naked, pale periophthalmic skin that is proportionally larger relative to the eye than in closely related *Aratinga* sensu stricto but that resembles in its extent that of *Thectocercus acuticaudata*, for example; the highly variable dusky blue-gray coloring of the feathering of the head that results from individual feathers being brownish proximally and bluish gray distally. The overall color of the head is thus highly variable due, we posit, to combined factors of wear and perhaps individual variation; we know of no evidence that there are sexual differences in its intensity, although this may warrant study.

Lastly, we note that Miranda-Ribeiro (1920) consistently misspelled the epithet *weddellii* as *weddelli*. The orthography introduced by Deville (1851) was indeed the former, i.e., *weddellii*, having double *d*, double *l*, and double *i*.

Cyanopsitta

Cyanopsitta is a small blue macaw of northeastern Brazil. It is one of the rarest birds in the world and the subject of intense in situ and ex situ conservation management (Hammer and Watson, 2012). It was sister to a clade containing the majority of other macaws (except *Anodorhynchus* and *Diopsittaca*), diverging 8.1 Mya (3.5–11.4; fig. 9). Its phylogenetic position is stable across multilocus phylogenies (e.g., Tavares et al., 2006; Wright et al., 2008; Schirtzinger et al., 2012) and the concatenated and species trees.

Orthopsittaca

Orthopsittaca manilatus of Amazonian savannas and swamp forests is predominantly dark green but for its large patch of bare facial skin and maroon abdominal (belly) patch, thus resembling some of the more plainly plumaged species of *Pyrrhura*. It is diet-specialized to *Mauritia* palms within which it also nests (Forshaw and Knight, 2010). Despite its large geographic distribution across Amazonia, no subspecies have been described. After *Cyanopsitta*, it represents the next divergence in the macaws, sharing a common ancestor with *Ara* and *Primolius*, 7.4 Mya (3.1–10.4; fig. 9).

Lastly, here, we make a nomenclatural note about this species. Whitney's (1996) reinstatement of monotypic *Orthopsittaca* Ridgway, 1912, for this species has since become conventional. When Ridgway (1912) introduced *Orthopsittaca*, however, he cited *Orthopsittaca manilata* as the type species, implying that *manilata* was adjectival and feminine. Dickinson and Remsen (2013), in contrast, argued that usage should return to the masculine form *manilatus* of the species epithet, i.e., *Orthopsittaca manilatus*, noting that the name *manilatus* was invariable. We have been advised (see Acknowledgments) that in Boddaert's (1783: 52) naming of the bird as *Psittacus manilatus*, the specific epithet *manilatus* means "broad hand." We are further advised that under Article 31.2.1 of ICZN (1999) *Orthopsittaca manilatus* would be the correct nomenclature. Patterns of usage also argue that despite a long familiarity of the feminine *manilata* when the species was in *Ara* and since *Orthopsittaca* was reinstated by Whitney (1996), the masculine *manilatus* has prevailed since Dickinson and Remsen (2013). A cursory "Catalog" search of the Biodiversity Heritage Library on 19 March 2024 returned 52 instances of *Orthopsittaca manilata*, only two of which were later than 2013, and eight instances of *O. manilatus* all of which were after 2013. Further, other global checklists (e.g., Clements et al., 2022; Gill et al., 2021, 2022, 2023, 2024) have used *manilatus*. Given the apparent trend toward the use of manilatus since 2013, we concede, albeit reluctantly, that usage of *Orthopsittaca manilatus* should remain.

Primolius

Primolius consists of three smaller, predominantly green macaws. *Ara* and *Primolius* are estimated to have shared a common ancestor 7.1 Mya (3.1–10), a depth of divergence comparable to other intergeneric splits in Arini (fig. 9). There was discordance between the phylogenomic concatenated and species trees, but relationships in both trees are highly supported. In the concatenated tree, *P. couloni* was sister to *P. maracana* and *P. auricollis*, whereas in the species tree, *P. auricollis* was sister to *P. couloni* and *P. maracana*. The topology from Provost et al. (2018) is concordant with the phylogenomic tree presented here. Despite the apparent lack of strong phenotypic patterns favoring one topology versus the other, both nodes have divergences estimated to have occurred within the Late Pliocene to Pleistocene. The case for the priority of *Primolius* over *Propyrrhura* as the correct genus for these three species has been made by Penhallurick (2001) and cf. Whitney (1996).

Ara

Ara contains the other group of extant large-bodied brightly colored macaws, and we note that at least one smaller species, *A. tricolor*, is extinct (Forshaw and Knight, 2017). *Ara* has a crown age of 6.4 Mya (2.8–9.2), and maximum likelihood divergence time estimates among species in the genus ranged from 1.7–6.4 Mya (fig. 9). Relationships within *Ara* differ between the concatenated and species tree and relative to previously inferred trees. All trees support three different groups, but relationships among and within them vary. One group comprises four species, the two large red (*A. macao* and *A. chloropterus*) and two large green macaws (*A. militaris* and *A. ambiguus*). A phylogenetic study on *Ara* using mitochondrial DNA with incomplete species-level placed the extinct *A. tricolor* as sister to the red and green macaws (Johansson et al., 2018). The second group is the closely related blue-and-yellow macaws (*A. glaucogularis* and *A. ararauna*), our data robustly affirming the species status of *A. glaucogularis* (see Ingels et al., 1981; Hesse and Duffield, 2000) and the phenotypically distinct *A. rubrogenys*, which was not included in previous phylogenetic studies. The third group consisted solely of *A. severus*. In the phylogenomic trees, *A. severus* was sister to all other *Ara*. The concatenated and species trees differed with respect to the monophyly of the large green and red macaws. Only the concatenated tree showed that the red (*A. macao* and *A. chloropterus*) and green macaws (*A. militaris* and *A. ambiguus*) were respectively monophyletic for each color group (fig. 9). Phylogeographic studies have found genetic structuring across the ranges of *A. macao* (Schmidt et al., 2020; Aardema et al., 2023), and *A. militaris* (Eberhard et al., 2015, Rivera-Ortíz et al., 2023), and no structuring in *A. ambiguus*. The critically endangered *A. glaucogularis* of Bolivia shows weak genetic differentiation between northern and southern populations (Campos et al., 2021).

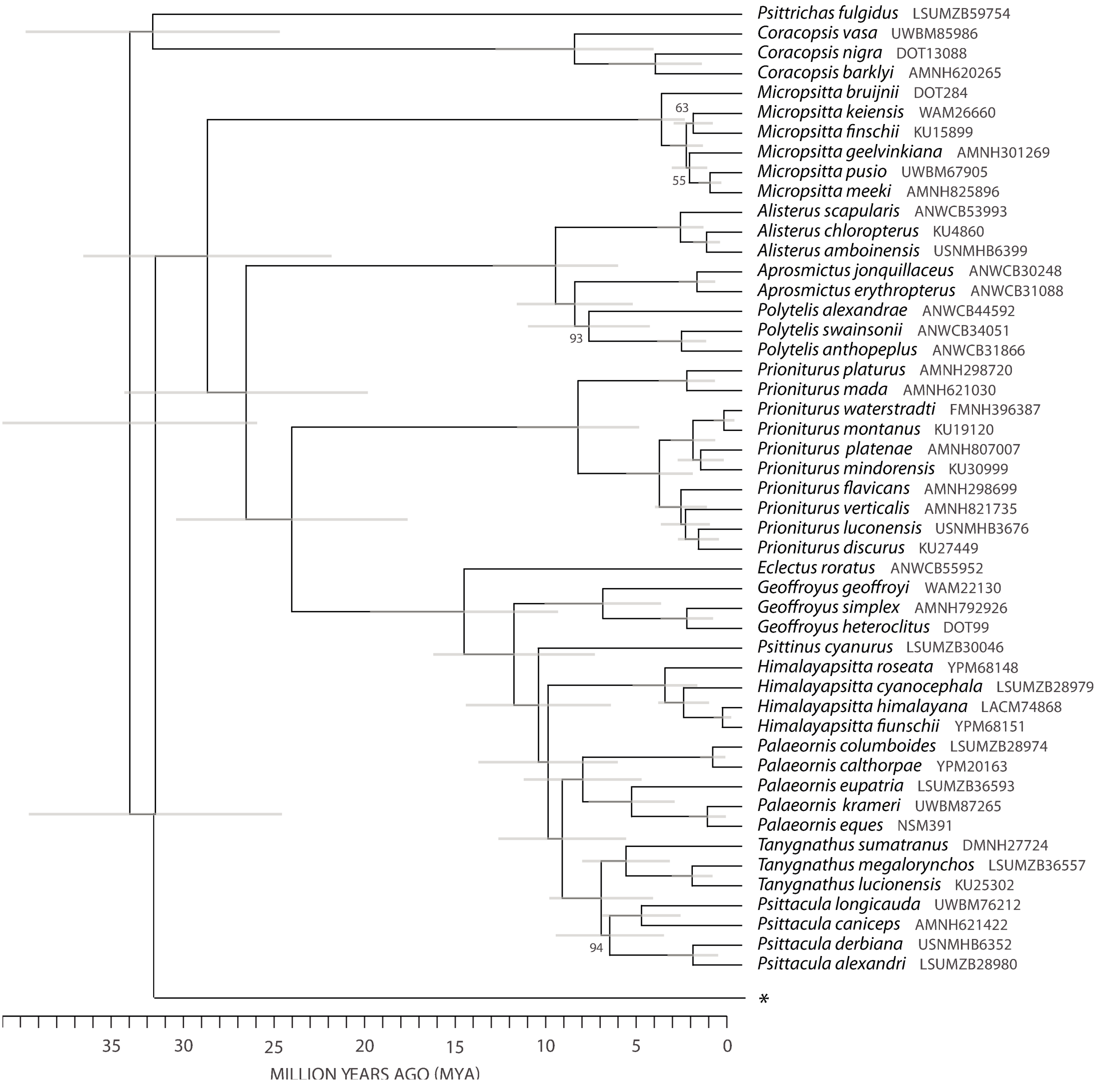


FIGURE 10. Time-calibrated topology of Psittaculinae, Psittrichasinae, and Coracopseinae. Nodes have ultrafast bootstrap values of ≥95% otherwise noted. Gray bars represent divergence time ranges were estimated from 100 bootstrap trees. * denotes clades outside of the focal groups.

Psittrichasidae

Psittrichasinae and Coracopseinae

Psittrichas and *Coracopsis*

The family Psittrichasidae is phenotypically and biogeographically diverse but comprises a low number of species in two monotypic subfamilies Psittrichasinae for *Psittrichas* and Coracopseinae for *Coracopsis* and is consistently placed as closely related to Psittaculidae. Psittrichasidae exhibits an unusual transoceanic distribution, where the monotypic subfamily Psittrichasinae (*Psittrichas fulgidus*) of New Guinea was sister to small radiation in Coracopseinae (*Coracopsis*) found in Madagascar and adjacent islands. The approximately

7000 km gap across the Indian Ocean between the ranges of these lineages was also unusual in that the divergence date was 30.4 Mya (22.3–35.4) (figs. 1, 10), some 40 million years after proposed Gondwana vicariant events observed in other sister taxa that show this disjunct distribution (Chakrabarty et al., 2012). The historical biogeography that accompanied this astonishing pattern of phylogeny warrants comment. Selvatti et al. (2022) reject Schweizer et al.'s (2011) proposal of dispersal across exposed land in the southern Indian Ocean, the Kerguelen Plateau–Broken Ridge hypothesis. They instead provided geological data in favor of an alternative history involving dispersal through Indomalaya and then south across the now submerged microcontinent of Mauritia.

Psittrichas fulgidus has an elongate bill, is among the largest parrots, and is utterly unlike any other parrot in its distinctive black and red plumage and black facial skin (Forshaw and Knight, 2010). It occurs widely across montane forests in New Guinea and has no described subspecies.

Coracopsis comprises 2–4 grayish-brown species that occur on Madagascar, Seychelles, and Comoro Islands, one of which, *C. vasa*, has extraordinary reproductive biology reviewed by Ekstrom et al. (2007). The uncertainty in species limits reflects that some recognize the *C. nigra* subspecies *sibilans* and *barklyi* as species. In our study we included *C. nigra*, *C. vasa*, and *C. barklyi* and found discordance between the concatenated and species tree topologies. The species tree topology matches the mtDNA tree of Podsiadlowski et al. (Podsiadlowski et al., 2017) where *C. barklyi* was sister to *C. nigra* and *C. vasa*. The time-calibrated concatenated topology has *C. nigra* and *C. barklyi* diverging 4.5 Mya (1.7–6.5) and subsequently coalescing to a common ancestor with *C. vasa* 8.6 Mya (3.9–12.1; fig. 10).

PSITTACULIDAE

Psittaculidae comprises five subfamilies (Psittaculinae, Psittacellinae, Platycercinae, Agapornithinae, Loriinae) that span the Old World. The high diversity of this radiation is reflected in the high number of recognized tribes and genera that are geographically cohesive. Psittaculinae (Polytelini, Psittaculini, Micropsittini) was sister to all other groups within Psittaculidae (fig. 1). Within the Psittaculinae, Micropsittini (pygmy parrots) was sister to Polytelini/Psittaculini (fig. 1). Next, Psittacellinae (tiger parrots) was sister to a clade containing Platycercinae, Loriinae, and Agapornithinae (fig. 1). The placement of Agapornithinae (lovebirds, hanging parrots, and Guaiabero) differed between phylogenomic trees. In the concatenated tree, Agapornithinae was sister to Loriinae (lorikeets, fig parrots, and Budgerigar) whereas in the species tree it grouped with Platycercinae, albeit with low support (LPP = 63%). Our results do not support monophyly of Mayr's (2008) Loricoloriinae, its key defining character of hypotarsal morphology likely indicating convergent evolution rather than relationships. For example, we confirm earlier findings (Joseph et al., 2011) that Micropsittini falls well outside the other taxa (Mayr, 2008) united in Loricoloriinae.

The supermatrix phylogeny of Provost et al. (2018) showed instability in the monophyly of Platycercinae, but phylogenomic data validated the group. The subfamilies have estimated crown ages dating from the late Oligocene to the early Miocene. The Platycercini and Pezoporini share a common ancestor estimated as the crown age of Platycercinae dated at 27.5 Mya (19.7–32.8; fig. 1).

Psittaculinae

Micropsittini

Micropsitta

Micropsitta are the smallest parrots. They are largely green with modified, strengthened tail shafts and metatarsals having long claws, which are adaptations for foraging on tree trunks. The clade has a deep stem age of 27.6 Mya (19.8–32.6) and crown age of only 4.1 Mya (2.8–5.2) indicating that extinction was responsible for the long branch (figs. 1, 10). There was considerable discordance between the phylogenomic concatenated and species trees within *Microp-*

sitta. In the concatenated tree, *M. bruijnii*, which ranges from Moluccas, Indonesia, across all of New Guinea to the Solomon Islands, was sister to the other two clades. Although with low support in the concatenated tree, *M. keiensis* was sister to *M. finschii* and these two were sister to a clade in which *M. geelvinkiana* was in turn sister to *M. meeki* and *M. pusio* (fig. 10). In contrast, *M. keiensis* and then *M. geelvinkiana* on consecutive nodes, were sister to the remaining *Micropsitta* in the species tree with strong support. The discordant relationships in the species tree were likely due to gene tree estimation error caused by low quality samples (Smith et al., 2023).

Polytelini

Polytelini contains three genera (*Alisterus*, *Aprosmictus*, and *Polytelis*) of midsized parrots that occur in Indonesia, New Guinea, and Australia. Relationships among the genera are stable across the phylogenomic trees in this study and in previous work (Provost et al., 2018), with the exception of the placement of *Polytelis alexandrae*, which is discussed below. *Aprosmictus* and *Polytelis* share a common ancestor 8.6 Mya (5.3–11.3), and their ancestor split from *Alisterus* 9.6 Mya (6.1–12.5; fig. 10).

