



Systematics and biogeography of the whistlers (Aves: Pachycephalidae) inferred from ultraconserved elements and ancestral area reconstruction

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ABSTRACT

The utility of islands as natural laboratories of evolution is exemplified in the patterns of differentiation in widespread, phenotypically variable lineages. The whistlers (Aves: Pachycephalidae) are one of the most complex avian radiations, with a combination of widespread and locally endemic taxa spanning the vast archipelagos of the Indo-Pacific, making them an ideal group to study patterns and processes of diversification on islands. Here, we present a robust, species-level phylogeny of all five genera and 85% of species within Pachycephalidae, based on thousands of ultraconserved elements (UCEs) generated with a target-capture approach and high-throughput sequencing. We clarify phylogenetic relationships within *Pachycephala* and report on divergence timing and ancestral range estimation. We explored multiple biogeographic coding schemes that incorporated geological uncertainty in this complex region. The biogeographic origin of this group was difficult to discern, likely owing to aspects of dynamic Earth history in the Indo-Pacific. The Australo-Papuan region was the likely origin of crown-group whistlers, but the specific ancestral area could not be identified more precisely than Australia or New Guinea, and Wallacea may have played a larger role than previously realized in the evolutionary history of whistlers. Multiple independent colonizations of island archipelagos across Melanesia, Wallacea, and the Philippines contributed to the relatively high species richness of extant whistlers. This work refines our understanding of one of the regions' most celebrated bird lineages and adds to our growing knowledge about the patterns and processes of diversification in the Indo-Pacific.

1. Introduction

Islands provide ideal settings to study evolution and biogeography due to their geographic isolation, discrete boundaries, and relatively well-studied geological histories. The generation of biodiversity on oceanic islands depends on two factors: colonization from continents (MacArthur and Wilson, 1963; 1967) and subsequent lineage diversification (Ricklefs and Bermingham, 2007; Moyle et al., 2009). True species diversity of birds in the Indo-Pacific is masked by decades of over-lumping phenotypically distinct, allopatric island populations (Mayr, 1942; Kearns et al., 2019). However, recent advances in molecular phylogenetics and our understanding of the speciation process have led to widespread re-evaluation of species limits in island bird lineages, specifically those in the Indo-Pacific.

The Indo-Pacific encompasses the Australo-Papuan continental region and island archipelagos spanning Wallacea and the Greater Sundas

to Melanesia and Polynesia. This region has complex geologic histories. Vast archipelagos, from the Philippines to Melanesia, were created by the convergence of the Australian and Pacific tectonic plates over the past ca. 43 Ma (Hall, 1998; 2002; 2013). These new islands—for which connectivity has waxed and waned with sea-level fluctuation—provided new opportunities for species to colonize and diversify (Esselstyn et al., 2009; Jonsson et al., 2011). Molecular systematic studies of terrestrial vertebrates have shown that current species distributions are influenced by long-distance dispersal and back colonization, tectonic processes, and Plio-Pleistocene eustasy (Filardi and Moyle, 2005; Heaney et al., 2005; Irestedt et al., 2014; Jonsson et al., 2018; Esselstyn et al., 2009; Oliver et al., 2020). Additionally, New Guinea is an important regional center of species richness (Marshall and Beehler, 2007), though its importance as an origin of the region's diversity is debated (Jonsson et al., 2011, 2017; Moyle et al., 2016). Although the orogeny of New Guinea is complex and far from certain, it is thought to have emerged subaerially

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in the Miocene (Hall, 2002; van Ufford and Cloos, 2005; Toussaint et al., 2014).

