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Southern hemisphere tectonics in the Cenozoic shaped the pantropical distribution of parrots and passerines

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Abstract

Aim: Explanations of pantropical distributions are challenging for taxa that diverged during the Cenozoic, after Gondwana broke apart. The 'boreotropics hypothesis' suggests that pantropical birds originated in the Laurasian forests. Extant parrots (Psittaciformes) are one the most species-rich pantropical avian clades, but their known evolutionary history does not fit a boreotropical origin. Most living parrots and the earliest diverging lineages of the Psittaciformes inhabit the remnants of Gondwana, whereas the oldest stem and crown fossils are from the remnants of Laurasia. Our study proposes a biogeographic hypothesis that focuses on the Cenozoic connections between Laurasia and Gondwana to explain extant and fossil geographical distributions.

Location: Global.

Taxon: Psittaciformes.

Methods: We generated a time tree using previously derived data from 32 molecular markers for 312 parrot species and reconstructed their biogeographic history using maximum likelihood. Two scenarios were compared: one with dispersal constrained to adjacent areas, including the connections between the Northern and Southern Hemispheres, and one without this constraint.

Results: Our results indicate that the pantropical distribution of parrots was shaped by two major geological events. First, the final breakup of parts of Gondwana may have caused the first splits within crown parrots, establishing two parallel radiations: Psittacidae in the Neotropics and Psittaculidae in Australasia. Second, igneous palaeo-provinces could have connected major biogeographic realms. It seems that Atlantogea and Eurogondwana were important, as they connected South America, Africa and Europe, thus reconciling the Gondwanan crown splits and the early Laurasian fossils.

Main Conclusions: Our time tree allowed more concise biogeographic correlations between parrots and their sister group, the passerines and Earth's tectonic history. The crown lineages of Psittacopasseres appear to have originated in the Southern Hemisphere remnants of Gondwana, but stem lineages appear to have been able to disperse into the Northern Hemisphere through palaeobiogeographic provinces in the Cenozoic.

1 | INTRODUCTION

Disjunct geographical distributions are of interest in biogeographical analyses. One example are pantropical distributions, that is, lineages inhabiting tropical areas that are separated by vast oceans (Bartish et al., 2011). The origin of pantropical biodiversity is associated with the fragmentation of the supercontinent Gondwana, which occurred in the Mesozoic (252–66 Ma; Upchurch, 2008). The resulting biogeographic patterns, which are mainly due to vicariance, may explain the extant distributions of frogs (Feng et al., 2017), harvestmen (Boyer & Giribet, 2007) and plants (Barker et al., 2007) that diverged in the Mesozoic.

The disjunctions of groups that diverged in the Cenozoic, however, are not so easily understood, as these landmasses were well separated at that time. The Cenozoic radiation of birds has produced many pantropical clades (Claramunt & Cracraft, 2015; Gill et al., 2021), but they are not a consequence of continental fragmentation. A Boreotropics hypothesis suggested a Northern Hemisphere origin of the pantropical taxa (Wolfe, 1975). This hypothesis proposes an origin in a Laurasian forest in the Palaeocene followed by dispersal and isolation in the tropics in the Eocene. The extant distributions of kingfishers and allies (Coraciiformes; McCullough et al., 2019) and trogons (Trogoniformes; Oliveros et al., 2020) are congruent with the Boreotropics hypothesis as the first splits between their fossil and extant lineages are centred in the Holarctic.

The Boreotropics hypothesis, however, encounters some problems in explaining the distribution of groups in which the first splits occurred in the Southern Hemisphere. This is particularly true for parrots (Psittaciformes), which are one the most species-rich pantropical avian clade, with 385 living species (Gill et al., 2021). A recent large-scale multilocus phylogenetic tree was built for parrots (Provost et al., 2018), but in that study, neither divergence times nor ancestral geographical ranges were estimated, both of which are required to develop a diversification scenario for the group.

Extant parrots fall into four lineages. The New Zealand parrots Strigopoidea (kakapo, kaka and kea; three extant spp.) are the sister group of all extant parrots. The next branch is the Australian Cacatuoidea (cockatoos; 21 extant spp.), the sister taxon of a diverse and cosmopolitan clade Psittacoidea, which includes Psittaculidae (Old World parrots; 184 extant spp.) and Psittacidae (Afro-American parrots; 177 extant spp.) (Gill et al., 2021; Schweizer et al., 2011; Wright et al., 2008). The fossil record of the Psittaciformes is congruent with the Boreotropics hypothesis, as the oldest fossils of stem (Eocene) and crown (Miocene) parrots have been recovered in Europe and North America (Mayr, 2010; Wetmore, 1926). Nonetheless, as most living species inhabit the Southern Hemisphere and the first parrot clades to diverge occur in the Australo-Pacific region (Schweizer et al., 2011; Wright et al., 2008), a boreotropical origin for parrots must consider land connections between Laurasia and Gondwana in the Early Cenozoic.

Current divergence time estimates for crown parrots, however, do not agree with the boreotropical hypothesis, as they set the diversification of crown group parrots in the middle Eocene at approximately 40 Ma (Claramunt & Cracraft, 2015; Schweizer et al., 2011). At that time, Australia had barely split from Antarctica, and a vast ocean stood between it and Eurasia (Hall, 2002) and faunal exchange would have been barred, especially for nonmarine birds, such as parrots. Therefore, these divergence times are far too early to match the geologic data, but they were based on time trees that did not use any parrot calibrations (Schweizer et al., 2011; Tavares et al., 2006; Wright et al., 2008). This is known to cause unreliable time estimates (Yang & Rannala, 2006; Yang & Yoder, 2003). In fact, a more recent diversification of Psittaciformes at approximately 29 Ma was obtained using internal calibrations for the group (Oliveros et al., 2019), but only seven species of extant parrots were included in that dataset.

Here, we used 28,466 bp of mitochondrial and nuclear DNA sequences to present a comprehensive time-scale with multiple internal calibrations for 312 parrots (81% of extant species). We provide a comprehensive biogeographic scenario for pantropical distributions strongly supported by geological data. Finally, we compare the diversification of Psittaciformes and Passeriformes, sister groups, that have many interesting biogeographic patterns in common.

2 | MATERIALS AND METHODS

2.1 | Sampling and datasets

Species nomenclature followed the International Ornithological Committee 11.2 (Gill et al., 2021), and higher taxa names were based on Joseph et al. (2012). A total of 7301 sequences were downloaded from GenBank (Benson et al., 2010).

We sampled loci for which sequences were available for at least 10 species and all parrot superfamilies (Strigopoidea, Cacatuoidea and Psittacoidea). Our final dataset included 312 living Psittaciformes species, of the 385 living species, and 96 of 97 (all but the Arinae *Ognorhynchus*) currently recognized extant genera (Gill et al., 2021). We also sampled five extinct parrots, namely, *Conuropsis carolinensis*, *Psephotellus pulcherrimus*, *Psittacula wardi*, *Psittacula exsul* and *Mascarinus mascarin*. In the case of *M. mascarin*, we used the sequence generated by Podsiadlowski et al. (2017); see also Joseph et al. (2012). As outgroups, eight passerines, two falconiforms, the chicken (*Gallus gallus*) and the ostrich (*Struthio camelus*) were included. Not all markers were available for all species (Supplementary File S1).