Alisterus

The king parrots (*Alisterus*) comprise three species that are largely red ventrally and green dorsally and that have long, broad tails. A streak of a lighter green in the upper wing coverts in two species is strongly UV-fluorescent (Nemesio, 2001). They occur in Australia, Indonesia, and New Guinea. Relationships among the species were consistent and highly supported across previous topologies (Provost et al., 2018) and the one presented here. At approximately 3.2 Mya (1.8–4.2) *A. scapularis* (Australia) diverged from the ancestor of *A. amboinensis* (Moluccas, western New Guinea) and *A. chloropterus* (remainder of New Guinea), which in turn diversified at 1.8 Mya (1.1–2.5; fig. 10).

Aprosmictus

Aprosmictus parrots are two predominantly green species with varying extents of red on the upper wing coverts. *Aprosmictus erythropterus* of Australia and New Guinea has a black back and, in males, the most extensive red in the upper wing coverts, relative to the other species *A. jonquillaceus* of Timor, Roti, and Wetar, Lesser Sunda Islands, Indonesia (Forshaw and Knight, 2010). Both species have two generally accepted but poorly differentiated subspecies. Our estimate of divergence time between *A. erythropterus* and *A. jonquillaceus* was 2.3 Mya (1.3–3.2; fig. 10).

Polytelis

Polytelis comprises three species endemic to Australia. They are long-tailed, slender-bodied parrots and have vocalizations that are as notably unique to the genus as they are similar among the three species themselves. Phenotypically disparate relative to each other, they share at least one plumage trait, a distinctively colored wing-covert patch. Notably, however, this patch is most easily visible in one species, *P. swainsonii* when safely viewed under a "black" light where ultraviolet pigments reflect as yellow (L.J., personal obs.). Similarly, *P. swainsonii* is sexually dimorphic in its coronal plumage but UV-fluorescent pigments are again only visible when safely viewed under a "black" light (L.J., personal obs.).

Previous multilocus phylogenetic studies analyzed only two of the three species, *P. anthopeplus* and *P. alexandrae*, and not *P. swainsonii* (Wright et al., 2008; Schweizer et al., 2010, 2011). Further, these earlier multilocus studies sampled only single individuals each of *P. anthopeplus* and *P. alexandrae* that, moreover, had been reared in captivity either in Europe or North America and presumably were descended from many generations bred in captivity. Wild-collected specimens of *Polytelis alexandrae* are rare in museum collections, and we know of no cryofrozen tissue samples of it from natural populations. Given that background and taxon sampling, we note that the earlier multilocus studies consistently and unexpectedly found that *P. anthopeplus* and *P. alexandrae* were not each other's closest relatives. In particular, *P. alexandrae* consistently was more closely related to *Aprosmictus erythropterus* than to *P. anthopeplus* (reviewed in Provost et al., 2018).

In an ongoing phylogenomic study of this unexpected result, we have sequenced all three species using multiple samples, whether toe pads of older museum specimens or cryofrozen tissue samples, from the natural ranges of all species, as well as captive-bred samples of *P. alexandrae* (note again that there are no cryofrozen tissue samples of wild *P. alexandrae*). We specifically probed the unexpected paraphyly of *Polytelis*. We wished to test, for example, whether it was due to the use in earlier work of captive birds in Europe and North America. Specifically, such birds could have been descended, albeit by many generations, from well-known hybridization between *P. alexandrae* and *A. erythropterus* in captivity, although there is no evidence of backcrossing after such hybridization (Forshaw, 2002; Sindel and Gill, 2003) during the 20th century. The concatenated tree found that *P. alexandrae* was sister to *P. anthopeplus* and *P. swainsonii* with 93% UFBS (fig. 10). In contrast, the species tree affirmed earlier multilocus work showing *P. alexandrae* as sister to *Aprosmictus* with 100% support. The divergence time estimate for *P. alexandrae* was approximately 7.9 Mya (4.7–11). This phylogenetic discordance could indicate several possibilities: ancient introgression occurred between between *P. alexandrae* and *A. erythropterus* (or their ancestral lineages); *P. alexandrae* is of hybrid origin; or *P. alexandrae* warrants full generic, not subgeneric, separation from *Polytelis*. Concerning the last alternative, we note that *Spathopterus* North, 1895, was erected solely for this species based on the spatulate tip of one primary feather in males. Mathews (1912) noted, however, that the name is preoccupied by *Spathoptera* Audinet-Serville, 1835, in the Coleoptera (see Schodde and Mason, 1997). *Northipsitta* Mathews, 1912, is available for it if *Spathoptera* is truly unavailable. Currently, we do not favor its generic separation from *Polytelis* (pace Provost et al., 2018). We instead argue that ancient introgression within the past natural ranges of these birds, not in captive populations, is potentially an equally good explanation of the data bearing on this problem. We are planning a separate publication specifically to address this surprisingly intransigent conundrum in more detail and our approach to its resolution.

Psittaculini

Eclectus, *Geoffroyus*, *Tanygnathus*, and *Psittinus* are all genera with low species diversity that radiated across Indonesia, the Philippines, and New Guinea. Their plumage is often described as sleek. Much of the diversity is reflected in subspecies that are allopatrically distributed across islands. Generic-level relationships remain stable and more supported with phylogenomic data. The branching pattern starts with *Eclectus* then *Geoffroyus* then a clade containing *Psittacula*, *Tanygnathus*, and *Psittinus.*

The relationships within Psittaculini are mostly well resolved, but there is still scope for clarifying relationships within paraphyletic *Psittacula* sensu lato, and the placement of *Psittinus* varies between our tree and previous work (Braun et al., 2019). The 10 species of racquet-tailed parrots (*Prioniturus*) form a clade that was sister to all other members of Psittaculini. Phylogenomic relationships among the 10 species are largely congruent with an mtDNA tree (Schweizer et al., 2012). Within the sister clade of *Prioniturus*, *Eclectus*, then *Geoffroyus*, on successive branches were sister to a subclade containing *Tanygnathus*, *Psittinus*, *Psittacula*, and *Prioniturus*. All these relationships were highly supported and consistent among phylogenies.

Prioniturus

The racquet-tailed parrots (*Prioniturus*) comprise a small radiation in the Philippines and Indonesia. The species are largely green and stocky with rounded tails in which the central tail feathers have extended bare shafts protruding from the distal end of the tail and terminating with a racquet of feather barbs (Forshaw and Knight, 2010). An mtDNA phylogeny of *Prioniturus* inferred three separate clades (Schweizer et al., 2012): (1) *mada* and *platurus*; (2) *waterstradti*, *montanus*, *platenae*, and *mindorensis*; and (3) *discurus*, *luconensis*, *verticalis*, and *flavicans*). Our phylogenomic results are largely congruent but with some notable exceptions. We confirm the finding of Schweizer et al. (2012) that *P. discurus* is paraphyletic. All phylogenetic data showed that *P.* [*discurus*] *mindorensis* was highly supported as a member of clade 2, which does not include nominotypical *P. d. discurus*. The species recognition of *P. mindorensis* appears further warranted, although its phenotypic divergence is primarily in iris color (pale, not dark) and much reduced blue throughout the plumage. Within clade 2, the position of *P. montanus* differed between the mtDNA and phylogenomic tree. The phylogenomic tree had *P. montanus* as sister to *P. waterstradti* (UFBS = 100%), whereas the mtDNA tree places the taxon as sister to all other members of clade 2. The trees also differed with the placement of *P. flavicans*. In the phylogenomic tree, *P. flavicans* was sister to all other members of clade 3, whereas in the mtDNA tree *P. flavicans* was sister to only *P. discurus* and *P. luconensis*. The phylogenomic species tree places *P. flavicans* outside clade 3 as sister to clades 2 and 3. It is unclear to what extent the position of *P. flavicans* in the species tree was driven by a lower-quality sample. The *P. flavicans* sample was retained after more moderate data filtering, but in the most stringent approach the sample was dropped. The radiation of *Prioniturus*, which was estimated to have begun 8.4 Mya (4.9–11.2; fig. 10), reflects the complex relationships among islands within the Philippines and Indonesia (Brown et al., 2013).

Eclectus

Eclectus occurs from across New Guinea and its surrounding islands to the Solomon Islands in the east, far northeastern Australia in the south and Sumba in the Lesser Sundas in the west. Across its range it exhibits considerable geographic variation in size and plumage color while maintaining the oft-remarked exceptional sexual dichromatism of red and blue (female) and green (male) forms (Heinsohn et al., 2005). The phylogenetic placement of *Eclectus* has remained stable and the genus is unquestionably monophyletic. The remaining taxonomic questions deal with whether subspecies should be elevated to species. Using captive individuals and mtDNA, Braun et al. (2016) inferred phylogenetic relationships among six of the nine described subspecies. They found deep phylogeographic structure representing an Indonesian clade and a New Guinea/Solomon Islands clade. The available data indicate there are up to four phylogenetic species in the clade, but until genomic data from wild specimens is published, the recognition of a single species should be maintained.

Geoffroyus

Geoffroyus are midsized parrots that are largely green with contrastingly colorful head plumage in two species and a distinctive blue nuchal collar in one. They occur in Australia, Indonesia, Papua New Guinea, and the Solomon Islands. Traditionally, three species have been recognized: *G. geoffroyi*, *G. simplex*, and *G. heteroclitus*. *Geoffroyus heteroclitus* of the Bismarck Archipelago, Bougainville Island, and the Solomon Islands has a subspecies on Rennell Island (*G. h. hyacinthinus*) that differs in size and plumage color. Del Hoyo and Collar (2014) elevated it to species rank, but *hyacinthinus* was not included in our sampling. We found a deep divergence between *G. geoffroyi* and *G. simplex*/*G. heteroclitus* dating to 7.2 Mya (3.7–9.7; fig. 10). The subsequent split between *G. simplex* and *G. heteroclitus* was dated to 2.8 Mya (1.3–4; fig. 10). The underlying historical biogeography of *Geoffroyus* is unclear. We suggest that initial divergence between *G. geoffroyi* and the ancestor of *G. simplex*/*G. heteroclitus* likely occurred within New Guinea, and that subsequent dispersal out of New Guinea and into the Bismarck Archipelago and Solomon Islands could have been involved in the speciation of *G. heteroclitus*.

Psittinus, Psittacula, Himalayapsitta, and *Palaeornis*

Long treated in *Psittacula* sensu lato, the genera *Psittacula*, *Himalayapsitta*, and *Palaeornis* comprise medium- to large-sized long-tailed parrots that are predominantly green in plumage and often with colored or bicolored bills. They variously have distinctively colored heads and nuchal collars or, in the absence of a collar, distinctively colored facial areas and bold, black submalar stripes. Colored patches on the wing coverts vary in size from a small shoulder patch to large covering most of the greater wing coverts.

Nonmonophyly of *Psittacula* has been reported in several studies, which have all found *Tanygnathus* to be nested within it (Groombridge et al., 2004; Kundu et al., 2012; Jackson et al., 2015; Podsiadlowski et al., 2017). However, taxonomic recognition of *Psittacula* sensu lato has persisted despite its established nonmonophyly for two decades. Braun et al. (2019) proposed a major taxonomic revision of a subclade within Psittaculini (*Tanygnathus*, *Psittinus*, *Psittacula*, and *Prioniturus*) to recognize only monophyletic genera as follows († denoting extinct species): *Himalayapsitta* (*himalayana*, *finschii*, *roseata*, *cyanocephala*), *Nicopsitta* (*columboides*, *calthrapae*), *Belocercus* (*longicauda*), *Psittacula* (*alexandri*, *derbiana*), *Palaeornis* (†*wardi*, *eupatria*; see Hume, 2007, and Podsiadlowski et al., 2017, for placement of †*Mascarinus* Lesson, 1831, within this group), and *Alexandrinus* (*krameri*, †*exsul*, and *eques* including *echo*).

Psittinus

The mono- or ditypic genus *Psittinus* of continental Southeast Asia, Borneo, and Sumatra is morphologically divergent relative to *Psittacula*. *Psittacula* sensu lato are slender bodied, long-tailed birds perhaps recalling *Polytelis*, whereas *Psittinus* has a short, rounded tail and a stocky body recalling the "true parrots" of older literature such as *Geoffroyus*. Largely green, various populations have blue or black distributed in distinctive patches on the head and dorsal surface. The bill is bicolored, the maxilla being red and the mandible black. Traditionally treated as comprising one species with three subspecies, a recent trend has been to elevate *P. c. abbotti*, found on two islands of western Sumatra, to species rank on the basis of its larger size and different pattern of sexual dimorphism in plumage (del Hoyo et al., 2014; Eaton et al., 2016; Gill et al., 2023).

The phylogenomic trees show discordance between the concatenated and species tree topologies, but the trees certainly support the need for a taxonomic revision. A prominent difference between the Braun et al. (2019) tree and both the phylogenomic trees was in the placement of *Psittinus*. Braun et al. (2019) found that *Psittinus* was sister to a clade containing *Tanygnathus*, *Psittacula longicauda*, *Psittacula alexandri*, and *Psittacula derbiana*. In contrast, the phylogenomic tree showed that *Psittinus* was strongly supported as sister to the entire clade containing *Psittacula*/*Tanygnathus* (fig. 10), and that pattern was also recovered in the species tree. These two basal lineages shared a common ancestor 10.5 Mya (6.2–13.7; fig. 10). The position of *Psittinus* does not impact the proposed generic revision of Braun et al. (2019), but it is important for understanding the evolutionary history of the clade.

For the remaining lineages, the phylogenomic tree favors fewer new monophyletic genera. It supports *Himalayapsitta* (*roseata*, *cyanocephala*, *himalayana*, *and finschii)* as represented by a clade stemming from the basal node in the entire *Psittacula-Tanygnathus* group 10 Mya (5.9–13; fig. 10). Braun et al. (2019) further proposed *Nicopsitta*, *Palaeornis*, and *Alexandrinus* to account for the nonmonophyly among the group more broadly. Our phylogenomic analyses place all the species that would be subsumed in the first two of these genera (*calthrapae*, *columboides*, *wardi*, *eupatria*) as well as *eques* in a clade for which we advocate recognition under the oldest available name, *Palaeornis* Vigors, 1825. The generic variation characterized by Braun et al. (2019) was reflected in the relatively deep crown age of *Palaeornis* at 8.2 Mya (4.8–10.8; fig. 10). Note that if the phylogenetic position of extinct *Mascarinus mascarinus* (Linnaeus, 1771) found by Podsiadlowski et al. (2017)

is confirmed then this species would also be placed within *Palaeornis*, which is the older generic name. Braun et al. (2019) inferred *longicauda* with weak support to be sister species to *derbiana/alexandri* and accordingly suggested placing *longicauda* in a monotypic genus, *Belocercus* S. Muller, 1847. We have found support for that relationship among these species in the phylogenomic tree (UFBS = 94%; fig. 10). This includes *caniceps*, which was not sampled in Braun et al. (2019), as sister to *longicauda* in our tree. We dated the basal divergence of *Psittacula* sensu stricto (*derbiana*, *alexandri*, *longicauda*, *caniceps*) at 6.8 Mya (3.8–9.4; fig. 10). Accordingly, we favor retention of the two sister species pairs that comprise there four taxa, (*longicauda*, *caniceps*, *alexandri*, and *derbiana*) within *Psittacula* Cuvier, 1800 (type species is *Psittacus alexandri* Linnaeus, 1758; see Schodde et al., 2012; ICZN, 2014), rendering *Belocercus* synonymous with it. However, the species tree has *longicauda* and *caniceps* (the latter not sampled by Braun et al., 2019) as sister to *Tanygnathus* (LPP = 1.0). This relationship, if eventually confirmed, could be expressed by the adoption of *Belocercus* to avoid a paraphyletic *Psittacula*, but we do not recommend its adoption yet.