The whistlers and allies (Aves: Pachycephalidae) are one of the most geographically widespread and taxonomically complex avian radiations in the Indo-Pacific. Current classifications recognize five genera, 64 species, and 164 subspecies (Gill et al., 2020). Over time, discrepancies in the number of species within the family reflect the evolving nature of pachycephalid systematics. Sibley and Ahlquist, (1982)—based on DNA-DNA hybridization—included a broad array of genera within the family: *Daphoenositta*, *Mohoua*, *Oreica*, *Falcunculus*, *Pitohui*, *Rhagologus*, *Pachycephala*, *Colluricincla*, *Pachycare*, *Hylocitrea*, *Eulacestoma*, and *Coracornis*. The past three decades of molecular systematics have brought phylogenetic clarity to the group, especially concerning taxonomic family limits (Aggerbeck et al., 2014; Aidala et al., 2013; Dumbacher et al., 2008; Moyle et al., 2016; Norman et al., 2009a; b; Spellman et al., 2008). For example, *Daphoenositta* and *Mohoua* are now thought to be sister to each other and outside of the taxonomic superfamily to which whistlers belong (Orioloidea; Moyle et al., 2016; Oliveros et al., 2019). The Sulawesi endemic *Hylocitrea bonensis*, formerly thought to be a whistler and even named as such in its English common name, is now thought to be part of the Passerides radiation (Alström et al., 2014; Jönsson et al., 2008; Spellman et al., 2008). Our current understanding is that Pachycephalidae comprises five genera: *Pseudorectes*, *Colluricincla*, *Melanorectes*, *Coracornis*, and *Pachycephala* (Jönsson et al., 2016). *Pachycephala* is the most species-rich genus, comprising about 70% of the taxa within the family. The family's modern species richness is centered in New Guinea (four genera, 26 species) and Australia (two genera, 14 species), but other species span a large area from Sundaland to Oceania.

To date, no study has used genome-wide data to address the phylogeny and biogeography of whistlers and their allies. All prior work on this group has relied on multi-locus datasets and mitochondrial clocks to estimate phylogeny and calibrate divergence times across the clade (Jönsson et al., 2010; Marki et al., 2018). Although these approaches have been sufficient to elucidate certain relationships within the family, many nodes remain unresolved. Given the species richness in the Australo-Papuan region, it is unsurprising that previous biogeographical analyses highlighted that region as the ancestral origin of the family (Jönsson et al., 2010; 2014). Here, we use ultraconserved elements (UCEs; Faircloth et al., 2012) to infer a whistler phylogeny, estimate divergence times based on secondary fossil-calibrated nodes from the literature, and to reconstruct ancestral areas of the group. This study furthers our understanding of the evolutionary relationships within the whistlers, their ancestral biogeographic history, and insular colonization patterns that characterize the group.

2. Materials and methods

2.1. Taxon sampling

The dataset comprised 58 ingroup and eight outgroup taxa (Table 1), representing all pachycephalid genera and all but 10 species recognized by the IOC World Bird List v10.1 (Gill et al., 2020). We lacked *Coracornis sanghirensis*, *Pseudorectes incertus*, *Pachycephala melanorhyncha*, and *P. caledonica*, along with six newly recognized *Colluricincla* species (Marki et al., 2018). These were unsampled because either toepad samples did not enrich effectively, or, in the case of *Colluricincla*, the taxonomic updates occurred after we finished our sampling. Approximately 78% of samples were derived from fresh muscle tissue with associated museum voucher specimens, whereas 22% of the samples were derived from toepad clips (Table 1). Seven outgroup and 11 ingroup taxa were previously sequenced (Moyle et al., 2016; Oliveros et al., 2019; Table 1) and those data were downloaded from GenBank and added to our dataset. We sampled two individuals from widely separated populations of the recently recognized Western Whistler in Australia (*P. f. fuliginosa* and *P. f. occidentalis*; Joseph et al., 2014a,

2021).