We tested three datasets (Supplementary File S2). Dataset I included all mitochondrial genes (protein coding and ribosomal), 322 taxa (312 Psittaciformes) and 12,620 bp. Dataset II comprised 15,846 bp of 17 nuclear genes (exons and introns) from 268 taxa (256 Psittaciformes). Finally, Dataset III merged the two previous datasets with a total of 329 taxa (317 Psittaciformes) and 32 genes (28,466 bp).

2.2 | Alignments and tree estimations

Alignments were conducted for each marker with MAFFT 7.13 (Katoh & Standley, 2013). Protein-coding genes were inspected for stop codons in SeaView 4.7 (Gouy et al., 2010) and ribosomal genes were aligned considering the secondary structure. The sequences were concatenated using the PHYLOCH package (Heibl, 2008) for R 3.6 (R Core Team, 2013).

For Datasets I, II and III, we used Gblocks (Castresana, 2000) with the least stringency criteria to eliminate saturated positions. For Dataset III, we included other versions of the alignment: one using the most stringent criteria in Gblocks and another without Gblocks (329 spp., 32 loci, 47,018 bp). We performed partitioning tests using PartitionFinder 2.1.1 (Lanfear et al., 2012), considering each gene and the *fgb* intron as separate partitions based on the corrected Akaike information criterion.

The trees generated in this study are shown in Supplementary File S3. We performed partitioned maximum likelihood (ML) analyses with RAxML 8.2.9 (Stamatakis, 2006) using the general time reversible model (Lanave et al., 1984) with four gamma categories at the Cipres Science Gateway (Miller et al., 2012). Tree searches included 100 independent runs and branch support was evaluated with 1000 bootstrap pseudoreplicates. The topologies for the three versions of Dataset III were virtually the same, with slightly higher support values for the version with the least stringent Gblocks (Dataset III; 329 spp., 32 loci, 28,466 bp). The latter was considered our final tree (Figure 1), and the alignment and partition scheme are shown in Supplementary File S4. We also inferred a species tree using the multispecies coalescent approach (Mirarab & Warnow, 2015), considering, in this case, a single mitogenomic tree built with Dataset I. In this coalescent analysis, the mitogenomic tree and the 17 individual nuclear gene trees were compared based on species quartets.

Divergence times were estimated using the approximate likelihood in MCMCTree 4.8 (Yang, 2007) with the topology and partition scheme of our final ML tree. We selected six fossils (Table 1; Supplementary File S5) as time priors to calibrate three internal and three external nodes following the best practices for fossil calibrations (sensu Parham et al., 2012). We used Dataset III to estimate the divergence times, but as mitochondrial and nuclear rates differ particularly among birds (Allio et al., 2017), we also calculated the divergence times for the nuclear and mitochondrial datasets separately (Table 2). The HKY model with five gamma categories and the alpha shape parameter for rate variation of 0.5 were set for a relaxed molecular clock analysis with independent rates. Two independent runs converged for all the parameters with high effective sample size values (>200; Rambaut & Drummond, 2007). Our time tree in newick format is shown in Supplementary File S6.
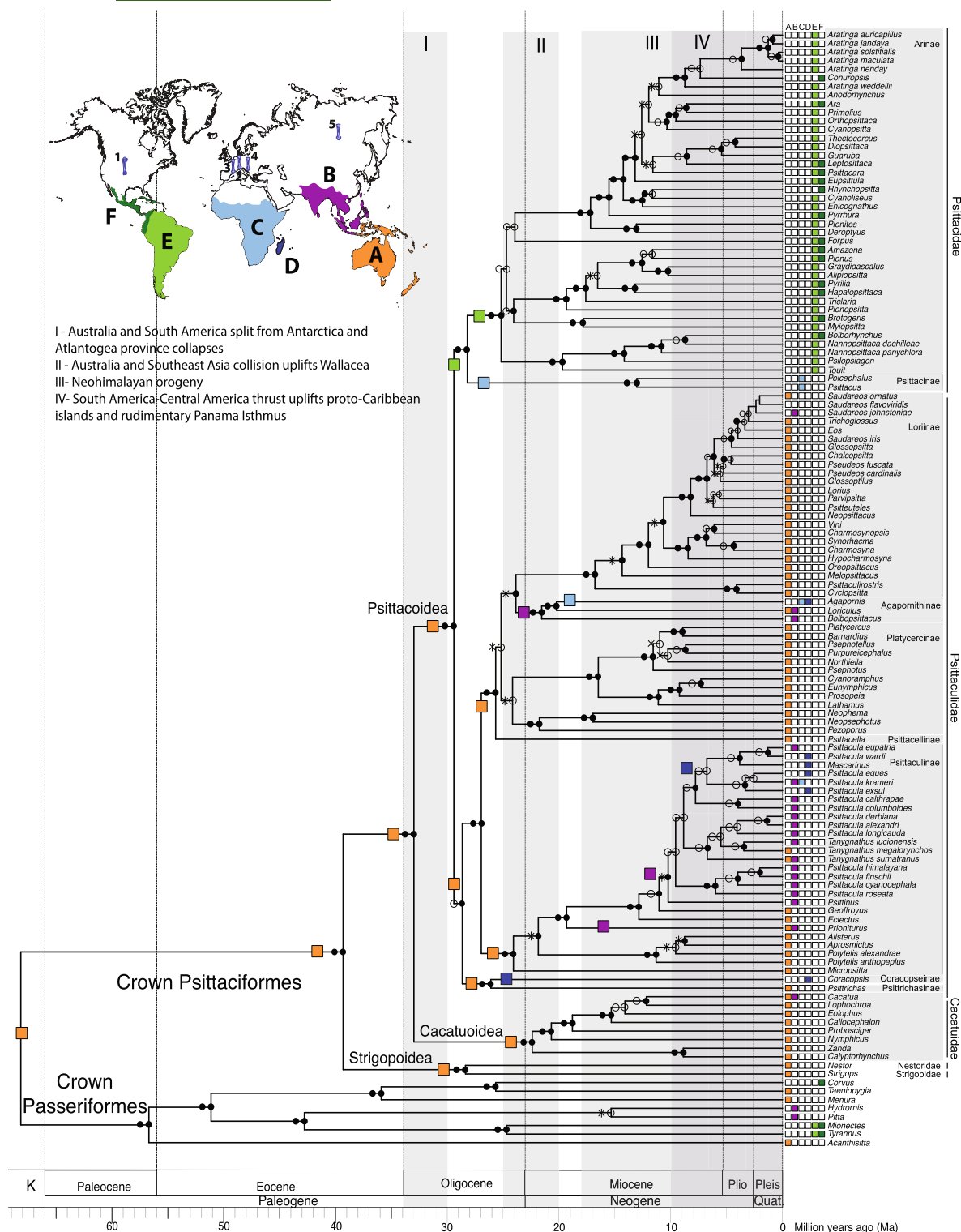
2.3 | Biogeography and ancestral range estimation