Braun et al. (2019) also found some cases of paraphyletic species, *derbiana* being nested within *alexandri*, and *echo* within *krameri*. Because the sampling of the entire group has relied on using captive birds, samples from wild birds will be required to verify these patterns. We do not yet advocate placing *derbiana* within *alexandri* but urge closer study.

Tanygnathus

Tanygnathus are predominantly green, round-tailed parrots with large or massive bills, and in most species, at least partly red. The four usually recognized species (see below) are distributed in the Philippines and Indonesia. The genus is nested deeply within *Psittacula* sensu lato, so the large bill and rounded tails of these birds are likely derived traits, but this depends on the position of *Psittinus*. *Tanygnathus gramineus* occurs only on Buru (Moluccas, Indonesia). It is monotypic and extremely rare in collections and we have been unable to sample it. The other species all show geographic variation expressed with up to six described subspecies.

Provost et al. (2018) and Braun et al. (2019) each inferred relationships for *Tanygnathus*, but each of those studies drew on samples of two species (*T. sumatranus*, *T. megalorhynchos*), whereas Arndt et al. (2019) and the present study included *T. sumatranus*. The best estimation of phylogenetic relationships among the other species based on our analyses and that of morphology (plumage, iris color) and mitochondrial DNA sequences (Arndt et al., 2019) was that *T. megalorhynchos* and *T. lucionensis* were sister species, and that *T. sumatranus* sensu lato was sister to both (fig. 10). This topology was not comparable to other trees. The position of *T. lucionensis* in the species tree was unreliable because the sample was of lower quality. Despite the lower diversity of *Tanygnathus*, the clade had a crown age of 6.0 Mya (3.4–7.9; fig. 10).

Arndt et al. (2019) argued on grounds of morphology (plumage, iris color) and *cytochrome b* sequences from mitochondrial DNA that Philippine populations of *T. sumatranus* should be elevated to species rank as *T. everetti*. We agree that further work is needed to accurately place *T. e. burbidgii* (Sulu Islands) and *T. s. sangirensis* (Talaud Islands) before species limits in *T. sumatranus* sensu lato are resolved.

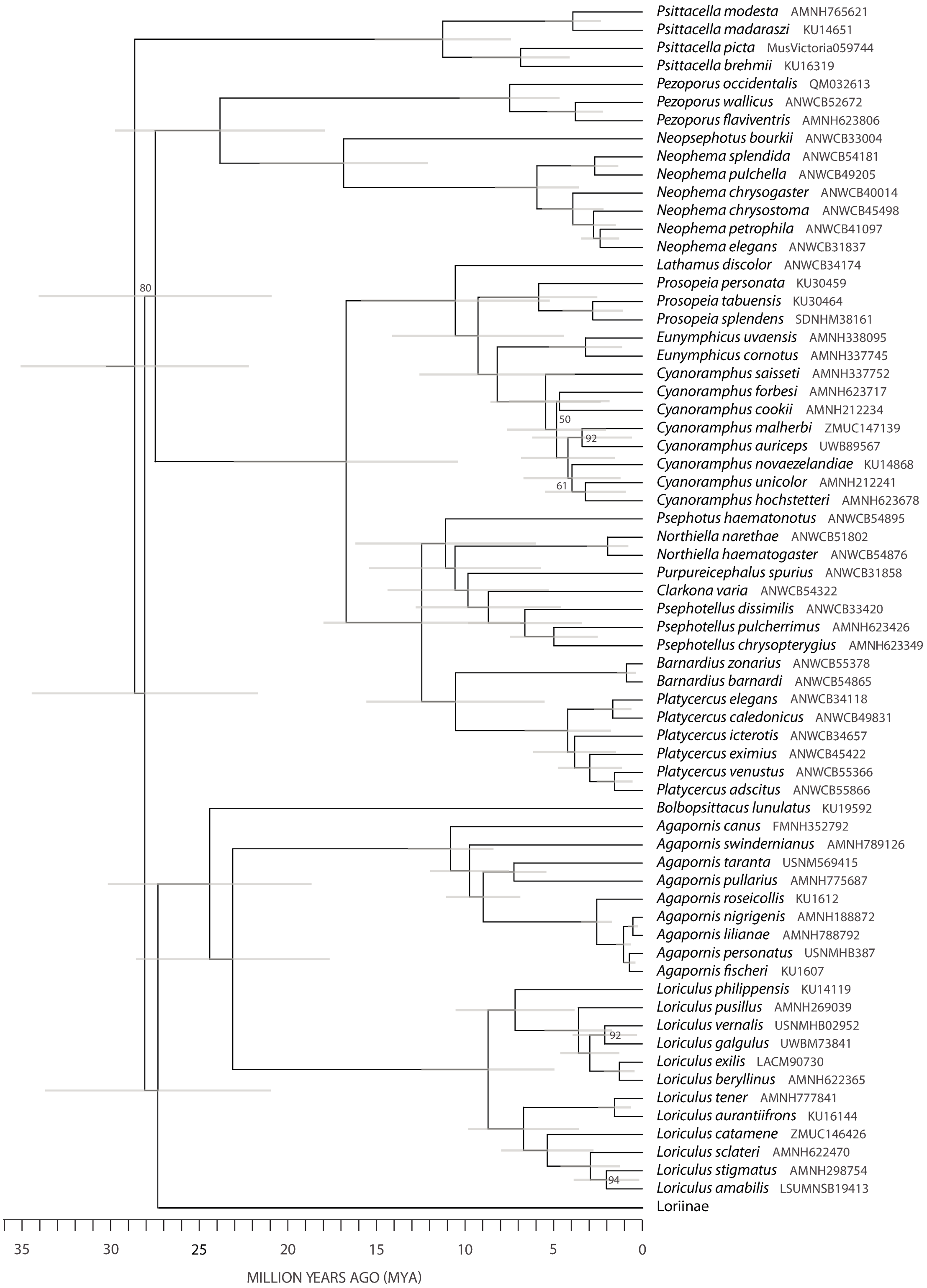
Psittacellinae

Psittacella

The tiger parrots (*Psittacella*) are stocky, small to midsized with short round tails (Forshaw and

→

FIGURE 11. Time-calibrated topology of Psittacellinae, Platycercini, Pezoporini, Neophemini, and Agapornithinae. Support values come from the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted. Gray bars represent divergence time ranges were estimated from 100 bootstrap trees.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Psittacella madaraszi KU14651
Psittacella picta MusVictoria059744
Psittacella brehmii KU16319
Pezoporus occidentalis QM032613
Pezoporus wallicus ANWCB52672
Pezoporus flaviventris AMNH623806
Neopsephotus bourkii ANWCB33004
Neophema splendida ANWCB54181
Neophema pulchella ANWCB49205
Neophema chrysogaster ANWCB40014
Neophema chrysostoma ANWCB45498
Neophema petrophila ANWCB41097
Neophema elegans ANWCB31837
Lathamus discolor ANWCB34174
80
Prosopeia personata KU30459
Prosopeia tabuensis KU30464
Prosopeia splendens SDNHM38161
Eunymphicus uvaensis AMNH338095
Eunymphicus cornotus AMNH337745
Cyanoramphus saisseti AMNH337752
Cyanoramphus forbesi AMNH623717
Cyanoramphus cookii AMNH212234
50
Cyanoramphus malherbi ZMUC147139
92
Cyanoramphus auriceps UWB89567
Cyanoramphus novaezelandiae KU14868
61
Cyanoramphus unicolor AMNH212241
Cyanoramphus hochstetteri AMNH623678
Psephotus haematonotus ANWCB54895
Northiella narethae ANWCB51802
Northiella haematogaster ANWCB54876
Purpureicephalus spurius ANWCB31858
Clarkona varia ANWCB54322
Psephotellus dissimilis ANWCB33420
Psephotellus pulcherrimus AMNH623426
Psephotellus chrysopterygius AMNH623349
Barnardius zonarius ANWCB55378
Barnardius barnardi ANWCB54865
Platycercus elegans ANWCB34118
Platycercus caledonicus ANWCB49831
Platycercus icterotis ANWCB34657
Platycercus eximius ANWCB45422
Platycercus venustus ANWCB55366
Platycercus adscitus ANWCB55866
Bolbopsittacus lunulatus KU19592
Agapornis canus FMNH352792
Agapornis swindernianus AMNH789126
Agapornis taranta USNM569415
Agapornis pullarius AMNH775687
Agapornis roseicollis KU1612
Agapornis nigrigenis AMNH188872
Agapornis lilianae AMNH788792
Agapornis personatus USNMHB387
Agapornis fischeri KU1607
Loriculus philippensis KU14119
Loriculus pusillus AMNH269039
Loriculus vernalis USNMHB02952
92
Loriculus galgulus UWBM73841
Loriculus exilis LACM90730
Loriculus beryllinus AMNH622365
Loriculus tener AMNH777841
Loriculus aurantiifrons KU16144
Loriculus catamene ZMUC146426
Loriculus sclateri AMNH622470
Loriculus stigmatus AMNH298754
94
Loriculus amabilis LSUMNSB19413
Loriinae
35
30
25
20
15
10
5
0
MILLION YEARS AGO (MYA)

Knight, 2010). The English name tiger-parrot is derived from the yellow-and-black barring in the chest (upper ventral) plumage in females of three of the four species. There are two small and two larger species, clearly forming two species pairs that were reflected in our phylogeny (fig. 11).

The clade is on a deep branch, sharing a common ancestor with the clade containing the subfamilies Platycercinae, Loriinae, and Agapornithinae 20.6–33.5 Mya (fig. 1). Across this relatively long evolutionary period, there are only four species that diversified in the mountains of New Guinea. Phylogenetic relationships are stable and consistent across concatenated and species tree approaches in the phylogenomic data. Prior phylogenetic work only sampled *P. brehmii* and *P. picta* (Provost et al., 2018). *Psittacella modesta* and *P. madaraszi* are sister and have olive-brown heads with green backs. The other sister pair, *P. brehmii* and *P. picta*, have black barring on their backs. The crown age of *Psittacella*, 11.3 Mya (6.8–14.5; fig. 11), was among the oldest of all parrot genera, as are the species-level divergence time estimates. One subspecies of *P. picta*, *P. p. lorentzi*, has occasionally been elevated to species rank (Mayr, 1941; del Hoyo and Collar, 2014) based on plumage differences, Mayr (1941) only further noting that they "form a superspecies." Gregory (2017) commented that they differ "significantly in plumage," *lorentzi* seeming "as distinct from Painted [*P. picta*] as Modest [*P. modesta*] and Madarasz's Tiger-Parrots [*P. madaraszi*] are from each other." More recently, Collar et al. (2020) imply that they will retain the two species arrangement, although at the time of our writing (11 May 2024) had not yet not employed it. We agree with Beehler and Pratt (2016) in stressing that this is premature until the nature of any contact where *P. p. lorentzi* and *P. p. excelsa* meet is explored, especially with genetic data. Beehler and Pratt (2016) noted that the likely area of contact, near the Strickland River gorge, is a barrier for a number of montane species. The details of this case, to reiterate, need further study.

We know of no proposal to separate the large- and small-bodied species pairs of *Psittacella* into two genera (fig. 12). Given their ages, this is not without merit. That differently sized but otherwise extraordinarily similar species with a sister-group relationship should be placed in different genera finds support elsewhere in Aves, e.g., the meliphagid genera *Entomyzon* and *Melithreptus*. In that case, there is no extant species of clearly intermediate size whereas in *Psittacella* the four species more smoothly intergrade in size between extremes. Further, subclades in *Psittacella* cannot be diagnosed by yellow-and-black barring in the chest of females because three out of four of the species have the character state. We refrain from breaking up *Psittacella* here primarily for those reasons.

Platycercinae

Pezoporini

The Pezoporini are restricted to Australia. The phylogenomic trees confirm the results of Joseph et al. (2011) that *Neopsephotus*, *Neophema*, and *Pezoporus* form a clade, the Pezoporini, and that *Pezoporus* is monophyletic. Estimated divergence times among these three genera are deep. *Neopsephotus* and *Neophema* share a common ancestor 16.9 Mya (11.2–20.7), and this lineage coalesces with *Pezoporus* 23.8 Mya (16.7–28.5; figs. 1, 11). Both the concatenated and species trees inferred from phylogenomic data are topologically concordant for higher-level and the majority of species-level relationships within the Pezoporini. Our data affirm that *Melopsittacus undulatus* is not closely related to Pezoporini as had been thought prior to the advent of molecular studies. Lastly, here, we argue that Pezoporini warrants being broken into two tribes, monogeneric Pezoporini and a second tribe for *Neophema* and *Neopsephotus.* We name that tribe below after closer review of our data and the biology of these birds.

Pezoporus

Pezoporus contains three midsized and highly terrestrial species with varying tail lengths rela-

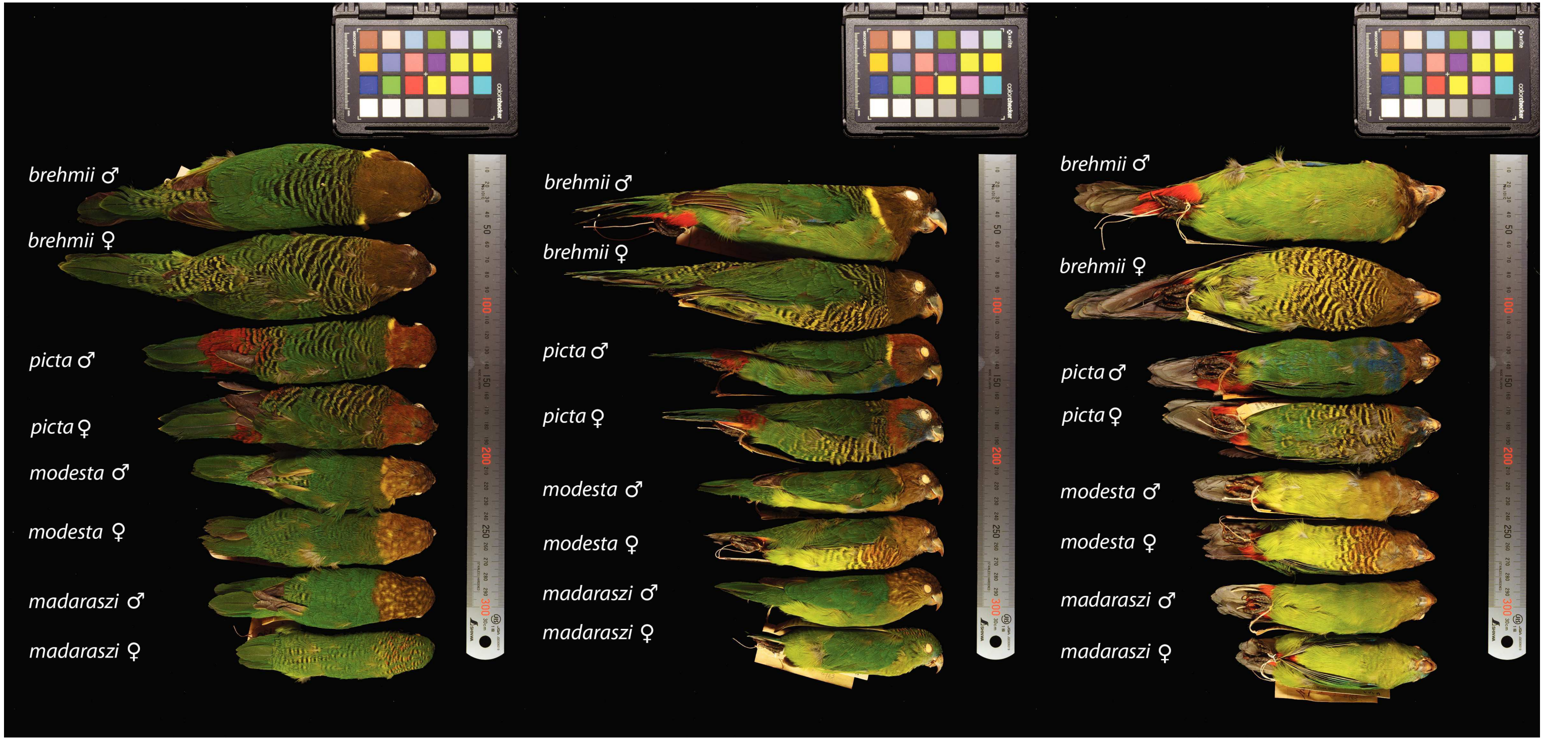


FIGURE 12. Specimens from the American Museum of Natural History (AMNH) of the four traditionally recognized species of *Psittacella* to show the size difference between the sister pairs of larger (*P. brehmii* AMNH 293610 ♂, AMNH 339594 ♀; *P. picta* AMNH 419599 ♂, AMNH 622039 ♀) and smaller (*P. modesta* AMNH 339630 ♂, AMNH 622046 ♀; *P. madaraszi* AMNH 419061 ♂, AMNH 622057 ♀) species. Photographs: Sahid Robles Bello.

tive to body size. They are either nocturnal (*P. occidentalis*) or active at dawn and dusk (*P. wallicus*, *P. flaviventris*). They are essentially green, finely mottled black and yellow, having very few other differences in plumage (e.g., red frons absent in *P. occidentalis* but present in the other two; yellower belly in *P. flaviventris* relative to *P. wallicus*). Their plumage pattern is strikingly convergent with that of *Strigops*.