2.2. Genetic analysis and genomic preparation

We extracted genomic DNA from tissue samples using a Qiagen DNeasy extraction kit following the manufacturer's protocol. For toepad samples, we used a modified protocol adapted from McCormack et al. (2016). We rinsed toepad clippings with 250 μ L of 100% ethanol and rehydrated with UV-crosslinked molecular grade water. To ensure full digestion, we finely cut toepads and added 30 μ L of Proteinase K and Dithiothreitol (DTT; 0.1 g in 1000 μ L ddH₂O) to each sample. We monitored for contamination with a negative control and quantified DNA concentrations of all samples using a Qubit 3.0 Fluorometer (ThermoFisher). We sonicated extracted tissue samples using a Covaris M220 focused-ultrasonicator (50 W peak incident power, 10% duty factor, and 200 cycles per burst for 55–75 s, depending on extraction quality), but toepad samples were not sonicated due to their degraded (i. e., short) DNA strands.

We used a Kapa Biosystems Hyper Prep kit and methods outlined in Faircloth et al. (2012) to prepare Illumina libraries. We washed samples with AMPure XP beads, indexed using the iTruStub dual indexing system (Glenn et al., 2019), amplified via a 17-cycle PCR, and enriched resulting libraries in equimolar concentrations for each sample. We used the MYcroarray MYbaits probe kit to target 5060 UCE loci and pooled 6–8 dual-indexed tissue libraries (4–6 toepad libraries) before another round of PCR. We sent UCE-enriched pools for bioanalyzing prior to sequencing at the University of Oklahoma Medical Research Foundation on an Illumina HiSeq 3000. Several samples that failed the initial sequencing were re-enriched and subsequently sequenced on an Illumina NovaSeq 6000 (Table 1).

2.3. Alignment and phylogenetic analysis

We followed the PHYLUCE pipeline to process raw Illumina reads into UCE contigs (Faircloth, 2016). We trimmed low-quality bases and adaptor sequences from raw sequence reads using illumiprocessor v1 (Faircloth et al., 2013; Bolger et al., 2014). We assembled contigs from cleaned reads with trinity v2.0.6 (Grabherr et al., 2011) and extracted contigs for each taxon that matched UCE loci. We aligned loci using mafft (Katoh and Standley, 2013) without trimming. We trimmed alignments using gblocks v0.91 (Castresana, 2000) with default parameters except for the minimum number of sequences for a flank position, b2, which we set to 0.65.

We assembled a 75%-complete matrix such that 75% (50 out of 66 taxa) were present per UCE alignment (locus) and inferred a maximum likelihood tree (Fig. 1). We input gene partitions to PartitionFinder v2.1.1 (Lanfear et al., 2014), which determined the best partitioning scheme and the best-fit model of sequence evolution for the concatenated dataset to be a general time-reversible model of nucleotide substitutions with gamma distributed rates among sites (GTR + G). We then performed maximum likelihood tree searches of the partitioned, concatenated data matrices using RAXML v8.2.10 (Fig. 1; Stamatakis, 2006) on the CIPRES gateway (Miller et al., 2010).

We estimated the species tree from independent gene trees in ASTRAL-III v5.15.4 (Fig. 2; Mirarab et al., 2014; Zhang et al., 2018). ASTRAL uses dynamic programming to search for the tree that shares the maximum number of quartet topologies with input gene trees, restricting itself to a predefined set of bipartitions. We restricted our ASTRAL dataset to 54 tips by removing most of the toepad-derived samples, because samples with short gene contigs tend to get pulled erroneously toward the base of a tree (Moyle et al., 2016). We generated 4283 gene trees using RAXML-ng (Kozlov et al., 2019), including 100 bootstrap replicates for multi-locus bootstrapping using ASTRAL. We report the main ASTRAL tree as the result of running ASTRAL on the best ML input gene trees with support values based on the 100 bootstrap replicate trees.