The continental landmasses were divided into six major regions (biogeographic areas) with unique, cohesive biogeographic history throughout the Cenozoic, which also represent the endemism of the major parrot clades (Holt et al., 2013; Joseph et al., 2012). The regions were South America; North America plus the Caribbean; Africa; Madagascar; Eurasia including Indomalaya and islands west of Wallace's Line; and the Australo-Pacific region comprising the islands east of Wallace's Line plus Australia, New Zealand and the Pacific archipelagos. In this analysis, only parrots and passerines were included. The distribution of each species was coded for the six areas according to the Handbook of Birds of the World webpage (Billerman et al., 2020). The maximum range size was set to three as the maximum range of any parrot species spans three or less of these areas.

The distribution matrix was analysed in the R package BioGeoBEARS 1.1.2 (Matzke, 2013) using RStudio 1.2.1335 and R 3.6. Ancestral ranges were estimated using the three implemented biogeographic models, namely, likelihood-based dispersal extinction cladogenesis (DEC; Ree et al., 2005), the Bayesian-based program BayArea (Landis et al., 2013) and parsimony-based dispersal–vicariance (DIVA; Ronquist, 1994). For each model, three parameters are estimated: the extinction rate or range contraction (*e*), the dispersal rate or range expansion (*d*) and the founder event speciation (*j*) (Matzke, 2013).

The unconstrained analysis seems inadequate for Cenozoic biogeography, as it assumes equal dispersal probabilities between areas that were considerably isolated (Scotese, 2004). Thus, we run a constrained analysis penalizing dispersal to nonadjacent biogeographic areas (Van Dam & Matzke, 2016). In this analysis, dispersal between nonadjacent areas scored a low (0.01) probability, whereas those between adjacent areas scored the maximum probability (1.0). Area adjacency was based on the following. In the Paleogene, biotic interchange was possible through two major geologic connections: between South America and the Australo-Pacific region through Antarctica until the Oligocene (34 Ma; Reguero et al., 2014) and between South America and Africa through a series of volcanic islands in the South Atlantic Ocean until 30 Ma (Oliveira et al., 2009; Pérez-Díaz & Eagles, 2017). During the Neogene, new connections formed as continents coalesced, namely, Eurasia and the Australo-Pacific region through Wallacea since 25 Ma (Hall, 2011, 2013); North America and Eurasia through Beringia until 5 Ma (Gladenkov et al., 2002); Africa and Eurasia through the Arabian Peninsula since 23 Ma (Reuter et al., 2007); and South and North America through the Panama Isthmus since 3 Ma (O'Dea et al., 2016).

As the vertebrate fauna of Madagascar is an intricate mixture of African and Asian stocks (Warren et al., 2010), Eurasia and Africa

I - Australia and South America split from Antarctica and Atlantogea province collapses
II - Australia and Southeast Asia collision uplifts Wallacea
III- Neohimalayan orogeny
IV- South America-Central America thrust uplifts proto-Caribbean islands and rudimentary Panama Isthmus

FIGURE 1 Dated maximum likelihood (ML) tree and ancestral ranges of the Psittacopasseres with emphasis on the Psittaciformes. Multispecies monophyletic genera were collapsed in a single branch. Circles indicate high (>70%; black) or low (<70%; white) node support for ML (right) and multispecies coalescent (left) topologies, and asterisks indicate nodes not recovered in each respective analysis. Top left: Map of present-day continents and biogeographic regions used here: Australo-Pacific region (A), Eurasia (B), Africa (C), Madagascar (D), South America (E), North America and Caribbean (F). Numbered light blue silhouettes are pre-Quaternary (Late Oligocene–Miocene) fossils of crown Psittaciformes in the Northern Hemisphere with approximate location and main bone in original description: *Conuropsis* (1; humerus, North America) and tarsometatarsi attributed to *Mogontiacopsitta* and *Bavaripsitta* (2; Germany), *Archaeopsittacus* (3; France), *Xenopsitta* (4; Czech Republic) and Psittacoidea gen. Indet. (5; Siberia). Shaded time intervals with Roman numbers indicate major geologic events that may have influenced Psittacopasseres evolution.

were both considered adjacent biogeographic areas to Madagascar to accommodate such biogeographic complexity. Finally, the following landmasses, which were never connected in the Cenozoic, were considered nonadjacent (Blakey, 2008; Collins, 2003): Africa and the Australo-Pacific region; North America and the Australo-Pacific region; South America and Eurasia; and North America and Africa. The detailed ancestral range results are shown in Supplementary Files S7–S9.

3 | RESULTS

Our phylogeny of Psittaciformes (317 sampled species; 100% bootstrap probability [BP]) includes three monophyletic superfamilies (see also Joseph et al., 2012; Figure 1): Strigopoidea (3/4; 100 BP), Cacatuoidea (20/21; 100 BP) and Psittacoidea (294/357; 100 BP). Among the living genera, 35 were monotypic, and 10 (*Bolborhynchus*, *Charmosyna*, *Charmosynopsis*, *Cyclopsitta*, *Enicognathus*, *Geoffroyus*, *Myiopsitta*, *Prosopeia*, *Psittacus*, *Psittinus*) were sampled for a single species. Thus, of the 51 genera formally tested, eight (*Aratinga*, *Nannopsittaca*, *Polytelis*, *Pseudeos*, *Psittacula*, *Saudareos*, *Tanygnathus*) were not monophyletic. The monophyly and relationships among superfamilies, families and subfamilies were usually strongly supported (Figure 1), indicating that current classifications reflect the evolutionary history of the parrots (Provost et al., 2018). Our final time tree (Figure 1) was built by collapsing multispecies monophyletic genera and plotting the distribution of species and genera and the ancestral ranges of the major clades using the R package APE (Paradis et al., 2004).

Among crown Psittaciformes, the Strigopoidea are the sister taxon of all remaining parrots, and the next split is that of the Cacatuoidea–Psittacoidea. Within Cacatuoidea, we recovered the three subfamilies (Joseph et al., 2012; White et al., 2011) with the black cockatoos of the genus *Calyptorhynchus* in the subfamily Calyptorhynchinae (5/5; 100 BP) branching first and sister to the clade including the monotypic grey Nymphicinae and the species-rich and white–grey Cacatuinae (14/15; 99 BP; Figure 1). A first split between the Nymphicinae and the remaining cockatoos, black and white, as suggested by White et al. (2011), was not recovered in any of our analyses.