The estimated split of *Pezoporus wallicus* and *P. flaviventris* was 3.8 Mya (2.1–5.2; fig. 11), which is older but overlaps with the level divergence in mtDNA that was used to elevate the two to species rank (Murphy et al., 2011). The enigmatic and recently rediscovered *P. occidentalis* diverged from the ground parrots early in their history at 7.5 Mya (4.4–10). Shute et al. (2023) have reexamined the cranial osteology of the arid zone, nocturnal *P. occidentalis*. They summarize its osteological distinctiveness in the title of their paper as adaptive and also note it as an evolutionary trade-off between the need for species to have good hearing and vision in its largely nocturnal biology. Taxonomically, they raised the specter of reinstating monotypic *Geopsittacus* for *P. occidentalis*. As their work clearly suggests adaptive differentiation relative to the other two *Pezoporus* species, we do not advocate breaking up *Pezoporus*.

Neophema and *Neopsephotus*

The seven species long placed in *Neophema* are the smallest-bodied Platycercinae and have long tails. One group of four species (*chrysostoma*, *elegans*, *petrophila*, *chrysogaster*) for which the genus-group name *Neonanodes* is available, is predominantly yellow-green with species-specific patterns of shades of blue about the face, forehead and wing. A further pair of species (*pulchella*, *splendida*), one of which, *pulchella*, is the type species of *Neophema*, have distinctive blue faces and red in the wings or chest. Lastly, a seventh species, usually now placed in monotypic *Neopsephotus*, is pastel pink and blue. The clade, excluding *Neopsephotus*, began diversifying 6 Mya (3.4–8.1; fig. 11). We affirm the now well-established transferal of *Neophema bourkii* to monotypic *Neopsephotus* as sister to the six species we advocate leaving in *Neophema*. In addition to our genomic support for this, *Neopsephotus bourkii* is ecologically and phenotypically highly distinctive. Its plumage is uniquely pastel pink and blue, it has distinctive, musical vocalizations unlike the high-pitched *tzeet* like contact flight vocalizations made by the other six species, it inhabits arid zone *Acacia* scrubs, and is markedly crepuscular, i.e., noticeably active at dawn and dusk.

Among the six species remaining in *Neophema*, four are strictly or partially migratory, although the scale of movements varies. *Neophema chrysostoma* of southeastern Australia and the critically endangered *N. chrysogaster* are typical long-distance migrants crossing Bass Strait between Tasmania and the Australian mainland, *N. chrysostoma* migrating still further north deep into arid central Australia. As some of these movements occur at night, we reiterate the observation of Joseph et al. (2011) that crepuscular or nocturnal activity characterizes a number of species in Pezoporini as currently construed, suggesting its early origin in the tribe's history. *Neophema elegans* in the west of its range is partially migratory with at least a part of its population regularly migrating seasonally up to several hundred kilometers between the arid and temperate zones (Davis and Burbidge, 2008). *Neophema elegans* in eastern Australia moves locally with some suggestion of seasonality (Collar and Boesman, 2020) and *N. petrophila* certainly undergoes pronounced postbreeding dispersal and probably some seasonal movement (Baxter and Parker, 1981; Higgins, 1999). The sister species *N. splendida and N. pulchella* are in turn sister to the preceding four species and geographically replace each other in low woodlands in arid central-southern Australia and mesic southeastern Australia, respectively.

Wolters (1975) introduced Neophemini at tribal rank to accommodate the genera *Neopsephotus* and *Neophema*. He gave neither a description nor a reference to one as is required for new family-group names introduced after 1930. Therefore, his name is a nomen nudum and unavailable. Our colleagues R. Schodde and I. Mason have independently concluded that there is merit in recognizing *Neophema* and *Neopsephotus* at tribal or subtribal rank. We here join with them in introducing a family-group name to accommodate the genera *Neopsephotus* and *Neophema* either at tribal rank or as a subtribe within Pezoporini. We introduce a new family-group name at the rank of tribe as:

Neophemini Schodde, Mason, Smith, Thom, and Joseph, 2024, new tribe

ZooBank registration: urn:lsid:zoobank.org:act:7156B56E-42BF-4410-AAB4-2C3A84628231

Diagnosis: Small, usually plain-plumaged parrots without transverse barring or black chevroning, e.g., dorsal feathers in *Pezoporus* are transversely barred black and yellow in their centers but broadly fringed with green, whereas in *Neophema* and *Neopsephotus* the dorsal feathers are plain green or dusky brown, respectively; unmarked outer rectrices with extensive yellow (or white) tips and dark bases; remiges with white to yellowish white bar on inner vanes evanescent, earliest in adult males, hardly extending on to outer vanes and usually obscure on upper surface of wing; pale "submissive" spot present in nape down; underwing coverts rich dark blue, often brighter on bend of wing; hypotarsal flexor tendon arrangement approaching ancestral condition: deep flexor tendons enclosed in separate bony canals, superficial tendon musculus flexor perforatus digiti II enclosed in a separate canal, and remaining superficial tendons external and separated in two separated shallow grooves on plantar wall; usually colonial, in small groups; foraging on ground and low shrubs and nesting in tree hollows (scrapes under rocks in *Neophema petrophila*); nestling begging call a husky quavering note that increases in time-frequency with age developing into bursts of brief whistles. In accordance with Article 13.1.2, we note that gross phenotypic differences have been well-illustrated and described on many occasions in the literature and we cite as examples reference works on the world's parrots (e.g., Forshaw and Knight, 2010; Juniper and Parr, 1998). This tribe comprises the genera *Neophema* and *Neopsephotus*.

Type genus: *Neophema* Salvadori, 1891, *Catalogue of the Birds in the British Museum* 20: 539, 569, by original designation. Type species: *Psittacus pulchellus* Shaw, 1792 = *Nephema (Neophema) pulchella* (Shaw, 1792).

Taxonomic position of the tribe: Subfamily Platycercinae in the Family Psittaculidae.

Component genera: *Neopsephotus* and *Neophema*.

- *Neopsephotus* Mathews, 1912. *Novitates Zoologicae* 18: 279 – type species: *Euphema bourkii* Gould, 1841 = *Neopsephotus bourkii* (Gould, 1841), by monotypy.
- *Neophema* Salvadori, 1891. *Catalogue of the Birds in the British Museum* 20: 539, 569 – type species: *Psittacus pulchellus* Shaw, 1792 = *Neophema (Neophema) pulchella* (Shaw, 1792), by original designation.
- subgenus *Neophema*
- subgenus *Neonanodes* Mathews, 1912. *Novitates Zoologicae* 18: 279 – type species: *Psittacus chrysogaster* Latham, 1790 = *Neophema (Neonanodes) chrysogaster* (Latham, 1790), by monotypy.

Geographical distribution: Australia and some of its offshore islands including Tasmania.

Platycercini

The broad-tailed parrots (Platycercini) consist of nine genera and 38 extant species distributed across Australasia. The clade includes the radiation of rosellas (*Platycercus*) in Australia and *Cyanoramphus* (New Zealand and islands of the South Pacific). The seven other genera contain up to a maximum of four species. Four of these genera are monotypic, i.e., *Purpureicephalus*, *Lathamus*, *Psephotus*, and *Clarkona*, the last-named here reinstated (see below). There are also four species in *Cyanoramphus* that went extinct upon European colonization of their islands, and *Psephotellus pulcherrimus* of Australia is extinct. There are two well-supported subclades in Platycercini that are repeatedly inferred across different studies, datasets, and phylogenetic methods. Intergeneric relationships are also resolved and stable. One clade comprises *Barnardius*, *Platycercus*, *Purpureicephalus*, *Psephotus*, *Psephotellus*, *Clarkona*, and *Northiella* (figs. 1, 11). *Barnardius* and *Platycercus* are closely related, which reflects some authors uniting them in *Platycercus* (e.g., Johnstone and Storr, 1998), but they diverged at 10.5 Mya (4.7–14.7) and we support retention of both (figs. 1, 11). The nonmonophyly of *Psephotus* sensu lato (Joseph et al., 2011) was corroborated with phylogenomic data, the type species *Psephotus haematonotus* not sharing a most recent common ancestor with the four species comprising *Clarkona* and *Psephotellus.* Phylogenetically between these genera are ditypic *Northiella* and monotypic *Purpureicephalus*. The other major subclade within the Platycercini (*Lathamus*, *Prosopeia*, *Eunymphicus*, *Cyanoramphus*) is more widely distributed, ranging from Australia, New Caledonia, Fiji, New Zealand, and various small islands in the South Pacific. As with previous phylogenetic work, the migratory and critically endangered *Lathamus discolor* was sister to *Prosopeia*, *Eunymphicus*, and *Cyanoramphus* (figs. 1, 11). In turn *Prosopeia*, which is restricted to Fiji, was sister to *Eunymphicus* of New Caledonia and the Loyalty Islands and *Cyanoramphus*. This suggests a key role for a propensity for long-distance movement in the evolution of this clade (see Joseph et al., 2011).

Our concatenated tree was concordant with previous phylogenies (Boon et al., 2008; Joseph et al., 2011) showing that *Eunymphicus* and *Cyanoramphus* are sister lineages, and that *Prosopeia* was sister to both. Some of the species trees had *Cyanoramphus* and *Prosopeia* as sister with strong support. However, interpreting the robustness of this alternative relationship will require new genetic data because the *Eunymphicus* samples were dropped in the most stringent data-retention filter.

Lathamus

The critically endangered *Lathamus discolor* is largely green and small bodied. In its nectarivory and associated aspects of morphology, such as slender, pointed wings and tail, and crude brush tongue, it is convergent with the lories and lorikeets (Loriini; see Gartrell et al., 2000; Kennedy and Tzaros, 2005). It is a seasonal migrant that breeds in Tasmania and winters in mainland southeastern Australia. As with the other monotypic genera in broad-tailed parrots, it is on a long branch that diverged 10.6 Mya (4.4–15) from a clade that radiated across New Zealand and nearby islands (*Cyanoramphus*), New Caledonia (*Eunymphicus*), and Fiji (*Prosopeia*) (fig. 11).

Prosopeia

Prosopeia (shining parrots) encompasses three species that are endemic to Fiji. They are large parrots dorsally green and ventrally red to yellow. *Prosopeia* likely colonized the archipelago at around 9.3 Mya (3.7–13.4), as this was the timeframe of its divergence from its common ancestor with *Eunymphicus* and *Cyanoramphus* (fig. 11). *Prosopeia personata* of Viti Levu diverged from *P. tabuensis* and *P. splendens* 5.9 Mya (2.3–8.9). Some authors (Forshaw and Knight, 2010) consider *P. splendens* of Kadavu, Ono, Viti Levu, a subspecies of *P. tabuensis* of Vanua Levu, Kioa, Koro, and Gau. Our time-calibrated tree has the two species diverging at 2.8 Mya (1–4.4; fig. 11).

Eunymphicus

The two species of *Eunymphicus* are midsized green parrots that have a black mask and crest, red and yellow crowns and long tails. They occur in the New Caledonian archipelago. Boon et al. (2008) found genetic, morphological, and behavioral data supporting recognition of two species, *E. cornutus* of Grande Terre (New Caledonia's main island) and *E. uvaeensis* of Ouvéa in the Loyalty Islands. Our time-calibrated tree dates this split at 3.2 Mya (1–5.1; fig. 11).

Cyanoramphus

Cyanoramphus are small to midsized, largely green with long tails that radiated in New Zealand and surrounding islands of the South Pacific as well as eastward to the remote archipelago of the Society Islands. *Cyanoramphus* was estimated to have diverged from *Eunymphicus* of New Caledonia and the Loyalty Islands 8.2 Mya (3.2–12) and diversification within the group was estimated to have begun 5.5 Mya (2–8.2; fig. 11). Systematic relationships with *Cyanoramphus* have been and still are hampered by incomplete taxon and genetic sampling, a reminder that we have not sampled the extinct *Cyanoramphus ulietanus* and *C. zealandicus*. Comparison of the phylogenomic tree with mtDNA data (Rawlence et al., 2015) was limited because of the low support in our concatenated tree. These conditions are analogous to that of *Pyrrhura*—a rapid radiation and degraded DNA from historical specimens. The phylogenomic results confirm that classifying taxa together based on color of head plumage was not consistent with the phylogeny, an observation that was used to elevate several taxa to species rank. All trees agree that *C. forbesi* and *C. auriceps* are not sister species. *Cyanoramphus forbesi* was previously classified as a subspecies with *C. auriceps* because both have a red frontal band and yellow crown. The phylogenomic tree has C. *forbesi* as sister to the endangered *C. cooki*, of Norfolk Island, albeit with low support (UFBS = 51%). The mtDNA tree has *C. cooki* as sister to all other *Cyanoramphus*, excluding *C. forbesi*. Regardless, if *C. cooki* and *C. forbesi* were sister or on successive nodes, then they shared a common ancestor 4.7 Mya (1.7–7.3). The mtDNA tree and our phylogenomic trees agree that *C. saisseti* was sister to all other *Cyanoramphus* whereas species tree had the more plainly patterned *C. unicolor* in this position. *Cyanoramphus hochstetteri*, which was formerly a subspecies of *C. novaezelandiae*, was most closely related to *C. malherbi* and *C. unicolor* in the mtDNA and the concatenated phylogenomic tree (fig. 11).

Platycercus

Rosellas (*Platycercus*) are small to midsized parrots that have radiated entirely within Australia including Tasmania. They are among the most easily diagnosable of any parrot genus on plumage by their uniquely mottled upperparts and prominent mono- or bicolored cheek patches. The phylogenomic trees parallel the results from prior multilocus data in supporting two groups sometimes recognized as subgenera (Shipham et al., 2015). The nominotypical subgenus *Platycercus* comprises blue-cheeked species *Platycercus caledonicus* of Tasmania and islands of Bass Strait, and the *P. elegans* complex of mainland southeastern Australia (the blue-cheeked crimson rosella complex); those sometimes placed in subgenus *Violania* comprises species having white, bicolored blue and white, or yellow cheeks (*icterotis*, *eximius*, *adscitus*, and *venustus*). Both a multilocus (Shipham et al., 2015) and the phylogenomic tree presented here showed the placement of *P. icterotis* of southwestern Western Australia as unresolved or poorly supported as sister to the rest of *Violania*. Our analyses accord with those of Shipham et al. (2015, 2017) who showed that mtDNA of mainland *P. eximius* has been captured by that of nonsister species *P. adscitus*, which occurs to its north and with which it has a complex hybrid zone (Shipham et al., 2019); the mtDNA of *P. eximius diemensis* of Tasmania is “true” *P. eximius* mtDNA.