Table 1

Samples used in this study. Institutional abbreviations: AM, Australian Museum; AMNH, American Museum of Natural History; ANSP, Academy of Natural Science; ANWC, Australian National Wildlife Collection; CAS, California Academy of Science; DMNH, Delaware Museum of Natural History; FLMNH, Florida Museum; KUNHM, University of Kansas Biodiversity Institute; LSUMZ, Louisiana State University Museum of Natural Science; SNZP, Smithsonian National Zoological Park; UWBM, University of Washington Burke Museum of Natural History and Culture; WAM, Western Australia Museum; and YPM, Yale Peabody Museum. The sequencing platform, NCBI accession numbers, and number of UCE contigs recovered are noted. Areas used to infer historical biogeography in BioGeoBears are marked with an 'X': A) Mainland Asia (including New World for outgroup *Vireo*), B) Sundaland (including Palawan), C) Wallacea (Sulawesi, Moluccas, Lesser Sundas), D) Philippines and Palau, E) Australia, F) New Guinea, and G) Oceania (Bismarcks, Melanesia, Polynesia). Note that for biogeographic Scenario A, columns E and F were combined into one region. Numbers in 'Cleaned reads' column that are marked with * are reported as number of raw reads.

Taxon	Institution	Identifier	Source	Location	Platform	NCBI accession	Cleaned reads	No. UCE Contigs	Mean contig length	A	B	C	D	E	F	G
Outgroups																
<i>Vireo solitarius</i>	KUNHM	25186	Tissue	United States	GenBank	SAMN04301800	2404617	4189	537.9	X	–	–	–	–	–	–
<i>Psophodes occidentalis</i>	KUNHM	6205	Tissue	Australia: Western Australia	GenBank	SAMN10450353	–	4086	709.7	–	–	–	–	X	X	–
<i>Pteruthius aeralatus</i>	KUNHM	17806	Tissue	Malaysia: Borneo	GenBank	SAMN04301781	3106608	4124	465.7	X	X	–	–	–	–	–
<i>Sphecotheres vieilloti</i>	KUNHM	10752	Tissue	Australia	HiSeq 2500	SAMN22583359	3115560*	3990	905.2	–	–	X	–	X	X	–
<i>Oreocharis arfaki</i>	KUNHM	16440	Tissue	Papua New Guinea: Central	GenBank	SAMN04301753	7309007	4445	694.6	–	–	–	–	–	X	–
<i>Erpornis zantholeuca</i>	KUNHM	27942	Tissue	Vietnam: Lao Cai	GenBank	SAMN10450298	–	4209	967.4	X	X	–	–	–	–	–
<i>Oriolus chinensis</i>	KUNHM	10450	Tissue	China: Guangxi	GenBank	SAMN04301755	9693493	4587	606.7	X	X	X	X	X	X	–
<i>Pitohui dichrous</i>	KUNHM	12200	Tissue	Papua New Guinea: Madang	GenBank	SAMN10450344	–	4432	994.6	–	–	–	–	–	X	–
Ingroup																
<i>Colluricincla boweri boweri</i>	ANWC	B28851	Tissue	Australia: Queensland	HiSeq 3000	SAMN22583360	6415681	4373	1269.3	–	–	–	–	X	–	–
<i>Colluricincla harmonica brunnea</i>	ANWC	B56031	Tissue	Papua New Guinea: Central	HiSeq 3000	SAMN22583361	8057954	4381	629.9	–	–	–	–	X	X	–
<i>Colluricincla megarhyncha griseata</i>	ANWC	B56099	Tissue	Papua New Guinea: Western	HiSeq 3000	SAMN22583362	8036483	4277	1359.5	–	–	–	–	X	X	–
<i>Colluricincla tenebrosa</i>	KUNHM	12108	Tissue	Papua New Guinea: Mandang	HiSeq 3000	SAMN22583363	4262572	4350	1171.7	–	–	–	–	–	X	–