The species-rich Psittacoidea includes the main Australo-Pacific parrot diversity and all species that occur outside that region. The largest clade is Psittaculidae (145/180; 98 BP), whose seven subfamilies were recovered as monophyletic in our tree (Figure 1), including the clade (100 BP) formed by monotypic Psittrichasinae (1/1) and Coracopseinae (3/3), sister to all other Psittaculidae (Figure 1). Our phylogenies confirm the Psittrichasinae–Coracopseinae clade as the first split within Psittaculidae with high statistical support (98 BP; see also Provost et al., 2018). The next-branching subfamily was Psittaculinae (42/46; 100 BP), with three paraphyletic genera, *Psittacula*, *Tanygnathus* and *Polytelis*. The monotypic *Mascarinus* and the paraphyletic *Tanygnathus* fell within the *Psittacula* radiation with strong support (see also Braun et al., 2019; Kundu et al., 2012;

Provost et al., 2018; Schweizer et al., 2011), whereas two (out of three) sampled species of *Polytelis* branched sequentially as sisters to a clade containing the genera *Aprosmictus* and *Alisterus*, but statistical support was weak (Figure 1). This suggests that *Polytelis* might require full taxon sampling to be properly resolved. The sister group of Psittaculinae was a clade composed of the remaining four subfamilies, in which Psittacellinae (2/4; 100 BP) split first, followed by Platycercinae (34/38; 56 BP) and finally Loriinae (46/64; 100 BP) plus Agapornithinae (17/24; 100 BP). In our results, the relationships among the Psittaculidae subfamilies showed low support (see also Braun et al., 2019; Provost et al., 2018) due to the scarcity of available molecular markers (Supplementary File S1), particularly for the Loriinae radiation. Our results show paraphyly of two Loriinae genera, namely, *Pseudeos* and *Saudareos* (Figure 1), but recent genomic and phenotypic data clarified many uncertainties in the lorikeet phylogeny and taxonomy (Joseph et al., 2020; Smith et al., 2020), including the highly supported monophyletic status of these two genera.

The final clade Psittacidae (150/177; 100 BP) includes 45% of all parrot species. Our tree shows Psittacidae and Psittaculidae to be reciprocally monophyletic (Figure 1; see also Joseph et al., 2012; Provost et al., 2018; Schweizer et al., 2011). Psittacidae is split between Psittacinae (8/12; 100 BP) and the more diverse Arinae (141/165; 100 BP), and most genera were monophyletic, with two exceptions in Arinae (*Aratinga* and *Nannopsittaca*). Ten genera classified as *incertae sedis* (Joseph et al., 2012) were well resolved in our analyses. The genera *Touit*, *Psilopsiagon*, *Nannopsittaca* and *Bolborhynchus* formed a strongly supported clade (100 BP) sister to all the remaining Arinae, although *Nannopsittaca* was paraphyletic with *Bolborhynchus* nested in that clade (Figure 1). Next, we recovered a split that corresponds to the clades traditionally divided by tail length: the long-tailed Arini and the short-tailed Androglossini (65 BP). However, the two long-tailed *incertae sedis* genera *Myiopsitta* and *Brotogeris* formed a clade that is the sister taxon of the Androglossini, whereas the short-tailed *incertae sedis* taxon *Hapalopsittaca* nested within the Androglossini as a sister group of *Pyrilia* with high support. The three remaining *incertae sedis* genera are all short-tailed and clustered at the root of the Arini with low support (56 BP), with *Forpus* branching first, followed by the clade with *Deroptyus* and *Pionites* (100 BP), which is sister to the Arini (100 BP). The last paraphyletic genus was *Aratinga* due to the insertion of the extinct North American *Conuropsis*. A particularly poorly resolved clade was Arini, which includes the large macaws and conures (*Psittacara*–*Aratinga* clade; Figure 1) and most of the severely endangered New World species (Olah et al., 2016).

In our BioGeoBEARS results, the ancestral ranges for all the major clades (families and superfamilies) were identical in all the analyses (DEC, BayArea and DIVA), but the constrained DEC model showed the highest likelihood, and the inclusion of the jump dispersal parameter *j* improved model performance (Supplementary Files S7–S9). The unconstrained results were the same as in our constrained analysis, but the likelihood values were lower in the unconstrained analysis (Δ lnL = −28.37). Hence, our biogeographical discussion will be based on the constrained DEC + *j* analysis (Figure 1).

TABLE 1 Summary of the age and diagnostic apomorphies of fossil specimens used as time priors for each major clade in the molecular dating analysis

Fossil specimen	Stratigraphy	References (description, stratigraphic dating and phylogenetic placement)	Calibrated clade	Key apomorphic diagnosis	Hard minimum age (Ma)	Soft maximum age (Ma)	Calibration configuration in MCMCTree
Vegavis iaai	Locality VEG9303 of the 1992/1993 IAA expedition, lithostratigraphic unit K3, Cape Lamb, Vega Island, Antarctica	Clarke et al. (2005), Mayr (2013, 2016)	Neognathae	Unambiguous features that are unique to the Neognathae, such as a complex hypotarsal morphology containing many sulci and crests	66	86.5	SN (66.5, 7, 10)
Eozygodactylus americanus	Tynsky Quarry (F2), Kemmerer, Lincoln County, Wyoming, USA	Mayr (2015), Weidig (2010)	Psittacopasseres	The family Zygodactylidae is a stem member of the Parapasseres clade that includes the Passeriformes, which are the living sister group of the Psittaciformes. All Parapasseres share exclusively a large processus intermetacarpalis and a long and slender tarsometatarsus that is significantly longer than the humerus and exhibits a crista plantaris lateralis	51	66	SN (51.81, 4, 10)
Wieslochia weissi	Frauenweiler south of Wiesloch (MP 21–25), Germany	Mayr and Manegold (2006)	Eupasseres	Apomorphic features shared between *Wieslochia* and the Tyranni are a large processus procoracoideus and a well-developed tuberculum ligamenti collateralis ventralis on the proximal portion of the ulna	33	51	SN (33, 7, 10)
Mogontiacopsitta miocaena	Mainz-Weisenau Basin (MN1), Germany	Mayr (2010)	Crown Psittaciformes	This and other contemporaneous taxa exhibit key apomorphies of living Psittaciformes, such as a strongly medially offset trochlea of metatarsal II and a furrow between the throchlea accessoria and the trochlea of metatarsal IV	28	51	SN (28, 8, 10)
Cacatua sp. Indet.	RSO Site, Riversleigh Station, Queensland, Australia	Boles (1993)	Cacatuini	The forward nostril openings and the wide and saddle-shaped cere region suggest a close affinity of this fossil with the members of the Cacatuini tribe in the Cacatuoidea superfamily	17	28	SN (16, 4, 10)
Nelepsittacus minimus	Bed HH2b, Manuherikia River section, Otago, New Zealand	Worthy et al. (2011)	Crown Strigopoidea	Among other characteristics, *Nelepsittacus* and *Nestor* (Strigopoidea) share a synapomorphy of an elongate groove preceding the foramen distale on the dorsal facies of the tarsometatarsus	19	28	SN (19, 3, 10)

Note: For detailed justification of each time prior, see Supplementary File S5.