Notably, the *P. elegans* group has long been a focus of work in speciation and systematics particularly after it was proposed by Cain (1955) as an example of a ring species. Our sampling was not designed to address these issues, but genomic testing of earlier work by Joseph et al. (2008) rejecting the ring species hypothesis is long overdue.

Barnardius

The Australian ringneck parrots, *Barnardius* spp., are the sister group of *Platycercus* rosellas.

The two genera are each phenotypically distinct and easily recognizable. Mostly, *Barnardius* are arid and semiarid zone replacements of *Platycercus*, with notable exceptions of broad sympatry or parapatry in southwestern Australia, the Flinders Ranges, and in and near riparian zones of some inland river systems in eastern Australia. Our molecular dating indicates divergence within *Barnardius* beginning at 0.9 Mya (0.4–1.4; fig. 11) was consistent with the 1.72% divergence between two mtDNA-based clades (Joseph and Wilke, 2006).

Until Schodde and Mason's (1997) review recognizing one species, most texts treated two species: *Barnardius zonarius* having subspecies *B. z. zonarius* and *B. z. semitorquatus*; and *Barnardius barnardi* more controversially having two subspecies, *B. b. barnardi* and *B. b. macgillivrayi*. Ford and Parker (1974) had noted that the phenotypically more complex plumage pattern of *barnardi* set it apart from the simpler patterned *macgillivrayi*, which they argued to be closer to the similarly patterned *zonarius* and *semitorquatus*. This was clearly supported in mtDNA phylogeographic data, which showed two clades, 1 and 2, having 1.72% net divergence between them (Joseph and Wilke, 2006). Clade 1 comprised samples of the *barnardi* phenotype, and clade 2 included all four subspecies (*zonarius*, *semitorquatus*, *macgillivrayi*, and *barnardi* and their phenotypic intergrades). Mitochondrial haplotypes in clade 2 were weakly differentiated and unstructured among the phenotypic groups. The lack of reciprocally monophyletic taxa in mtDNA data of *Barnardius* and the multiple zones of contact including between nonsister taxa *barnardi* and *macgillivrayi* can now be reasonably attributed to post-isolation gene flow.

Given that phenotypic signals of introgression of *zonarius* into *barnardi* are known to extend well east of their primary zone of contact (Schodde and Mason, 1997; Joseph and Wilke, 2006), we chose a sample of *barnardi* as far as possible from zones of its contact with *zonarius* and *macgillivrayi* and from where it shows minimal phenotypic signal of introgression from other taxa. Allowing that we were examining the world's parrots and not focusing in detail on any one species complex, we hoped this would be adequate. However, mtDNA extracted from UCE reads (not reported) showed that *barnardi* was nested within *zonarius*, a result inconsistent with Joseph and Wilke (2006). We must allow for several possibilities, assuming that the shallow mtDNA divergences in our samples are not due to contamination or a laboratory mix-up. One is that genetic introgression extends even further than we had anticipated and that our sampling has been obviously inadequate to place any introgression into full context. Alternatively, there is a puzzling discrepancy between large and small mitochondrial and nuclear DNA divergences, respectively, within *Barnardius*. For now, we reiterate Schodde and Mason's (1997) call for a full study of introgression across *Barnardius* and, of course, that it be a genomic assessment. This should be done before disrupting the current, if less than ideal, taxonomic practice of recognizing one species. We predict that the species-level taxonomy will eventually settle on the merit of recognizing monotypic *B. barnardi* and polytypic *B. zonarius*, however.

Psephotus

Psephotus haematonotus is a small-sized parrot with an attenuated tail, and it occurs broadly in southeastern Australia from the Lake Eyre Basin deep in the continent's interior south and east to the coasts. It diverged at 11.1 Mya (5.2–15.3; fig. 11). Its sexual dimorphism generally recalls that of *Clarkona* in that males are extensively green and females are grayish olive, but details of plumage patterning differ profoundly. *Psephotus haematonotus* has unique, whistled vocalizations. Although previously thought to be the eastern member of a vicariant sister pair with *Clarkona varia* (e.g., Ford, 1974) clarification of their phylogenetic positions dispelled this.

Northiella

Northiella are small-bodied parrots, with attenuated tails, but uniquely grayish-olive plumage punctuated by distinctively yellow or red wing-covert patches, blue facial feathering, (two-toned blue in *N. narethae*) and their prominent red or yellow abdominal (belly) patches. Their harsh contact calls recall those of *Platycercus* rosellas, but they also have a unique whistled vocalization. Phylogeographic work on what had been construed as one species, *N. haematogaster*, revealed genetic structuring to the extent of 2.16% mtDNA sequence divergence between what are now recognized as two species (Dolman and Joseph, 2015), *N. haematogaster* and *N. narethae*. In comparison to the temporal estimate of their divergence derived by converting the mtDNA distance with a standard 2% molecular clock, our phylogenomic estimate of divergence between these taxa is about twice as old at 2 Mya (0.8–3.1; fig. 11).

Purpureicephalus

Purpureicephalus spurius is a midsized, extraordinarily colored parrot. It has a strongly demarcated maroon-red crown, greenish yellow face, purplish underparts, yellow rump, green back and a long, attenuated blue tail. It has an unusually long maxilla with which it can extract seeds from the fruits of a cooccurring eucalypt, the marri *Corymbia calophylla*. It occurs in forest and woodland in southwest Australia and within this area shows no geographic variation. *Purpureicephalus* lies on a long branch diverging from the clade containing *Psephotellus* and *Clarkona* 9.8 Mya (4.6–13.6; figs. 1, 11). Its continued recognition as a monotypic genus is warranted on genomic, phenotypic, and biogeographical grounds. Notably among platycercine parrots, it is broadly sympatric with the largest and smallest of the *Barnardius* and *Platycercus* parrots, respectively. Any close affinity with *Platycercus adscitus* due to its unusually purplish blue ventral coloring has long been dispelled as has Cain's (1955) suggestion that *Purpureicephalus* and *Eunymphicus* should be synonymized.

Psephotellus and *Clarkona*

Psephotellus comprises a small radiation (here treated as three species) of midsized parrots endemic to Australia. Its three species (*Psephotellus dissimilis*, *P. chrysopterygius*, and the now extinct *P. pulcherrimus*) are almost unique in the entire Order Psittaciformes in nesting in terrestrial termite mounds in cavities dug out by the birds themselves. This well-supported clade has a crown age of 6.6 Mya (3.1–9.5; fig. 11). A fourth species, *varia*, was sister to the other three but on a long branch, having diverged from the other three species at (4–12.2 Mya; fig. 11). This species has usually been placed in *Psephotellus*. Unlike the three tropical or subtropical *Psephotellus* species, this species is an arid and semiarid zone species that nests unremarkably in tree hollows. Further, it is phenotypically unlike the other three in having, for example, uniquely patterned head plumage and distinctive vocalizations. On these collective grounds, we advocate recognition of *Clarkona* Mathews, 1917, as a genus for the species usually referred to as *Psephotellus varius* (cf. approach to recognizing *Gymnopsittacus weddellii* above), but which will become *Clarkona varia*. *Clarkona* was clearly and consistently treated as feminine by Mathews (1917a) and by CSIRO (1969). For example, Mathews (1917a) referred to the subspecies he recognized in this species as follows: "*Psephotus varius varius* or *Clarkona varia varia*," or "*Psephotus varius exsul* or *Clarkona varia exsul*," and so on.

Discordances in patterns of plumage color and phylogeny among the three species retained in *Psephotellus* are notable. The two species of Australia's tropics, *P. dissimilis* of the Northern Territory and *P. chrysopterygius* of Cape York Peninsula, are extremely similar in having aqua-green underparts and prominent yellow patches on the wing coverts. They occur either side of a well-established biogeographic barrier in northeastern Australia, the Carpentarian Barrier, which can explain the distribution of many similarly distributed pairs. Unexpectedly, therefore, our results and an earlier study based on mitochondrial DNA sequence data (Christidis and Norman, 1996) found that they are not sister taxa. Instead, the two eastern Australian species, *P. chrysopterygius* and the now extinct *P. pulcherrimus*, which had a red wing-covert patch and underparts of a similarly unique, if slightly different shade, of aqua-green, have emerged as sisters. Necessarily, both studies used DNA from historical specimens for the extinct *P. pulcherrimus*. Our study did likewise for the highly endangered *P. chrysopterygius*, that of *P. dissimilis*, with a sample derived from fresh tissue. We are currently sequencing DNA from a fresh *P. chrysopterygius* sample that has since become available to test this unexpected relationship.

If the pattern of relationships recovered in our study and by Christidis and Norman (1996) is confirmed, then it would imply that *P. dissimilis* diverged first from the common ancestor of *P. chrysopterygius* and *P. pulcherrimus* through vicariance across the Carpentarian Barrier. Next, divergence within eastern Australia led to separation of *P. pulcherrimus* and *P. chrysopterygius* (see Bryant and Krosch, 2016, for relevant biogeography). *Psephotellus pulcherrimus* was extinct by 1930, but genomic analyses show no evidence of a bottleneck prior to its extinction (Irestedt et al., 2019). Given the discordance just noted between color of wing coverts and relationships, it is notable that the reduced wing-covert patch is sexually dimorphic in *C. varia*, yellow in males and red in females and younger males.

Lastly, we note that the plumage patterning of adult male *P. dissimilis* and *P. chrysopterygius* is, at least within the constraints of natural selection, broadly similar to that of several species of African *Poicephalus* most especially *Poicephalus meyeri* (fig. 13) in showing dark upperparts, prominent yellow about the greater wing coverts, and a similarly unusual shade of green on the underparts. Study of the drivers of this convergence in the high-intensity light, mostly tropical savannas that these species inhabit would surely be rewarding.

AGAPORNITHINAE

Agapornithinae are small green parrots with short round or wedge-shaped tails. The clade consists of the monotypic *Bolbopsittacus lunulatus* of the Philippines, the hanging parrots (*Loriculus*), which occur from India to New Guinea, and the lovebirds (*Agapornis*) of the Afrotropics. *Agapornis* and *Loriculus* share the behavior of carrying nesting material in their feathers (Forshaw, 1973). Relationships among the three genera are stable. *Bolbopsittacus* diverged from the common ancestor of *Loriculus* and *Agapornis* at 24.4 Mya (17.4–28.8), and *Loriculus* and *Agapornis* then split at 23.1 Mya (16.4–27.3; figs. 1, 11) We advocate recognition of this phylogenetic depth and structure at least through recognition of a tribe for *Bolbopsittacus* and we note that two family-group names are available with which to recognize two other currently monogeneric tribes for *Loriculus* and *Agapornis*. In accordance with articles 13.1 and 13.2 of the Code (ICZN, 1999) we therefore introduce a new family-group name at the rank of tribe for the genus *Bolbopsittacus*:

Bolbopsittacini, new tribe

ZooBank registration: urn:lsid:zoobank.
org:act:6CB65343-DA33-4016-BE31-
B8348E1813A8

DIAGNOSIS: In accordance with Article 13.1.1, we note that diagnostic traits of Bolbopsittacini—the same as those of its sole genus and species, the Guaiabero *Bolbopsittacus lunulatus*—include the combination of the following: a small (~15 cm) parrot with a very short tail; proportionally broad, bicolored bill that is black distally and bluish gray proximally; predominantly green in plumage but with light blue around the face and a sexually dimorphic collar uniquely in parrots located across the mantle, which in males is blue concolorous with or slightly darker than blue of the face and in females is yellow with a black terminal band; yellow rump edged with black in females of *B. l. mindanensis*. We note convergent similarities in plumage with *Cyclopsitta diophthalma*, especially in the tone of blue about the face. In accordance with Article 13.1.2, we note that these differences have been well illustrated and

FIGURE 13. Photographs (not to scale) of an adult male *Psephotellus dissimilis* (left photo: David Cook) of Australia and *Poicephalus meyeri* (right photo: John Missing) of Africa and showing broadly similar plumage patterning that includes most unusual but similar shades of green on the underparts, dark brownish upperparts and a prominent patch of yellow about the wing coverts and bend of the wing. See text for discussion. Photographs reproduced with permission from the photographers.

described on many occasions in the literature and we cite as examples reference works on the world's parrots (e.g., Forshaw and Knight, 2010; Juniper and Parr, 1998).

Type-genus *Bolbopsittacus* Salvadori, 1891, *Catalogue of the Birds in the British Museum* 20: 388, 503 – type species: *Psittacus lunulatus* Scopoli, 1786 = *Bolbopsittacus lunulatus* (Salvadori, 1891), by original designation.

Taxonomic position of tribe: Subfamily Agapornithinae of Family Psittaculidae.

Component genera: Monospecific including only *Bolbopsittacus lunulatus* (Scopoli, 1786).

Geographic distribution: Philippines.

Bolbopsittacus

Bolbopsittacus lunulatus is a small green parrot with pale blue facial markings and is restricted to the Philippines. Our sampling has not addressed divergence within the species, which is currently divided into three subspecies (*callainipictus*, *intermedius*, and *mindanensis*). None of several recent studies of cryptic diversity in Philippine birds have addressed this species either (e.g., Peterson, 2006; Lohman et al., 2010; Hosner et al., 2014, 2018). Its phylogenetic placement as sister to *Loriculus* and *Agapornis* was well supported and stable across the phylogenomic trees and previous phylogenetic hypotheses for parrots (e.g., Wright et al., 2008).

Loriculini

Loriculus

Hanging parrots (*Loriculus*) are so named from their oft-quoted but rarely reported behavior of roosting while hanging by the feet from a branch like a pteropodid bat. The behavior has been described, however, for *L. galgulus* in captivity (e.g., Griffiths, 1947; Buckley, 1968). We would welcome modern data on this behavior in the wild, its consistency, or whether the birds have evolved responses to any physiological challenges caused by roosting upside down. Three out of up to 15 species recognized were not sampled in this study, namely *L. camiguinensis* of Camigun Sur, southern Philippines (Tello et al., 2006), *L. flosculus* of Flores Island, Indonesia, and *L. bonapartei*, also part of the *L. philippensis*–*L. camiguinensis* complex and debatably elevated to species rank (e.g., Collar and Kirwan, 2023). Forshaw and Knight (2010) treated the relatively recently described *L. camiguinensis* as a subspecies of *L. philippensis*; certainly the taxon is diagnosable by traits of plumage and size. Two subclades within *Loriculus* diverged 8.7 Mya (4.7–12.2; fig. 11), concordant with variation in bill color but not the presence of a red throat patch. Clade 1 is defined by taxa having black bills and contains *L. tener* and *L. aurantiifrons* of New Guinea and surrounding islands and the Bismarck Archipelago, and *L. catamene*, *L. sclateri*, *L. stigmatus*, and *L. amabilis* of Moluccas and Sulawesi and neighboring islands (fig. 11). Clade 2, which is defined by taxa with red bills, has a deep divergence whereby *L. philippensis* was sister to the other taxa in the clade (*L. pusillus*, *L. vernalis*, *L. galgulus*, *L. exilis*, and *L. beryllinus*) from which it diverged at 7.2 Mya (3.7–10.4), although *L. philippensis bonapartei* notably has a black bill (Forshaw and Knight, 2010; fig. 11). Within clade 2 *L. pusillus* of Java and Bali, Indonesia diverged from two sister pairs. One pair contains the widely distributed *L. vernalis* occurring in India through Southeast Asia and neighboring archipelagoes and its geographic replacement, *L. galgulus* of the Malay Peninsula, Sumatra, Borneo, and surrounding islands. The other sister pair is widely disjunct geographically and comprises *L. beryllinus* endemic to Sri Lanka and *L. exilis* of Sulawesi. The estimated divergence time between *L. beryllinus* and *L. exilis* was 1.3 Mya (0.5–2.2; fig. 11), indicating that this complex biogeographic pattern is a relatively recent pattern.