<i>Colluricincla woodwardi woodwardi</i>	ANWC	B55216	Tissue	Australia: Western Australia	HiSeq 3000	SAMN22583364	4877222	4306	1238.6	–	–	–	–	X	–	–
<i>Coracornis raveni</i>	AMNH	299556	Toepad	Indonesia: Sulawesi	HiSeq 3000	SAMN22583365	9957267	4447	380.6	–	–	X	–	–	–	–
<i>Melanorectes nigrescens nigrescens</i>	ANWC	B52558	Tissue	Papua New Guinea: Western	HiSeq 3000	SAMN22583366	9452805	4375	1020.8	–	–	–	–	–	X	–
<i>Pseudorectes ferrugineus</i>	KUNHM	9610	Tissue	Papua New Guinea: Morobe	HiSeq 2500	SAMN22583367	4304376*	4134	998.5	–	–	–	–	–	X	–
<i>Pachycephala albiventris crissalis</i>	KUNHM	21019	Tissue	Philippines: Luzon Island	HiSeq 3000	SAMN22583368	4110258	4161	1137.1	–	–	–	X	–	–	–
<i>P. arctitorquis arctitorquis</i>	WAM	A25087	Tissue	Indonesia: Moluccas: Tanimbar Island	HiSeq 3000	SAMN22583369	3183040	4275	1060.2	–	–	X	–	–	–	–
<i>P. aurea</i>	AMNH	302234	Toepad	Indonesia: West Papua	HiSeq 3000	SAMN22583370	8566773	4176	338.1	–	–	–	–	–	X	–
<i>P. balim</i>	AMNH	341498	Toepad	Indonesia: New Guinea	HiSeq 3000	SAMN22583371	8241080	4296	348.2	–	–	–	–	–	X	–
<i>P. chlorura intacta</i>	LSUMZ / FLMNH	B45791	Tissue	Vanuatu	HiSeq 2500	SAMN22583372	1238892*	3601	622.6	–	–	–	–	–	–	X
<i>P. chlorura littayei</i>	YPM	71205	Toepad	New Caledonia: Loyalty Islands	HiSeq 3000	SAMN22583373	7102672	4404	806.9	–	–	–	–	–	–	X
<i>P. cinerea plateni</i>	KUNHM	12751	Tissue	Philippines: Palawan	HiSeq 3000	SAMN22583374	4438825	4126	1101.9	X	X	X	X	–	–	–
<i>P. citreogaster goodsoni</i>	KUNHM	5615	Tissue	Papua New Guinea	HiSeq 3000	SAMN22583375	8008394	4283	857.2	–	–	–	–	–	–	–
<i>P. collaris collaris</i>	CAS	96792	Tissue	Papua New Guinea: Louisiade Archipelgo	HiSeq 3000	SAMN22583376	3182587	4301	937.1	–	–	–	–	–	X	–
<i>P. feminina</i>	AMNH	DOT-6601	Tissue	Solomon Islands: Rennell Island	HiSeq 2500	SAMN22583377	4973732*	4271	995.8	–	–	–	–	–	–	X
<i>P. flavifrons flavifrons</i>	KUNHM	104129	Toepad	Samoa: Savaii Island	HiSeq 3000	SAMN22583378	6938446	2494	374.7	–	–	–	–	–	–	X
<i>P. fuliginosa fuliginosa</i>	ANWC	B43329	Tissue	Australia: South Australia	HiSeq 3000	SAMN22583379	5859131	4225	1058.1	–	–	–	–	X	–	–
<i>P. f. occidentalis</i>	ANWC	B31698	Tissue	Australia: Western Australia	HiSeq 3000	SAMN22583380	8971975	4188	1015.7	–	–	–	–	X	–	–
<i>P. fulvotincta javana</i>	KUNHM	31158	Tissue	Indonesia: Lesser Sundas: Java	HiSeq 3000	SAMN22583381	6638021	4202	935.5	–	X	X	–	–	–	–
<i>P. groeffii</i>	KUNHM	22555	Tissue	Fiji: Viti Levu	HiSeq 2500	SAMN22583382	2291262*	4000	722.4	–	–	–	2291262*	–	–	X
<i>P. griseonota cinerascens</i>	YPM	76041	Toepad	Indonesia: Moluccas: Bacan Island	HiSeq 3000	SAMN22583383	8636387	3380	460.5	–	–	X	–	–	–	–
<i>P. homeyeri winchelli</i>	KUNHM	15340	Tissue	Philippines: Antique: Panay Island	HiSeq 3000	SAMN22583384	4708725	4082	1059.6	–	–	–	X	–	–	–
<i>P. hypertythra hypertythra</i>	KUNHM	31363	Tissue	Papua New Guinea: Western	HiSeq 3000	SAMN22583385	6382356	4343	1235.1	–	–	–	–	–	X	–
<i>P. hypoxantha hypoxantha</i>	LSUMZ	B36296	Tissue	Borneo	HiSeq 3000	SAMN22583386	6897108	4266	1209.9	–	X	–	–	–	–	–