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Today, Strigopoidea, Cacatuoidea and most of the Psittaculidae are confined to the Australo–Pacific region, which has been recovered as the ancestral area of extant parrots; thus, our results show that the ancestor of crown Psittaciformes originated in Gondwana (Figure 1). We recovered five branches stemming from the Australo-Pacific region, four of which belong to the Psittaculidae clade. The earliest diverging of these are the Malagasy Coracopseinae. The next two branches belong to the Psittaculinae, which colonized Asia independently through the genus *Prioniturus*, and the radiation including *Psittinus*, *Psittacula*, *Tanygnathus* and *Mascarinus*. The last Psittaculidae branch is Agapornithinae, which originated in Asia and later gave rise to lineages in Africa and Madagascar. Finally, the last out-of-Australo-Pacific branch in crown Psittaciformes is the ancestor of Psittacidae in South America, which subsequently split into the Neotropical Arinae and African Psittacinae.

4 | DISCUSSION

As one the most species-rich pantropical avian clade, parrots offer a unique study system to understand the origin and evolution of continental disjunction of lineages that diverged in the Cenozoic. Furthermore, our results show that crown parrots have deep roots in Gondwanan landmasses, so their pantropical distribution was shaped by a scenario not involving the Laurasian-centred Boreotropics routes. Here, we discuss our biogeographic hypothesis (Figure 2) to explain how the distribution of parrots became pantropical. We also compare our scenario for parrots with the diversification of their sister group, the passerines (Claramunt & Cracraft, 2015). Although the close affinity of parrots and passerines has long remained undetected due to their disparate morphologies, these lineages share many parallel spatiotemporal patterns and our results suggest that their origin and diversification could have been driven by similar geological and tectonic events.

4.1 | Reconciling stem Psittacopasseres in Laurasia with the Gondwanan roots of the crown clades

Together, the Psittaciformes (385 living species) and Passeriformes (6456 species) form a clade named Psittacopasseres containing over 60% of extant avian diversity (Mayr, 2015; Suh et al., 2011). The earliest representatives of the Psittacopasseres clade are fossils of early Eocene zygodactyl stem passerines, such as the Psittacopedidae and Zygodactylidae from the Eocene of Europe and North America (Ksepka et al., 2019; Mayr, 2016) and the Quercypsittidae, stem psittaciformes from the late Eocene of Europe (Mourer-Chauviré, 1992). The earliest crown fossils of parrots have been reported from Late Oligocene deposits of Eurasia and North America (Mayr & Göhlich, 2004), and there are crown passerines from the early Miocene in Australia and Zealandia (Boles, 1993).

Our time tree dates the Psittacopasseres split at the Cretaceous–Paleogene [K–Pg] (boundary 72–64 Ma; Table 2), and our biogeographical results indicate a Gondwanan origin for the clade (Figure 1; Supplementary File S7). During that time, the main block of Gondwana, formed by Antarctica, Australia and South America, and the Laurasian landmasses, including North America and Eurasia, was already fragmented and isolated from each other (Figure 2a). However, by the Eocene, Africa approached Europe exposing hills and floodplains in the northern rim of the Arabian plate that may have allowed biotic interchange (Sen, 2013), forming a unique mixture of Gondwanan biota in Europe characterizing the Eurogondwanan fauna (Ezcurra & Agnolin, 2012).

Additionally, at the K–Pg boundary, a major palaeobiogeographic province formed as volcanic activity peaked in the South Atlantic, where the now submerged magmatic provinces of the Rio Grande Rise and Walvis Ridge sit east and west, respectively, of the Mid-Atlantic Ridge (Pinheiro Praxedes et al., 2019). Seismographic assessment of deep-sea drilling revealed that intense volcanism during the Eocene caused uplift in the area, and relief and erosion patterns suggest that most of the Rio Grande Rise and Walvis Ridge were above or near sea level (Homrighausen et al., 2018; Pinheiro Praxedes et al., 2019). The South Atlantic magmatic provinces are key evidence for Atlantogea (Ezcurra & Agnolin, 2012; Oliveira et al., 2009), a palaeobiogeographic province that allowed biotic interchange between African and South American biotas throughout the Palaeogene (Figure 2a). This province explained the diversification of many vertebrate groups (see Ezcurra & Agnolin, 2012 and references therein), including passerines (Selvatti et al., 2015, 2017), and we suggest that it affected parrots as well. The recent discovery of *Namapsitta*, a Late Early/Early Middle Eocene Namibian parrot-like representative of the Psittacopasseres (Mourer-Chauviré et al., 2014; Mourer-Chauviré & Pickford, 2018), adds support to our hypothesis. Thus, along with the Atlantogean province, which is substantially supported by geological and phylogenetic data, we suggest that Africa played a key role, enabling the reconciliation of stem fossils in Laurasia and early crown lineages in the remnants of Gondwana (Figure 2a). Our biogeographic scenario may be tested by other Laurasia–Gondwana disjunctions of Mesozoic fossils and by robust time trees for the Neotropical–Afrotropical break. Furthermore, palaeontological surveys in Africa may provide additional evidence for the Atlantogea hypothesis; the discovery of *Namapsitta* exemplifies how little we know about the palaeornithology of the African continent.

4.2 | Earliest crown split: Strigopoidea and Acanthisitta in Zealandia

The earliest split in each of the two major clades of Psittacopasseres separates a New Zealand endemic lineage from the remaining diversity (Claramunt & Cracraft, 2015; Oliveros et al., 2019): Strigopoidea in parrots and Acanthisitti in passerines. In the Late Cretaceous, at approximately 85–82 Ma, New Zealand drifted away from the main Gondwanan block formed by Antarctica, Australia and South

Clade	All loci		Nuclear		Mitochondrial	
	Mean	95% HPD	Mean	95% HPD	Mean	95% HPD
Psittacopasseres	68.16	72–64	70.28	75–65	58.66	63–54
Crown Passeriformes	56.7	60–52	55.06	60–50	51.19	55–47
Eupasseres	51.14	54–47	46.61	51–42	47.85	52–43
Oscines	35.91	39–32	33.66	39–28	33.87	37–29
Suboscines	42.79	46–38	39.53	44–34	38.71	43–33
Crown Psittaciformes	39.32	42–36	41.58	45–37	36.96	40–34
Strigopoidea	28.37	31–25	24.66	28–21	28.1	30–25
Psittacoidea/Cacatuoidea	32.99	35–30	34.14	37–30	32.71	35–30
Cacatuoidea	22.41	24–20	21.01	23–18	24.11	26–21
Psittacoidea	29.41	31–27	29.99	33–27	29.45	31–27
Psittaculidae	28.66	30–26	28.72	31–25	28.74	30–27
Coracopseinae/Psittrichasinae	26.11	28–23	22.56	27–16	26.24	28–23
Geoffroyus/Asian Psittaculinae	11.06	12–9	8.65	10–6	12.51	14–10
African Psittaculinae	6.78	8–5	6.87	8–5	7.7	9–6
Loriinae/Agapornithinae	23.86	25–22	21.73	24–19	24.5	26–22
Loriculus/*Agapornis*	20.23	22–18	16.71	19–13	21.8	24–19
Psittacidae	28.21	30–26	27.87	30–24	28.72	30–26
Arinae	25.18	27–23	22.31	25–19	26.84	28–24

TABLE 2 Divergence time results for each Dataset (I [mitochondrial], II [nuclear] and III [all loci]) for the splits discussed in the main text, including all the major Psittacopasseres lineages as well as clades with shifts in the ancestral ranges (see Figure 1)

HPD, highest posterior density.