Agapornithini

Agapornis

The lovebirds (*Agapornis*) are small, short-tailed, stocky parrots, mostly with colored bills and species-specific color patterns of the head and chest. The nine species of lovebirds have radiated within sub-Saharan Africa and Madagascar. Pioneering analyses of their evolution were based on morphology and environmental data by Moreau (1948) and courtship and nesting behavior (Dilger, 1960, 1962, 1964). Later, Racheli (1999) and Huynh et al. (2023), respectively, presented a cladistic morphological analysis and a phylogenomic analysis based on low-coverage whole-genome sequencing. The phylogenomic concatenated tree has high support (>95% UFBS) for all nodes, and the species tree had only one node (*A. nigrigenis* and *A. roseicollis*) with lower support (LPP = 0.88). The phylogenomic trees were discordant with the placement of *A. taranta* and *A. pullarius*, but this discordance was attributable to data quality. In analyses with more stringent filters for retaining samples, *A. pullarius* was excluded and the position of *A. taranta* became stable. In the concatenated tree *A. canus* of Madagascar then *A. swindernianus* were sisters to the other lovebirds (fig. 11). The next divergence was between a clade containing *A. pullarius* and *A. swindernianus* of western and central Africa from the five remaining species. The final relationships in the group had *A. roseicollis* of southwestern Africa as sister to two species pairs: *A. nigrigenis*/*A. roseicollis* and *A. personatus*/*A. fischeri*. This clade was also characterized by nest building in cavities: *A. roseicollis* builds a cup-shaped nest whereas the other four species build domed nests (Huynh et al., 2023).

The topology of Provost et al. (2018) is concordant with the phylogenomic tree for nodes with common sampling except *A. personatus and A. fischeri* were found not to be sisters. The whole genome phylogeny Huynh et al. (2023) also recovered the same topology as our concatenated tree except it had lower support for nodes *lilianae*/*nigrigenis* and *personatus*/*fischeri*. Maximum likelihood estimates of species-level divergences cover a large timeframe, ranging from 0.7 Mya to 10.8 Mya (fig. 11). We advocate retention of one genus, *Agapornis*, for all of these species.

LORIINAE

Relationships within the Loriinae are resolved and stable. The speciose lorikeets and lories (Loriini) and monotypic Budgerigar (Melopsittacini) are sisters and split 17 Mya (8.6–22.2). Cyclopsittini diverged from the ancestor of Loriini and Melopsittacini 19.3 Mya (10.9–24.8; figs. 1, 14).

Cyclopsittini

Suavipsitta, Cyclopsitta, and *Psittaculirostris*

The fig parrots are among the smallest of all parrots. Predominantly green (one species has orange underparts), they have richly colored and diversely patterned facial plumages characterized by shades of red and blue, sometimes black, and which are often sexually dichromatic. *Psittaculirostris* are the largest and have strikingly colored elongate, lanceolate facial feathers. They are frugivorous and, again almost uniquely in parrots, they excavate rather than use existing hollows for nests in rainforest trees. They range across Indonesia, New Guinea, and Australia.

Two genera, *Cyclopsitta* and *Psittaculirostris*, are currently recognized. We recognize long-running, contentious debate about whether *Cyclopsitta* should be used instead of *Opopsitta* (e.g., Mathews, 1916; Holyoak, 1970; Storr, 1973, Schodde, 1978; Schnitker, 2014) but follow the decision to use *Cyclopsitta*. Previous work by Mitchell et al. (2021) and phylogenomic trees show that *Cyclopsitta* was paraphyletic (fig. 14), and *Psittaculirostris*, while monophyletic, was nested within *Cyclopsitta*. The complexes of taxa long treated as subspecies of *C. gulielmitertii* and *C. diophthalma* have not been completely sampled for molecular data. With that caveat, *C. gulielmitertii* emerged as sister to a clade comprising *Psittaculirostris* and the similarly diverse, polytypic *C. diophthalma* complex. Note that this is based on the limited taxon sampling that has been done in a mitochondrial genome analysis (Mitchell et al., 2021) and in our phylogenomic analysis. In our study, as iterated before, we sampled only one individual per species. In contrast, Mitchell et al. (2021) sampled several but not every subspecies in *C. diophthalma*, and in *C. gulielmitertii* they sampled just one individual of *C. gulielmitertii melanogenia*. It is worth noting that the same *C. gulielmitertii* sample (ANWC B 56211) was used here and by Mitchell et al. (2021). Within *Psittaculirostris*, *P. edwardsii* and *P. salvadorii* diverged 0.8 Mya (0.4–1.6) and the ancestor of these taxa diverged from *P. desmarestii* 1.8 Mya (0.7–2.8; fig. 14).

A case to break up *Cyclopsitta* had been made on morphological and ecological grounds (Schnitker, 2014), reinforcing the molecular data that show the genus to be paraphyletic. *Suavipsitta* Mathews, 1917, is available for all taxa within the polytypic *gulielmitertii* complex (see Mathews 1917b), whether ascribed species or subspecies rank (see summary in Beehler and Pratt, 2016) in the recent trend to recognize more than one species within the *gulielmitertii* complex). The only alternative to not recognizing *Suavipsitta* would appear to be placing all these birds—including *Psittaculirostris*—in one genus. We argue that this would unhelpfully obscure the group's phenotypic and phylogenetic diversity. It also simply repeats the recognition of the group at tribe level in Cyclopsittini. We therefore endorse the recognition of *Suavipsitta*.

Satisfactory species-level taxonomies for both the *C. diophthalma* and *S. gulielmitertii* complexes await molecular studies with full taxon sampling.

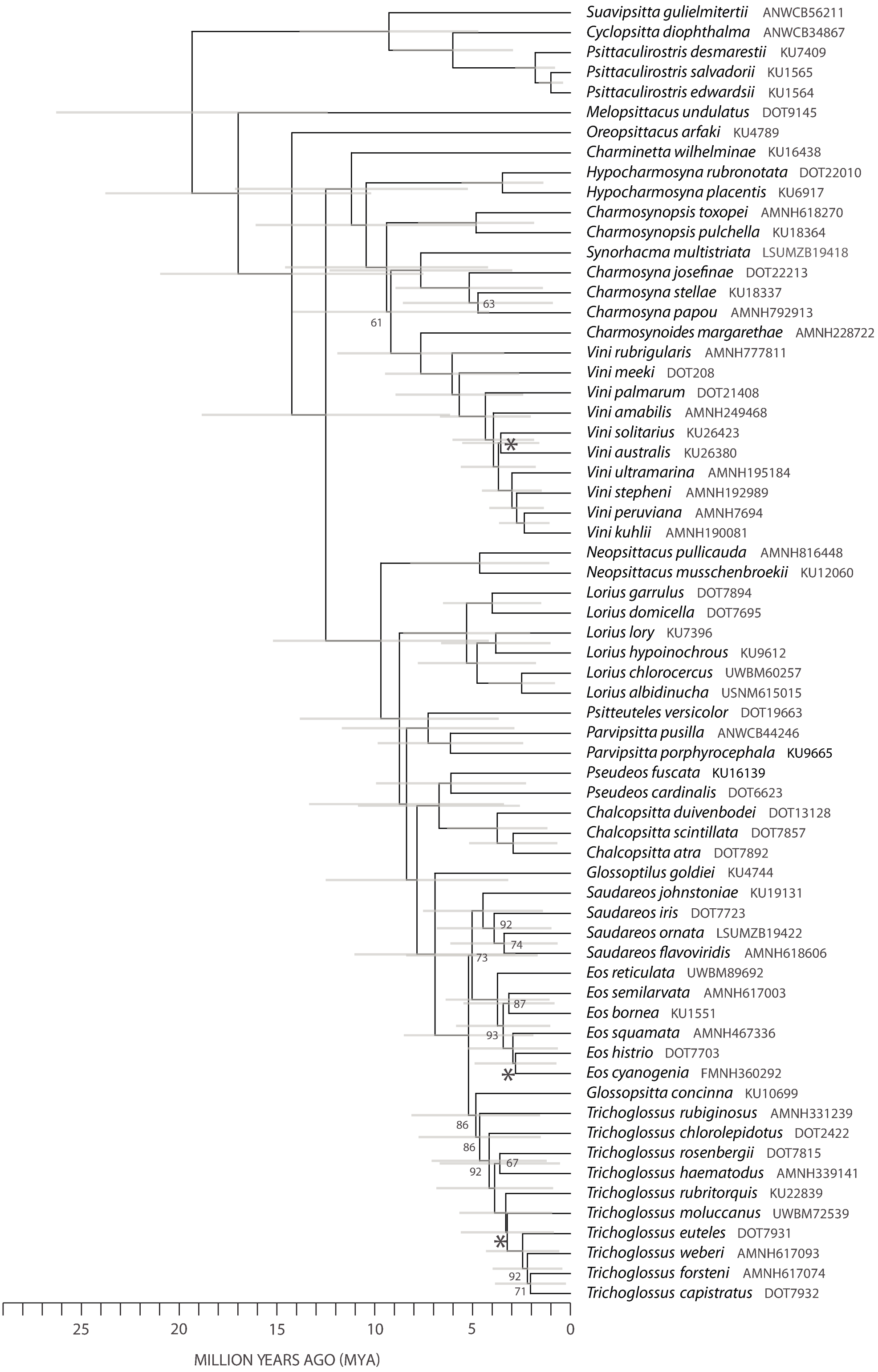
Melopsittacini

Melopsittacus

Melopsittacini contains a single genus and monotypic species (*Melopsittacus undulatus*), a small green parakeet that occurs throughout the interior of Australia. It is well known in captivity around the world (reviewed in Olsen, 2021).

Loriini

The nectarivorous lories and lorikeets (Loriini) are a diverse group that radiated across Indonesia, the Philippines, Australia, and the South Pacific, having their highest diversity on


Suavipsitta gulielmitertii ANWCB56211
Cyclopsitta diophthalma ANWCB34867
Psittaculirostris desmarestii KU7409
Psittaculirostris salvadorii KU1565
Psittaculirostris edwardsii KU1564
Melopsittacus undulatus DOT9145
Oreopsittacus arfaki KU4789
Charminetta wilhelminae KU16438
Hypocharmosyna rubronotata DOT22010
Hypocharmosyna placentis KU6917
Charmosynopsis toxopei AMNH618270
Charmosynopsis pulchella KU18364
Synorhacma multistriata LSUMZB19418
Charmosyna josefinae DOT22213
Charmosyna stellae KU18337
Charmosyna papou AMNH792913
63
61
Charmosynoides margarethae AMNH228722
Vini rubrigularis AMNH777811
Vini meeki DOT208
Vini palmarum DOT21408
Vini amabilis AMNH249468
Vini solitarius KU26423
*
Vini australis KU26380
Vini ultramarina AMNH195184
Vini stepheni AMNH192989
Vini peruviana AMNH7694
Vini kuhlii AMNH190081
Neopsittacus pullicauda AMNH816448
Neopsittacus musschenbroekii KU12060
Lorius garrulus DOT7894
Lorius domicella DOT7695
Lorius lory KU7396
Lorius hypoinochrous KU9612
Lorius chlorocercus UWBM60257
Lorius albidinucha USNM615015
Psitteuteles versicolor DOT19663
Parvipsitta pusilla ANWCB44246
Parvipsitta porphyrocephala KU9665
Pseudeos fuscata KU16139
Pseudeos cardinalis DOT6623
Chalcopsitta duivenbodei DOT13128
Chalcopsitta scintillata DOT7857
Chalcopsitta atra DOT7892
Glossoptilus goldiei KU4744
Saudareos johnstoniae KU19131
Saudareos iris DOT7723
92
Saudareos ornata LSUMZB19422
74
Saudareos flavoviridis AMNH618606
73
Eos reticulata UWBM89692
Eos semilarvata AMNH617003
87
Eos bornea KU1551
93
Eos squamata AMNH467336
Eos histrio DOT7703
*
Eos cyanogenia FMNH360292
Glossopsitta concinna KU10699
Trichoglossus rubiginosus AMNH331239
86
Trichoglossus chlorolepidotus DOT2422
86
Trichoglossus rosenbergii DOT7815
67
92
Trichoglossus haematodus AMNH339141
Trichoglossus rubritorquis KU22839
Trichoglossus moluccanus UWBM72539
Trichoglossus euteles DOT7931
*
Trichoglossus weberi AMNH617093
92
Trichoglossus forsteni AMNH617074
71
Trichoglossus capistratus DOT7932
25
20
15
10
5
0
MILLION YEARS AGO (MYA)

New Guinea. The clade exhibits a wide range of body sizes and plumage colors (Merwin et al., 2020). Relationships among genera are consistent across studies (Schweizer et al., 2015; Smith et al., 2020) and the phylogenomic tree presented here (Smith et al., 2023). The poorer-quality samples in the clade containing *Eos*, *Saudareos*, and *Trichoglossus*, which had the highest frequency of nodes in the Loriini with <95% UFBS support, prevented verifying its placement in the species tree. In our discussion below of species-level relationships, we exclude reference to the species tree from Smith et al. (2023) given the lower quality of sequence data, thus poorly resolved gene trees, for the lorikeets. We attribute the lower information content of lorikeet sequence data relative to the other parrots because the lorikeets were the first group for which we derived data from a commercial sequencing facility. Nonetheless, the concatenated phylogenomic tree provided a robust phylogenetic hypothesis that reaffirmed previous works and added nearly all described taxa.

Using the phylogenomic tree of the Loriini, Joseph et al. (2020) reclassified generic limits within the clade to align with phylogenetic history. This revision resulted in the splitting of several nonmonophyletic genera (*Trichoglossus*; *Charmosyna*; *Psitteuteles*). There are three main clades in the Loriini: (1) the monotypic and small-bodied *Oreopsittacus*; (2) includes diminutive to small lorikeets with long tails: *Charmosyna*, *Vini*, *Charminetta*, *Hypocharmosyna*, *Charmosynopsis*, *Synorhacma*, and *Charmosynoides*; and (3) species with a broad range in body size (small to large) and tails varying from short and square to long and attenuated: *Neopsittacus*, *Glossopsitta*, *Lorius*, *Parvipsitta*, *Psitteuteles*, *Pseudeos*, *Chalcopsitta*, *Glossoptilus*, *Eos*, *Trichoglossus*, and *Saudareos*. Clade 1 was sister to clades 2 and 3. The origin of the deepest clades within Loriini occurred at 14.2 Mya (6.0–19.5) and 12.5 Mya (4.8–17.5; fig. 14). Within clade 2, the topology forms a ladder with consecutive divergences of *Charminetta*, *Hypocharmosyna*, and *Charmosynopsis*. The remaining relationships were sister genera, *Synorhacma* and *Charmosyna*, and *Vini* and *Charmosynoides*, respectively (fig. 14). Maximum likelihood divergence dates among genera within clade 2 ranged from 6.1 to 10.4 Mya (fig. 14). Within clade 3, *Neopsittacus* then *Lorius* were sister to the remaining members of the group. The phylogenetic placement of *Neopsittacus* as sister to the diverse clade containing *Lorius*, *Saudareos*, *Eos*, *Trichoglossus*, *Glossopsitta*, *Pseudeos*, *Chalcopsitta*, *Psitteuteles*, and *Glossoptilus* was stable across phylogenies. *Parvipsitta* and *Psitteuteles*, and *Pseudeos* and *Chalcopsitta* were both sister pairs. The remaining members of clade 3 included *Glossoptilus*, which was sister to a group containing *Glossopsitta*, *Eos*, *Trichoglossus*, and *Saudareos*. The high generic diversity of clade 3 was estimated to have originated within a range of 5 to 9.7 Mya based on maximum likelihood divergence dates (fig. 14).