(continued on next page)

Table 1 (continued)

Taxon	Institution	Identifier	Source	Location	Platform	NCBI accession	Cleaned reads	No. UCE Contigs	Mean contig length	A	B	C	D	E	F	G
<i>P. implicata</i>	KUNHM	32803	Tissue	Solomon Islands: Guadalcanal	HiSeq 3000	SAMN22583387	3257972	4277	1060.3	–	–	–	–	–	–	X
<i>P. inornata inornata</i>	ANWC	B52274	Tissue	Australia: South Australia	HiSeq 3000	SAMN22583388	6121535	4270	1182.5	–	–	–	–	X	–	–
<i>P. jacquiniti jacquiniti</i>	DMNH	11332	Toepad	Tonga: Late Island	HiSeq 3000	SAMN22583389	10432085	4504	367.5	–	–	–	–	–	–	X
<i>P. johnei</i>	AMNH	658812	Toepad	Indonesia: Moluccas: Obi Island	HiSeq 3000	SAMN22583390	5823485	3694	339.6	–	–	X	–	–	–	–
<i>P. lanioides carnavoni</i>	KUNHM	6195	Tissue	Australia: Western Australia	HiSeq 3000	SAMN22583391	9380095	4296	1243.0	–	–	–	–	X	–	–
<i>P. leucogastra meeki</i>	SNZP	TKP2004067	Tissue	New Guinea: Rossel Island	HiSeq 3000	SAMN22583392	15785732	4305	1320.9	–	–	–	–	–	X	–
<i>P. lorentzi</i>	AMNH	765864	Toepad	Papua New Guinea: Mt Infal	HiSeq 3000	SAMN22583393	35133440	4355	363.0	–	–	–	–	–	X	–
<i>P. macrorhyncha</i>	WAM	A25185	Tissue	Indonesia: Moluccas: Tanimbar Island	HiSeq 2500	SAMN22583394	2154692*	4076	733.2	–	–	X	–	–	–	–
<i>P. melanura dahlia</i>	KUNHM	27797	Tissue	Papua New Guinea: New Ireland	HiSeq 3000	SAMN22583395	9138500	4393	1117.9	–	–	–	–	X	X	X
<i>P. mentalis mentalis</i>	YPM	76043	Toepad	Indonesia: Moluccas: Bacan Island	HiSeq 3000	SAMN22583396	10736338	4378	532.8	–	–	X	–	–	–	–
<i>P. meyeri meyeri</i>	ANSP	132275	Toepad	Indonesia: West Papua	HiSeq 3000	SAMN22583397	7020774	4362	423.7	–	–	–	–	–	X	–
<i>P. modesta modesta</i>	KUNHM	4736	Tissue	Papua New Guinea: Morobe	HiSeq 3000	SAMN22583398	6449453	4191	1317.5	–	–	–	–	–	X	–
<i>P. monacha lugubris</i>	YPM	128737	Toepad	Indonesia: Papua	HiSeq 3000	SAMN22583399	1402765	3641	428.7	–	–	–	–	–	X	–
<i>P. nudigula nudigula</i>	WAM	A22678	Tissue	Indonesia: Lesser Sundas: Flores Island	HiSeq 3000	SAMN22583400	3301865	4282	950.1	–	–	X	–	–	–	–
<i>P. olivacea olivacea</i>	ANWC	B46097	Tissue	Australia: Victoria	HiSeq 3000	SAMN22583401	4823326	4182	1165.9	–	–	–	–	X	–	–