America (Schellart et al., 2006). Bathymetric data and gravity anomaly data indicate that north-western New Zealand remained connected with Australia until the early Eocene (56–52 Ma), when the elongated seafloor trench named the Cato Trough, formed in the Tasman Sea that finally separated these landmasses and biotas (Muller et al., 2006; Schellart et al., 2006).

Molecular studies suggested a Late Palaeocene (58 Ma) mean date for the Strigopoidea split (Pacheco et al., 2011; Schweizer et al., 2011), but those estimates have credibility intervals from the Eocene to the Late Cretaceous (CI = 72–45 Ma, Schweizer et al., 2011; CI = 69–54 Ma, Pacheco et al., 2011). As no crown parrot fossils have been described from strata older than the Oligocene, a large gap in the fossil record of up to 30 Myr would have to be assumed to accommodate the Palaeocene age despite the rich avian diversity in these records (Mayr, 2016). We dated the Strigopoidea split in the late Eocene (39 Ma) with a narrow confidence interval (42–36 Ma; Table 2; Figure 1). This time interval holds even when we used mitochondrial-only (40–34 Ma) and nuclear-only data (45–37 Ma; Table 2), rejecting a Palaeocene age for crown Psittaciformes.

Our time tree suggests that the first split of Psittaciformes was not influenced by the formation of the Cato Trough, as was the case with passerines (Selvatti et al., 2015). Although the divergence date of the first split in crown passerines closely matches the age of the formation of the Cato Trough, the first split in parrots ensued 17 million years later (Figure 1; see similar results in Jarvis et al., 2014; Prum et al., 2015; Selvatti et al., 2015 and Oliveros et al., 2019).

Here, we suggest that volcanic provinces, such as the Lord Howe Rise and Fairway Rise in west New Zealand, which remained above

water during most of the Eocene, may have provided subaerial island chains and plateaus (Ung et al., 2016). Unlike early passerine lineages (e.g. Acanthisitti, basal Oscines), most extant psittaciformes have high flight capacity, covering large distances in a single day (Collar, 1997; Rowley, 1997). The Lord Howe Rise and Fairway Rise plateaus subsided below sea level around the late Eocene (40–35 Ma), coinciding with our divergence age for Strigopoidea (42–36 Ma) (Ung et al., 2016).

4.3 | Psittacopasseres in the East: Cacatuoidea, Psittaculidae and Oscines

The final step in the breakup of Gondwana separated Australia and South America from Antarctica. During the Eocene–Oligocene transition (40–30 Ma), seafloor spreading opened the deep-sea circulation of the Tasmanian Gateway in the east (Houben et al., 2019; Muller et al., 2006) and the Drake Passage in the west (Eagles & Jokat, 2014). This created the cold circum-Antarctic marine current, which prevented warm currents from reaching the Antarctic and altered current and wind patterns, triggering early Oligocene glaciation (Houben et al., 2019). As permanent icecaps spread across the continent they removed suitable habitats for most autochthonous Antarctic vertebrates, including birds (Reguero et al., 2014; Tambussi & Degrange, 2012). In our tree, Cacatuoidea split from a common ancestor with Psittacoidea at approximately 35–31 Ma in eastern Gondwana (Figures 1 and 2), with this event possibly driven by the current shifts and extensive forest fragmentation that took place during Eocene–Oligocene cooling (Hansen et al., 2013).
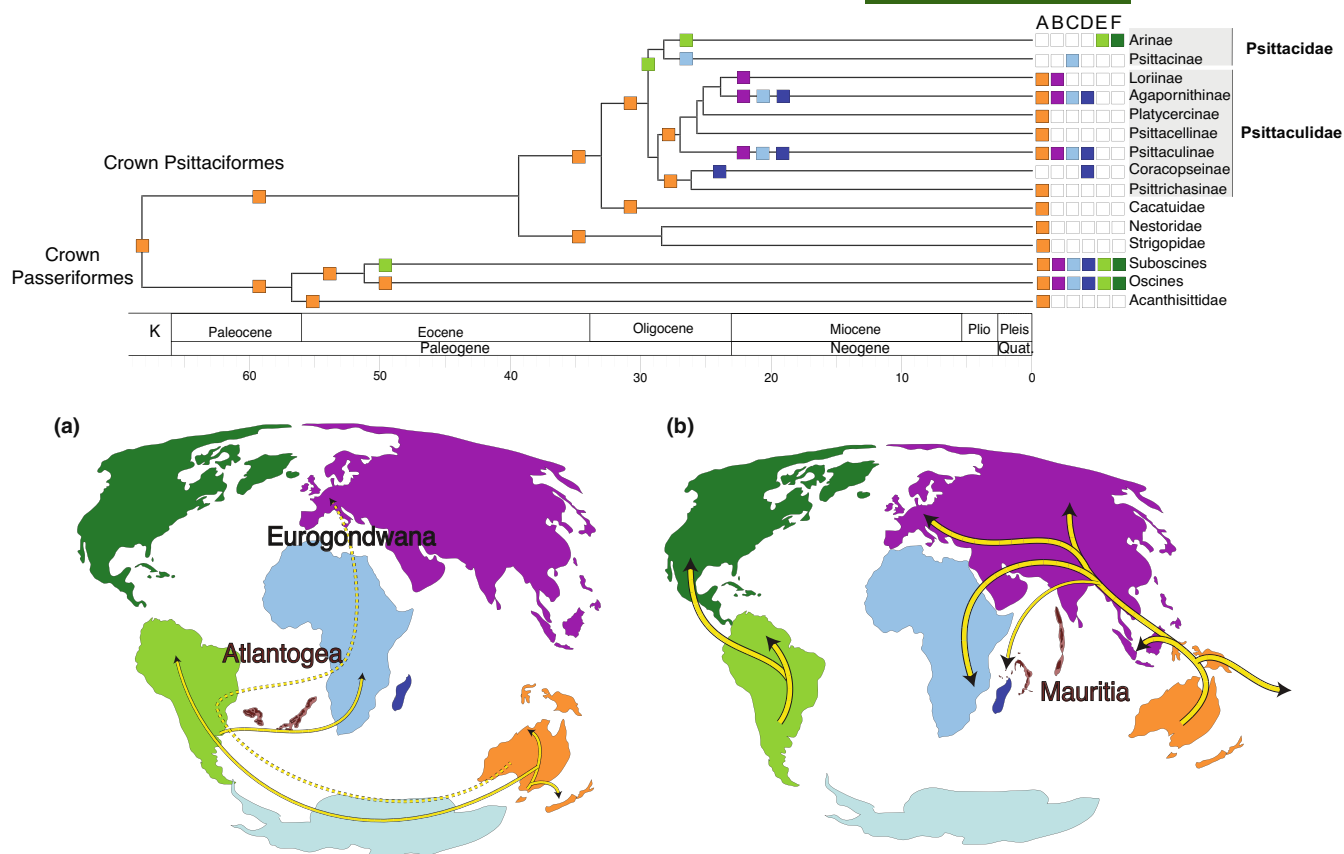
FIGURE 2 Our proposed hypothesis for the diversification of the Psittacopasseres major lineages (families and subfamilies). Approximate palaeobiogeographic reconstruction of major landmasses during the Paleogene (a) and Neogene (b). Igneous provinces of the Southern Hemisphere are coloured in dark red. Yellow lines suggest range expansions/dispersals of the crown (continuous) and stem (dashed) Psittacopasseres. Colour codes for the biogeographic areas and ancestral ranges at each node are the same as in Figure 1.