Oreopsittacus

Oreopsittacus is monotypic with geographic variation across the New Guinea highlands. *Oreopsittacus arfaki* is a small green lorikeet, with a long tail, and a distinct facial pattern of purple cheek patches and a broken “spotted” white malar stripe. As sister to all other lorikeets, it is on a long branch stemming from the basal divergence of the radiation dating to 14.2 Mya (6–19.5; fig. 14). Despite the significance of its evolutionary position in the lorikeet phylogeny, it is unclear how *Oreopsittacus* may inform the evolution of traits in the clade. Body size and plumage evolution are labile in lorikeets (Merwin et al., 2020). From a biogeographic perspective *Oreop-*

FIGURE 14. Time-calibrated topology of Loriinae. Support values come from the maximum likelihood tree. Support values come from the maximum likelihood tree. Nodes have ultrafast bootstrap values of ≥95% otherwise noted. Gray bars represent divergence time ranges were estimated from 100 bootstrap trees. * denotes an unsupported node where the topology of the presented time-calibrated phylogeny differs from that of the maximum likelihood tree.

sittacus helps reinforce the hypothesis that lorikeets originated in New Guinea.

Charminetta, Hypocharmosyna, Charmosynopsis, Synorhacma, and *Charmosyna*

Charmosyna was split into five additional genera to reflect phylogenetic relationships (Joseph et al., 2020). For simplicity, we will first discuss each of these newly circumscribed or reinstated genera (*Charminetta*, *Hypocharmosyna*, *Charmosynopsis*, and *Synorhacma*) and the current membership of *Charmosyna* followed by a section on *Vini* and *Charmosynoides.* The largest species in this clade are *Charmosyna papou* and *C. stellae*, but most taxa in this clade are small bodied with long tails.

Charminetta comprises one New Guinean species, *C. wilhelminae*. It is a very small lorikeet with distinctive red underwings and rump and a blue hindcrown, presumably a plesiomorphic trait in lorikeets similar to the maroon belly plumage of Arini.

Hypocharmosyna comprises two very similar species with sexually dichromatic elongated ear-covert feathers (blue in males, yellow in females) and red flanks or sides of the underparts. They occur on New Guinea and satellite islands.

Charmosynopsis comprises two phenotypically disparate species, *C. pulchella* of New Guinea, largely red below and green above; and the other, *C. toxopei*, of Buru in Maluku, Indonesia, almost entirely green but for its blue frond and forecrown.

Synorhacma of New Guinea although generally green shows yellow striations on its underparts, a patterning that is most unusual among all parrots, and uniquely in lorikeets, a bicolored bill.

Charmosyna, which formerly was a large paraphyletic assemblage, now comprises just three New Guinean species that are largely red below and green above with blue hindcrowns posteriorly edged with black. Two of the species, *C. stellae* and *C. papou*, have extraordinarily long central tail feathers. The third species, *C. josefinae*, resembles the other two but with nonelongated central tail feathers.

The phylogenetic pattern of elevational preference is interesting in that there have been multiple colonizations of the highlands and lowlands, where the number and directionality of the transition would be dependent on the ancestral state that is assigned. The sister to all remaining taxa in clade 2 was the smallest lorikeet *Charminetta wilhelminae*, which is a monotypic genus of the New Guinea highlands with no recognized geographic variation. There are then four subclades that reflect transitions between elevations. *Hypocharmosyna* (*H. rubronotata* and *H. placentis*) occur in the lowlands of New Guinea and surrounding islands. The widely distributed *Hypocharmosyna placentis* has deep phylogeographic structure that includes both mainland and insular forms (Smith et al., 2020; Joseph et al., 2020). More detailed populational-level sampling would be required to fully understand the evolutionary history of this taxon. *Vini* and *Charmosynoides* primarily occur in lower elevation habitats, but it is worth noting that montane conditions can be present at low elevations on Pacific islands (e.g., see *V. palmarum* in Gaua Island, Vanuatu; Andersen et al., 2017). *Charmosynopsis toxopei* occurs on Buru Island from 600–1000 m (Forshaw and Knight, 2010), Indonesia, and *Charmosynopsis pulchella* is another endemic species of the New Guinea highlands. Monotypic *Synorhacma* containing only *S. multistriata* occurs on the southern slopes of the central range in western New Guinea, occurring up to 1800 m (Forshaw and Knight, 2010).

Charmosyna sensu stricto now contains three species that occur in the highlands of New Guinea. *Charmosyna papou* and *C. stellae* have distinctly elongated central tail feathers and were taxonomically recognized as two species prior to molecular evidence. The phylogenomic data affirms the placement of subspecies within these species (Smith et al., 2020; Joseph et al., 2020): *wahnesi* and *goliathina* (UFBS <70%) was placed within C. *stellae*, and *papou* was rendered monotypic. The *Charmosyna* radiation was dated from 5.2 Mya (1.1–8.6; fig. 14).

Vini and *Charmosynoides*

The expanded *Vini* of Joseph et al. (2020) encompasses a radiation of diversely colored, small-bodied birds. We acknowledge informal discussion of the case to replace *Vini* Lesson, 1833, with *Coriphilus* Wagler, 1832. In contrast to the case of *Orthopsittaca manilatus* discussed above, we cautiously predict that *Vini* will warrant retention on the grounds of much more frequent usage, and therefore, stability. For example, in a search of the Biodiversity Heritage Library (https://www.biodiversitylibrary.org; accessed 8 January 2024) for references to "*Vini* Lesson" and "*Coriphilus* Wagler," we found 1871 vs. 223 full-text and 31 vs. 0 catalog references, respectively, citing these names, i.e., usage of *Vini* has demonstrably been more frequent than that of *Coriphilus*. Retention of *Vini* will promote stability and minimize disruption.

Vini as now construed exhibits high morphological diversity as it includes species formerly assigned to *Vini*, *Charmosyna*, and *Phigys*. It includes taxa with either short rounded tails (e.g., *V. solitarius*) through longer attenuated tails (e.g., *V. meeki*), species that are predominantly green with minimal red about the face and remarkably colored species with much red or blue, or both, in their plumage.

Charmosynoides was erected for the Solomon Islands endemic *C. margarethae*. Although *C. margarethae* certainly resembles the red and green species now placed in *Charmosyna* sensu stricto, traits such as its broad yellow pectoral band and its biogeographic distinctiveness were highlighted by placement in a monotypic genus. *Charmosynoides* and *Vini* are sister taxa that shared a common ancestor 7.7 Mya (2.7–11.2; fig. 14).

The more basal nodes in the radiation gave rise to mostly green birds, whereas more brilliantly and multicolored species (e.g., *V. peruviana*; *V. ultramarina*) stem from more derived nodes. This pattern of plumage evolution mainly follows a west-east expansion from Melanesia into Polynesia that occurred within the past 6.1 Mya (2.1–8.9; fig. 14). A still unresolved systematic puzzle within this clade is the placement of extinct *V. diadema*, which is known from a single specimen at the Paris Natural History Museum. *Vini diadema* was not included in Smith et al. (2020), but Joseph et al. (2020) advocated for its placement in *Vini* given its phenotypic similarity and geographic proximity to other small-bodied, green *Vini*.

Neopsittacus

Neopsittacus comprises two very similar, larger New Guinean lorikeets that, while dorsally green like most lorikeets, have extensive red underparts and underwings and yellow streaked facial plumage. They are placed on a long branch that coalesces with the other members of clade 3, 9.7 Mya (3.2–14.2; fig. 14). Smith et al. (2020) and Joseph et al. (2020) sampled two of three subspecies for each group that exhibits relatively shallow geographic structuring across their range.

Lorius

Lorius are midsized, stocky lories, mostly red with green wings and tail, and often with a dark crown. The six species form three sister pairs that are geographically coherent, a finding recovered in previous work using a small multilocus dataset (Schweizer et al., 2015). The three sister species pairs conform to a longitudinal geographic pattern of diversification and are: the westernmost pair, *L. domicella* and *L. garrulus* of Moluccas, Indonesia, was sister to the other two pairs, geographically central *L. lory* and *L. hypoinochrous* of New Guinea and surrounding islands; and easternmost *L. albidinucha* and *L. chlorocercus* of New Ireland and the Solomon Islands. The genus is absent from geographically intervening islands. The sister pairs *Lorius albidinucha*/*L. chlorocercus* and *L. lory*/*L. hypoinochrous* form a well-supported clade. *Lorius* had a crown age 5.3 Mya (1.7–8.2) in the tree presented here (fig. 14), and intraspecific variation continued to diversify into the late Pleistocene (Smith et al., 2020). Future systematic work on the group should resolve relationships among subspecies and assess whether any warrant species status. Smith et al. (2020) and Joseph et al. (2020) showed that species with geographic variation were monophyletic, but relationships often had lower support.

Parvipsitta and *Psitteuteles*

Parvipsitta comprises two Australian species, one of which (*P. pusilla*) is green with some red about the bill. As such, it closely resembles a number of other species now in newly circumscribed *Vini*, thus indicating the likely plesiomorphic nature of this predominantly green plumage with some facial red. *Parvipsitta porphyrocephala* in contrast has a more complex pattern of bluish underparts and purple crown, orange ear-coverts, and red underwing. It is the only lorikeet to range extensively into semiarid and arid zone habitats.

Psitteuteles now comprises just one species, *Ps. versicolor*, of tropical northern Australia. Predominantly green, it has a mauve chest and red crown, striated underparts, and a prominent naked, white periophthalmic ring.

Parvipsitta and *Psitteuteles* are deeply divergent lineages subject to previous reclassification (Schweizer et al., 2015). Although the distinction between *Parvipsitta* and *Psitteuteles* might be considered arbitrary, we reiterate the conclusions of Joseph et al. (2020) that placing all three species in *Psitteuteles* would form a very highly heterogeneous and differentiated group. *Parvipsitta* and *Psitteuteles* diverged from each other in the Pliocene at 7.3 Mya (2.1–11) and *Pa. pusilla* and *Pa. porphyrocephala* share a common ancestor dating back to 6.1 Mya (1.8–9.2; fig. 14). The three species are distinct in plumage, vocalization, and have nonoverlapping ranges in semiarid or mesic woodlands in Australia. For these reasons as well as to minimize nomenclatural change, we advocate their retention in *Parvipsitta* (cf. *Pseudeos fuscata* and *Ps. cardinalis* below). *Psitteuteles versicolor* of northern Australia, *Pa. pusilla* of eastern Australia, and *Pa. porphyrocephala* of southern and western Australia each exhibit no known geographic variation, a pattern observed in numerous highly vagile lorikeets that do not exhibit disjointed ranges caused by topographic or oceanic barriers. Network analysis of mtDNA also indicated that geographic genetic structure was lacking in *Pa. porphyrocephala* (Dolman and Joseph, 2015).

Chalcopsitta, Pseudeos, and *Cardeos*

Chalcopsitta are large lories with midlength tails and atypical colors. The three species in *Chalcopsitta* (*atra*, *scintillata*, and *duivenbodei*) occur in the New Guinea lowlands and some adjacent islands. We follow Beehler and Pratt (2016) in using the emended spelling of the epithet *scintillata* despite its introduction as *Psittacus sintillatus*. *Chalcopsitta scintillata* has generally green body plumage that is heavily striated yellowish, similar to *Synorhacma multistriata* and *Psitteuteles versicolor*. Apart from a red forecrown in adults, however, its head plumage is largely dark to black. Apart from the black crown of some *Lorius* and melanic individuals of *Charmosyna stellae*, this is not observed in the Loriini outside *Chalcopsitta*. Even more distinct is the nearly entirely black *C. atra* (save for yellow and red undertail in some populations) and the brown, yellow, and purple *C. duivenbodei* (which has very prominent yellow underwings). Relationships among the three species are consistent and well supported (fig. 14). *Chalcopsitta duivenbodei* was sister to *C. atra* and *C. scintillata*. The crown age of *Chalcopsitta* is 3.7 Mya (0.9–6.0; fig. 14).

Pseudeos and *Cardeos* both comprise single species and have been recently treated as congeneric (Joseph et al., 2020). We will argue below that separation into two genera can be justified. They are both characterized by extensive red or orange in their plumage.

Prior molecular work showed that *Pseudeos cardinalis*, long placed without comment in *Chalcopsitta*, is more closely related to *Pseudeos fuscata* than to the three species of its former genus, *Chalcopsitta* (Schweizer et al., 2015). Our phylogenomic work confirms this result, but the species tree showed *Pseudeos cardinalis* as sister to *Chalcopsitta*, and *P. fuscata* as sister to the whole clade (fig. 14). The phylogenetic discordance can be explained in part by the short internodal distance spanning the mean divergence between *Chalcopsitta* and *Pseudeos* at just 0.6 Mya with almost largely overlapping temporal ranges from the bootstrapped trees. The split between *Chalcopsitta* and *Pseudeos* was estimated at 6.7 Mya (2–10.3) and the divergence within *Pseudeos* was 6.1 Mya (1.9–9.5; fig. 14).

Concerning plumage traits in these five species, we stress the caveat of not giving undue taxonomic significance to similarities and differences. A general pattern of evolution in parrots, especially "radiations" of closely related species, is that relatively high diversity can evolve quickly under a range of evolutionary forces (Merwin et al., 2020). With that proviso, we make the following observations.

Pseudeos show atypical plumage patterns and indeed colors not only for lorikeets but for parrots generally (e.g., the peculiar light greenish rump color in *Pseudeos fuscata* unique in all Psittaciformes except perhaps a similar but not necessarily homologous color in *Poicephalus meyeri*, *Psephotellus dissimilis*, and *P. chrysopterygius*). The more uniformly "cardinal" red species *cardinalis*, recently transferred to *Pseudeos* but whose generic status we investigate here, is distinct from all species within the *Chalcopsitta/Pseudeos* clade, most strikingly from its closest relative, *P. fuscata*. The most common plumage in *P. fuscata* is a combination of brown, black, and orange, but it has a polymorphic plumage in which yellow largely replaces orange. Research into the pigment(s) underlying these colors in the two species of *Pseudeos* would be most interesting, e.g., are they all due to modified expression of psittacofulvins, the pigment underlying pigment-based red-to-yellow hues in parrots (McGraw and Nogare, 2004)? Striated plumage patterning is absent in *Pseudeos* whereas in *Chalcopsitta* all three species share unique nuchal streaking. Further, among all five of these species only *C. scintillata* is ventrally streaked, the ventral barring in the other four presumably an ancestral trait. Figure 15 illustrates these traits.

Concerning other characters, we note that in *Pseudeos* (including *cardinalis*) bill color is orange, or orange and black, whereas in *Chalcopsitta* it is black. The species *cardinalis* has an apparently autapomorphic trait of bare yellow skin around the base of the mandible. This skin of course is dark in museum specimens (fig. 15). Gross body size is disparate within both *Chalcopsitta* and *Pseudeos* sensu lato, with *P. fuscata* and *C. scintillata* the smaller species in their respective genus and the other three (*atra, duivenbodei*, and *cardinalis*) similarly large (see fig. 15). Lastly here, we note that *P. cardinalis* is endemic to a major center of avian endemism, the Solomon Islands.