The geographic ranges of Cacatuoidea and Psittaculidae also parallel those of passerines. Previous molecular estimates suggest an Australian origin for songbirds (Oscines) at approximately 38–47 Ma (Oliveros et al., 2019), as does our scenario for Cacatuoidea. In our hypothesis, the ancestral stocks of the Cacatuoidea and the Oscines ancestor coexisted in Australia and drifted away from Antarctica in the late Eocene. The first splits of the oscines—Menuridae, Atrichornithidae, Ptilonorhynchidae, Climacteridae and the superfamily Meliphagoidea—form a paraphyletic assemblage that, as in the Cacatuidae, is restricted to the Australo–Pacific realm (Oliveros et al., 2019). Coexisting with Cacatuoidea and the Oscines, psittacoid populations in eastern Gondwana originated the Psittaculidae ancestor (145/180; 98 BP), which led to an Australo-Pacific parrot radiation and some minor African and Eurasian crown clades. The emergence of the Wallacean archipelago, caused by the Australian and Asian plate collision (Hall, 2011), triggered the diversification of Oscines west of the Wallace Line (Oliveros et al., 2019). Surprisingly, the cockatoo expansion out of the Australian continent was somewhat restricted to the east of Wallace's line. Only nine species of the genus *Cacatua*, distributed in New Guinea, Wallacea, the Philippines and nearby archipelagos, represent the non-Australian Cacatuoidea. This pattern is strikingly different, however, for Psittaculidae, as our results suggest that after the emergence of Wallacean psittaculids,

they crossed Wallace's line at least four independent times (Figures 1 and 2).

The earliest split with a trans-Wallacean disjunction concerns the Psittrichasinae–Coracopseinae clade. The low diversity of this clade contrasts with a notable disjunction, that of the Australo-Pacific Psittrichasinae and the Malagasy Coracopseinae being separated by the Indian Ocean. The current hypothesis for this pattern suggests that the Coracopseinae stocks dispersed from Australia directly to Madagascar through large igneous provinces of the southern Indian Ocean, namely, the Broken Ridge and Kerguelen Plateau (Schweizer et al., 2010, 2011). However, gravimetric, bathymetric and palaeo-geographical data indicate widespread subsidence of those provinces since 60 Ma, and pelagic sedimentation has predominated over the area since 48 Ma (Bénard et al., 2010). Therefore, the igneous provinces of the southern Indian Ocean have been largely submerged and isolated since the Late Cretaceous, with over 1300 km of open ocean isolating the Kerguelen Plateau from any landmass (Ali & Aitchison, 2009). Isolation by extensive deep-water gaps increased as continents drifted apart during the Cenozoic, making dispersal through the southern Indian Ocean considerably difficult (Ali & Krause, 2011), especially for landbirds such as parrots and passerines.

As Madagascar and the Australo-Pacific were isolated by vast areas of open ocean, we suggest an alternative scenario in which the stem

Coracopseinae stocks crossed the Wallace Line into the Indomalayan region and reached Madagascar from there. Contrasting with the Kerguelen Plateau–Broken Ridge hypothesis, dispersal to Madagascar from Indomalaya has substantial geological support. Zircon crystals and tectonic plate reconstructions indicate that the Laccadives–Chagos Ridge and the Southern Mascarene Plateau in the western Indian Ocean formed the microcontinent Mauritia between India and Madagascar within Gondwana (Figure 2b; Ashwal et al., 2017). As the plates diverged, Mauritia fragmented in a ribbon-shaped volcanic chain over the last 65 Ma, and ocean drilling indicates that most of Mauritia rose above or very close to sea level in the Cenozoic, which may have connected India and Madagascar, especially during periods of low sea level (Warren et al., 2010). Our age for the Psittrichasinae–Coracopseinae split at approximately 28–24 Ma agrees with the Mauritia route (Figures 1 and 2), consistent with the patterns found in the passerine Malaconotoidea (Oliveros et al., 2019). This Australo-Pacific oscine radiation originated the vanga shrikes (family Vangidae), dispersed to Indomalaya and then to Madagascar slightly later (20–15 Ma) than our estimates for Coracopseinae (Oliveros et al., 2019; Reddy et al., 2012). The Indomalaya–Madagascar biotic connection is also supported by *Canarium* trees (Federman et al., 2015). The disjunctions in the Indian Ocean are one of the most challenging biogeographical patterns of biodiversity, and more time trees for different lineages are key to testing our hypothesis.

The next dispersals to Eurasia occurred in two Psittaculinae lineages, which stand out as the most diverse and widespread Psittaciformes in the Old World (Figures 1 and 2). The first lineage stems from within the genus *Prioniturus* and established a minor clade in Eurasia at approximately 8–5 Ma, whereas the second lineage was the radiation that involved the ancestral populations of *Psittinus*, *Psittacula*, *Tanygnathus* and *Mascarinus* at approximately 12–9 Ma (Figure 1). Then, by the late Miocene (8–5 Ma), the *Psittacula–Mascarinus* ancestor possibly established the first lineage of Psittaculinae in Africa and colonized the Mascarene Archipelago from there (Figure 1). Finally, the last Psittaculidae to disperse out of the Australo-Pacific was Agapornithinae, with living species in Eurasia, Africa and Madagascar (Figure 1).

The split dates of the Psittaculidae lineages that exist outside the Australo-Pacific region are centred in the Neogene (28–23 Ma for Coracopseinae, 25–22 for Agapornithinae and 12–9 Ma for Psittaculinae), coinciding with the increasing aridification of Australia (McGowran & Hill, 2015). As Wallacea and Southeast Asia are covered by rainforests (Frigola et al., 2018), ecological conditions may have favoured the arrival of Psittaculidae into Eurasian lands. The oldest crown-like fossils of Psittaciformes exhibit stout tarsometatarsus, which is found in Psittaculidae and Psittacidae, and the overall morphology resembles that of Psittaculidae (Mayr, 2015, 2016; Zelenkov, 2016). This evidence supports our hypothesis of an early Miocene parrot arrival in Eurasia. The arrival of psittaculids in Africa was probably through the Arabian Peninsula, which linked the rainforests of Eurasia and Africa in the early Miocene (Reuter et al., 2007). These palaeotropical forests were part of the Boreotropics, which were soon disrupted by the uplift of the

Himalayas and the ensuing desertification in central Asia and northern Africa in the mid-late Miocene. A Miocene split was also assumed for other African and Asian sister lineages in tropical birds (Oliveros et al., 2020; Selvatti et al., 2017). Our results suggest that those geological events left similar imprints in the evolution of Psittaculidae because all African and Asian disjunctions occurred after the Miocene (20–5 Ma; Figure 1).

4.4 | Psittacopasseres in the West: Psittacidae and Suboscines

Psittacidae is essentially a New World radiation, but the group also includes a dozen African species. This small geographic distribution overlap between the Psittacidae and the remaining Psittaciformes makes the geographic origin and dispersal routes of the Psittacidae an enigma in the evolution of parrots and constitutes a major challenge for explaining their pantropical distribution. The primary hypothesis currently recognized for the origin of the group points to Gondwana around the late Eocene (40–38 Ma; Schweizer et al., 2011; Wright et al., 2008). However, such a late Eocene split for Psittacidae conflicts with the ages of the two geological events that have been linked to the origin of the group in those studies. First, the orogeny of the transantarctic mountains, dividing eastern and western Gondwana, took place in the early Eocene (Wannamaker et al., 2018), which is considerably earlier (45–55 Ma) than the suggested late Eocene split. Second, the final separation of the Australian and South American landmasses from Antarctica, which led to the formation of the circum-Antarctic current, appears to have taken place much later, in the early Oligocene (33–30 Ma; Muller et al., 2006; Reguero et al., 2014).

Our age for the Psittaculidae–Psittacidae split (32–27 Ma) matches the South American breakup and the spread of permanent icecaps in Antarctica (Eagles & Jokat, 2014; Houben et al., 2019). According to this scenario, we suggest that as the Antarctic glaciation occurred during the Oligocene, Psittacidae stocks dispersed to South America shortly before the continent broke away from Antarctica (Figure 2a). This event produced parallel radiations of Psittacoidea that diversified independently east and west of each hemisphere (Figure 2b).

Our results recovered South America as the ancestral range of Psittacidae (Figures 1 and 2; Supplementary File S7), and a split between Psittacinae and Arinae occurred at approximately 30–26 Ma (Table 2), consistent with the increased seafloor spreading in the South Atlantic and the onset of deep-water circulation that caused Atlantogea to subside (Oliveira et al., 2009; Pérez-Díaz & Eagles, 2017). A South American origin followed by Atlantogean dispersal into the Old World has been reported in suboscine passerines (Selvatti et al., 2017). In that study, the South American ancestor of the Suboscines split into the Tyrannides radiation that produced over 1000 species in the New World. Tyrannides plus Arinae are a major component of the extant endemic Psittacopasseres diversity in the Americas. The sister clade of the Tyrannides, the Eurylaimides,

also diversified in South America, sprouting the family Sapayoidae, which today is monotypic. Finally, similar to the Psittacinae, the Eurylaimides ancestral stocks would have dispersed to Africa through Atlantogea and subsequently radiated in the Old World (Selvatti et al., 2017).

Our phylogeny shows that crown group Psittacinae (8/12; 100 BP) originated between 15 and 11 Ma. As there are no dispersal routes between Africa and South America after ~30 Ma (Figure 1; Table 2), our results support an ancient presence of Psittacinae in Africa. Therefore, the low diversity of this clade compared to the Arinae radiation agrees with the hypothesis of resource competition with the local fauna (Mayr, 2016). In this hypothesis, the diverse native fauna of arboreal rodents might have limited the diversification process on that continent. Furthermore, the floristic scarcity of important plant families associated with frugivorous birds in Africa, such as Lauraceae and Arecaceae (Snow, 1981), is also in accordance with the hypothesis of an older African arrival of the Psittacinae.

Finally, our results show that Arinae (141/165) radiated in South America at approximately 27–23 Ma and expanded to North America and the Caribbean multiple times in the late Miocene (Figure 1). Also, our ancestral range for all North American Arinae is in South America eliminating a boreotropical origin of the Psittacidae. Oroclinal bending formed as South America was pushed against the Central American plates from 15 Ma (O'Dea et al., 2016). This process transformed the Caribbean into a shallow sea with emerging islands that may have been used as a corridor by the Arinae. However, most of the North American/Caribbean Arinae split from the South American stocks after the Isthmus of Panama was formed at approximately 5 Ma (Figures 1 and 2b; O'Dea et al., 2016).

In summary, our time tree and historical biogeographical reconstruction indicate that the pantropical distribution of the Psittacopasseres could have been shaped by a combination of two major geological elements (Figure 2): first, the tectonic forces of the last continental fragmentation of the Cenozoic and, second, the now submerged magmatic islands that formed palaeogeographic provinces connecting major biogeographic realms. Particularly, the Atlantogea in the South Atlantic connected the Neotropics and Afrotropics and is a key component on the evolution of the pantropical distribution of parrots.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article. Supplementary File S1 contains markers and GenBank accession numbers for all species sampled in this study. Supplementary File S2 shows which loci were concatenated in each dataset. Supplementary File S3 contains all topologies estimated in this study. The alignment, partition scheme and topology used as our final results are provided as Supplementary Files S4 and S6. Supplementary File S5 details each fossil calibration used in the divergence time estimates. Biogeographic results are shown in Supplementary Files S7–S9. This paper is based entirely on previously published data.

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BIOSKETCHES

Alexandre Pedro Selvatti, Ana Galvão, Gerald Mayr, Cristina Yumi Miyaki and Claudia Augusta de Moraes Russo interests overlap in palaeontology, morphology, molecular evolution and biogeography, which allows a multidisciplinary approach to uncover the evolutionary history of parrots and the other major avian lineages. **Author contributions:** Alexandre Pedro Selvatti, Ana Galvão and Claudia Augusta de Moraes Russo conceived the ideas and interpreted the results; Alexandre Pedro Selvatti collected the data and conducted all analyses; Gerald Mayr provided input for fossil age and phylogenetic placement; Ana Galvão enriched the discussion of morphological characteristics; and Cristina Yumi Miyaki enriched the discussion on the diversification of parrots in the New World. Alexandre Pedro Selvatti wrote the manuscript with input from Ana Galvão, Claudia Augusta de Moraes Russo, Gerald Mayr and Cristina Yumi Miyaki.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.