In contrast to our earlier position (Provost et al., 2018; Joseph et al., 2020), we here acknowledge the collective weight of available genomic data coupled with biogeographic evidence and phenotypic data (notwithstanding the lability of color evolution in lorikeets) that warrants placement of *cardinalis* in monotypic *Cardeos* Verheyen, 1956. We acknowledge that the temporal divergence between *Cardeos cardinalis* and *Pseudeos fuscata* closely matches that between the two species of *Parvipsitta*, but we do not advocate generic separation of the latter. Very different biogeographical patterns and contexts apply in the two groups and we argue that the generic taxonomy should capture this.

Glossoptilus

Glossoptilus was reinstated for the New Guinean species *G. goldiei* once the paraphyly of *Psitteuteles* sensu lato was clarified. A small green lorikeet of the New Guinea highlands, it is distinguished by a full red crown and violet-purple facial plumage, and dark streaked underparts. It has no described geographic variation. *Glossoptilus goldiei* diverged from the clade containing *Glossopsitta*, *Eos*, *Saudareos*, and *Trichoglossus* 6.9 Mya (2.1–10.3; fig. 14).

Trichoglossus

Trichoglossus lorikeets often have clearly discrete colors across their heads, wings, chest, and bellies. A differently colored nuchal collar is also

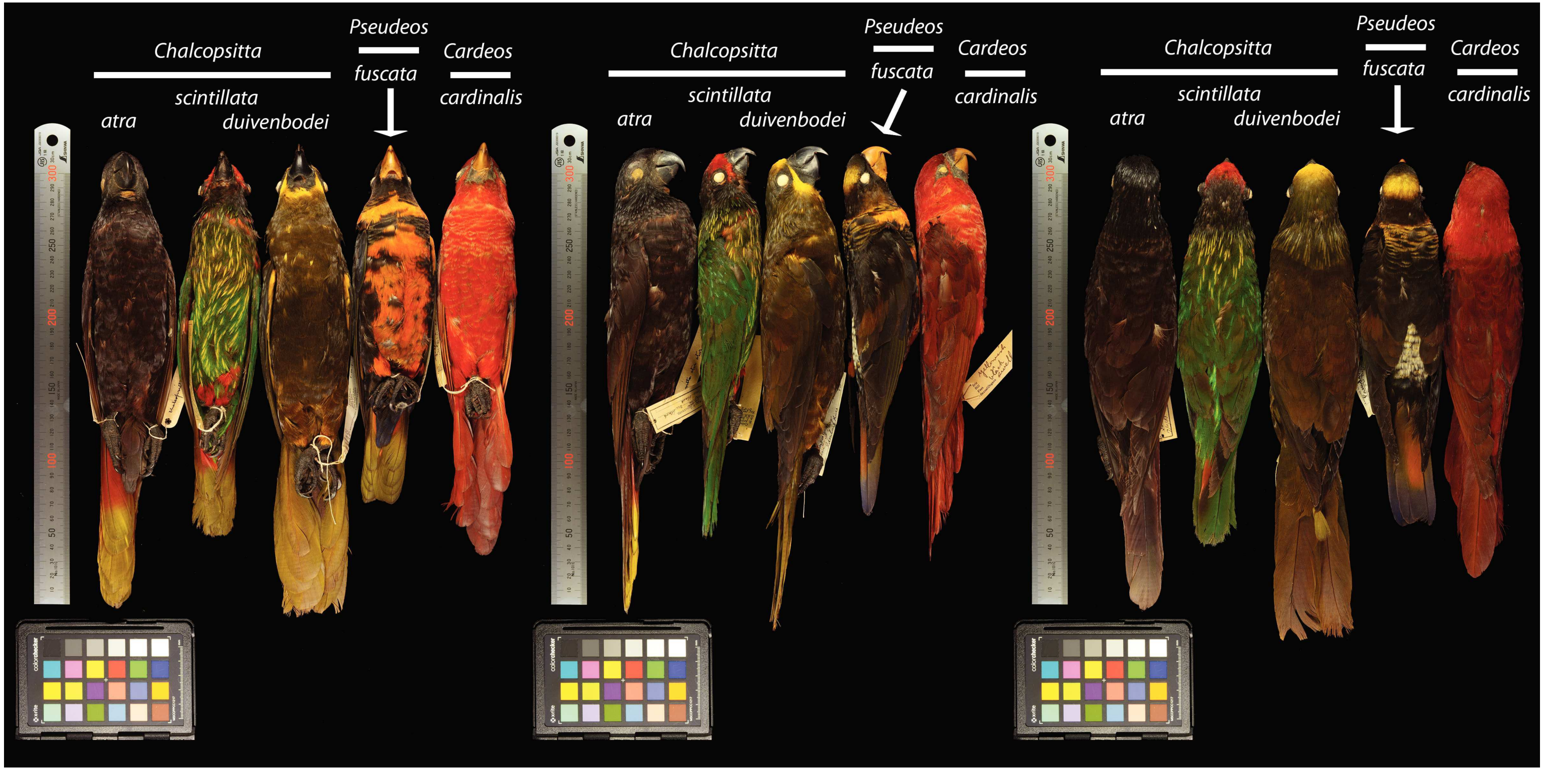


FIGURE 15. Specimens from the American Museum of Natural History (AMNH) of the species assigned to *Chalcopsitta* (*atra* AMNH 616728; *scintillata* AMNH 425529; *duivenbodei* AMNH 339804), *Pseudeos fuscata* AMNH 339121, and *Cardeos cardinalis* AMNH 217110. Ventral, side, and dorsal images from left to right. See text for discussion. Photographs: Sahid Robles Bello.

present in many forms. Narrow, dark terminal barring is on underparts' plumage.

The reconfigured *Trichoglossus* sensu Joseph et al. (2020) brought morphological homogeneity to the clade in that it now comprises species of similar size and gross morphology and that are also biogeographically cohesive, albeit occurring over a large geographic area. Despite improved circumscription of *Trichoglossus*, its extraordinary color variation still presents challenges in understanding species limits within it. Most of the current uncertainty lies with the Rainbow Lorikeet (*Trichoglossus haematodus*) complex, long considered one of the most polytypic bird species. Recent taxonomic revisions have led to recognition of 10 species, mostly from elevating variants of typically "rainbow" plumaged *T. haematodus* to species rank (*haematodus*, *rosenbergii*, *moluccanus*, *rubritorquis*, *capistratus*, and *forsteni*), as well as the yellow-billed and yellow-tailed but otherwise almost uniformly maroon-plumaged species usually treated at species rank (*rubiginosus*) and taxa that are mostly green-plumaged birds (*chlorolepidotus*, *euteles*, and *weberi*). Based on subspecific sampling and phylogenomic data it is unclear whether these currently recognized species limits define monophyletic groups (Smith et al., 2020; Joseph et al., 2020). Both *rubiginosus* and *chlorolepidotus* appear to be outside the main Rainbow Lorikeet radiation, although their exact relationships to each other and *Trichoglossus* was not stable. For this reason, we refrain from using *Oenopsittacus* Reichenbach, 1913, of which *T. rubiginosus* is the type species for either or both of these species. We are currently employing an approach that uses whole-genome data and population-level sampling to further attempt to differentiate relationships and species limits in *Trichoglossus*. The extraordinary *Trichoglossus* radiation has a crown age 4.6 Ma (1.2–7.4; fig. 14).

Glossopsitta

Glossopsitta is a monotypic genus of small green lorikeet with a red stripe of plumage through the eye and blue crown. *G. concinna* of mainland southeastern Australia and Tasmania shares a common ancestor with its sister lineage, *Trichoglossus* at 4.8 Mya (1.3–7.8; figs. 1, 14). Figure 16 indicates that the difference of more blue in the crown of mainland populations likely is valid for adult males and that while closer study is certainly warranted, we see merit to continued recognition of *G. c. didimus*.

Saudareos

Saudareos are smaller bodied, largely green lorikeets with long, attenuated tails. They are phenotypically disparate, perhaps reflecting evolutionary reshuffling of a number of plesiomorphic traits among them, e.g., distinctive ear-coverts, well-demarcated chest and belly plumage with narrow, dark terminal barring. This combined with their similarity to either the brightly colored (*Trichoglossus haematodus*) or mostly green *Trichoglossus* (*T. euteles*) caused confusion in premolecular classification. The taxonomic uncertainty extended beyond *Trichoglossus*. *Saudareos iris* was previously placed in *Psitteuteles*, which is now considered a paraphyletic assemblage of small lorikeets (Smith et al., 2020). Support for the *Saudareos* and *Eos* sister relationship varied across phylogenomic studies, which come from the same dataset but the sequence alignments varied slightly (phylogenomic tree presented here UFBS = 73%; subspecies tree from Smith et al., 2020, UFBS = 100%). The most northerly distributed lorikeet, *S. johnstoniae*, occurs in the mountains of Mindanao in the southern Philippines and diverged from other members of the genus 4.5 Mya (1.2–7.3; fig. 14). The following nodes reflect the divergence among and potentially within Indonesian archipelagos. *Saudareos iris* of Timor and Wetar Islands, Lesser Sundas, diverged from *S. flavoviridis* and *S. ornata* 3.9 Mya (1–6.9; fig. 14). *Saudareos flavoviridis* and *S. ornata* shared a common ancestor 3.4 Mya (0.8–6.3) and both occur on Sulawesi and neighboring islands. The species currently exhibit partial elevational segregation on Sulawesi, which may have contributed to the initial isolation. We note that in our earlier study (Joseph et al., 2020) *Saudareos flavoviridis meyeri* was closer to *S. ornata* than to

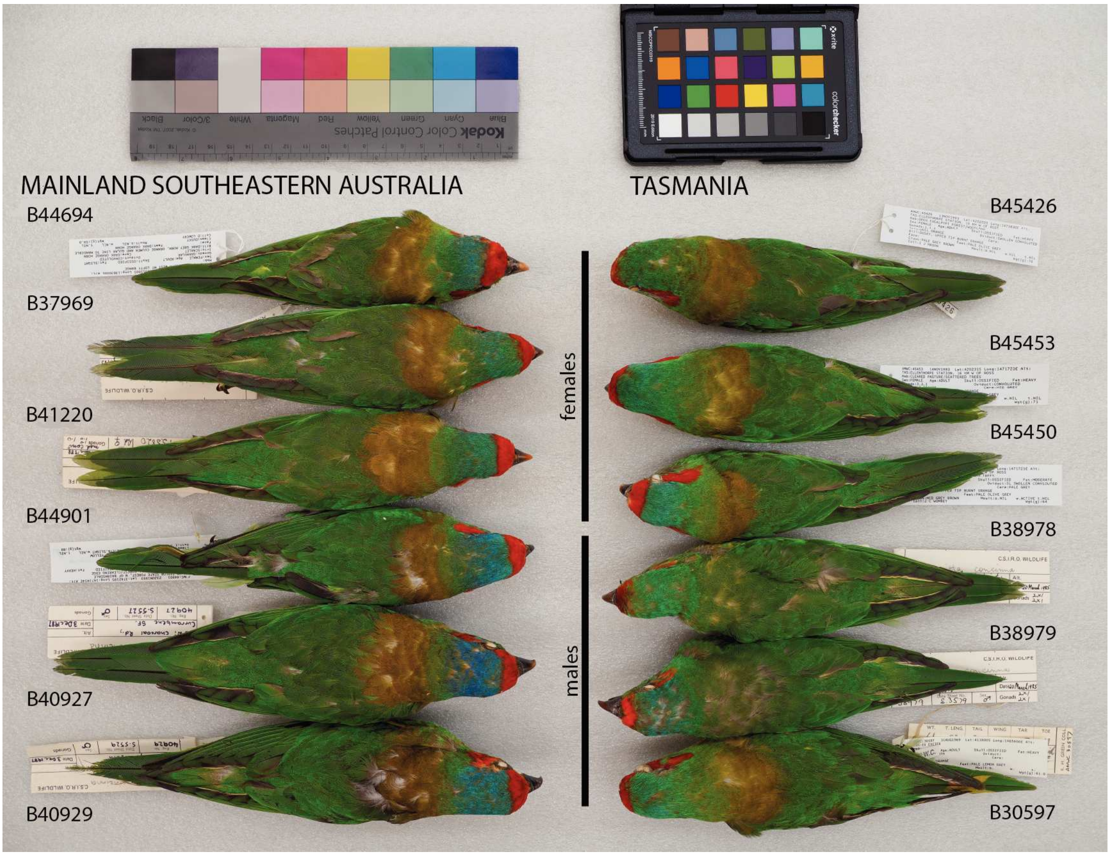


FIGURE 16. Dorsal view of specimens of *Glossopsitta concinna* from the Australian National Wildlife Collection (ANWC) showing variation within and between sexes and within and between mainland southeastern Australia versus Tasmania. Note the bluer coronal color in mainland males. Registration numbers from the bird collection at ANWC are shown. Photograph: Gordon Gullock.

other *S. flavoviridis*. Although we have not sampled to this extent in this study, we acknowledge the elevation of *meyeri* to species rank elsewhere (del Hoyo and Collar, 2014; Gill et al., 2023).

Eos

Eos comprises a fairly uniform clade of midsize lories with rounded tails and predominantly red plumage with blue and black patches, whose radiation dated to 3.7 Mya (1–6.3) occurred entirely in Indonesia; members of this clade are sister to *Saudareos* (fig. 14), the formerly Indonesian species of *Trichoglossus*. Relationships within *Eos* were poorly resolved (fig. 14) in our tree, likely due to poorer-quality samples. This lack of resolution limits what can be inferred about spatial history of the group. Smith et al. (2020) included subspecific sampling of all but two subspecies, and they found similar results of overall low support. It is of note that the *Eos squamata squamata* used in Smith et al. (2020) was mislabeled and is *Eos squamata riciniata*. *Eos* will require higher-quality genomic data to verify phylogenetic relationships.

CONCLUSION

If we have succeeded in providing a new benchmark in the taxonomy of the entire Psittaciformes, then we will have built a robust framework for downstream analyses of parrots in diverse fields such as ecology, ethology, physiology, conservation, and biogeography to name a few.

Several themes for further work have emerged. Apart from a few nomenclatural issues, we are confident that family-level systematics of parrots has largely stabilized. At the level of genera, however, challenges remain in resolving interrelationships, especially where very short internodes reflecting rapid evolutionary divergences have been detected. Relationships within the Arini are a clear example. This pattern was present in early molecular studies and continues to be observed in the phylogenomic dataset presented here. Genus-level taxonomy of parrots remains a challenging exercise. The relatively conserved psittaciform body plan along with plumage color that is subject to different degrees of natural and sexual selection still are at the root of remaining uncertainty. Study of the environmental and genomic drivers of the evolutionary forces that have produced similarly patterned taxa that are not closely related (*Strigops* vs. *Pezoporus*; *Touit costaricensis* and *T. dilectissimus* vs. *Cyclopsitta diophthalma*) and dissimilar taxa that are closely related (e.g., the species of *Aratinga*) would be rewarding. We hope that debates arising from our work on whether to recognize genera will be few. We predict that any that do arise ultimately will be grounded either in the non-predictability of morphological evolution or the complexities of introgression and, we hope, will be resolvable through the phylogenetic framework we have generated. If nothing else, we hope we have contributed substantially to understanding relationships.

Researchers should continue probing diversity within and between what are currently recognized as species to clarify species limits. Of course, much remains to be done in sampling geographic and intraspecific taxonomic diversity especially where species limits are debated or simply still need clarification (e.g., *Pionites leucogaster*, *Psittacella picta*, *Barnardius zonarius*, *Trichoglossus haematodus* sensu lato, *Psittinus cyanurus*, *Tanygnathus sumatranus* sensu lato). We hope these studies will be accompanied by disciplined discussion of rates of phenotypic evolution coupled with research into underlying patterns of gene flow and shared versus unique genetic diversity.

Further, we have often noted the lower quality of some of our data as likely due to the necessity in many cases of using historical museum specimens for DNA samples. That necessity will be difficult to overcome, but the use of genomic methodologies in achieving all of this work should be seen as de rigeur.

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