<i>P. orioides centralis</i>	UWBM	66075	Tissue	Solomon Islands: Western Province: New Georgia	HiSeq 3000	SAMN22583402	4927435	4354	1165.6	–	–	–	–	–	–	X
<i>P. orpheus orpheus</i>	WAM	23880	Tissue	Indonesia: Lesser Sundas: Timor Island	HiSeq 3000	SAMN22583403	12073401	4318	1108.1	–	–	X	–	–	–	–
<i>P. phaionota</i>	WAM	A24736	Tissue	Indonesia: Moluccas: Banda Island	HiSeq 3000	SAMN22583404	2287856	4329	942.7	–	–	X	–	–	X	–
<i>P. philippinensis illex</i>	KUNHM	10843	Tissue	Philippines: Cagayan: Camiguin Norte Island	HiSeq 3000	SAMN22583405	5426718	3942	1036.9	–	–	–	X	–	–	–
<i>P. richardsi</i>	AMNH	222850	Toepad	Solomon Islands: Bougainville	NovaSeq 6000	SAMN22583406	33680765	4423	–	–	–	–	–	–	–	X
<i>P. rufiventris</i>	UWBM	57510	Tissue	Australia: Queensland	HiSeq 3000	SAMN22583407	3126836	4073	1000.9	–	–	–	–	X	–	X
<i>P. rufogularis rufogularis</i>	ANWC	B38096	Toepad	Australia: Victoria	HiSeq 3000	SAMN22583408	9521653	4396	974.1	–	–	–	–	X	–	–
<i>P. schlegelii schlegelii</i>	KUNHM	121594	Tissue	Papua New Guinea: Central	NovaSeq 6000	SAMN22583409	57139942	4027	600.9	–	–	–	–	–	X	–
<i>P. simplex gagiensis</i>	WAM	A26551	Tissue	Indonesia: West Papua: Gag Island	HiSeq 3000	SAMN22583410	12795864	4175	741.9	–	–	X	–	X	X	–
<i>P. simplex simplex</i>	ANWC	B33535	Tissue	Australia: Northern Territory	HiSeq 3000	SAMN22583411	8265201	4254	1005.9	–	–	–	–	X	–	–
<i>P. soror soror</i>	KUNHM	7888	Tissue	Papua New Guinea: West Sepik	HiSeq 3000	SAMN22583412	4579981	4289	1188.2	–	–	–	–	–	X	–
<i>P. sulfuriventer sulfuriventer</i>	AMNH	DOT-12575	Tissue	Indonesia: Sulawesi	HiSeq 3000	SAMN22583413	4274373	4263	1199.2	–	–	X	–	–	–	–
<i>P. tenebrosa tenebrosa</i>	KUNHM	23676	Tissue	Palau: Peleliu Island	HiSeq 3000	SAMN22583414	3937741	4359	1092.3	–	–	–	X	–	–	–
<i>P. vanikorensis</i>	KUNHM	19410	Tissue	Solomon Islands: Temotu: Santa Cruz Island	HiSeq 2500	SAMN22583415	5725672*	4284	1143.9	–	–	–	–	–	–	X
<i>P. vitiensis kandavensis</i>	KUNHM	24411	Tissue	Fiji: Kadavu Island	HiSeq 3000	SAMN22583416	11350813	4393	1362.5	–	–	–	–	–	–	X
<i>P. pectoralis youngi</i>	ANWC	B29282	Tissue	Australia: New South Wales	HiSeq 2500	SAMN22583417	4736700*	4261	954.9	–	–	–	–	X	–	–

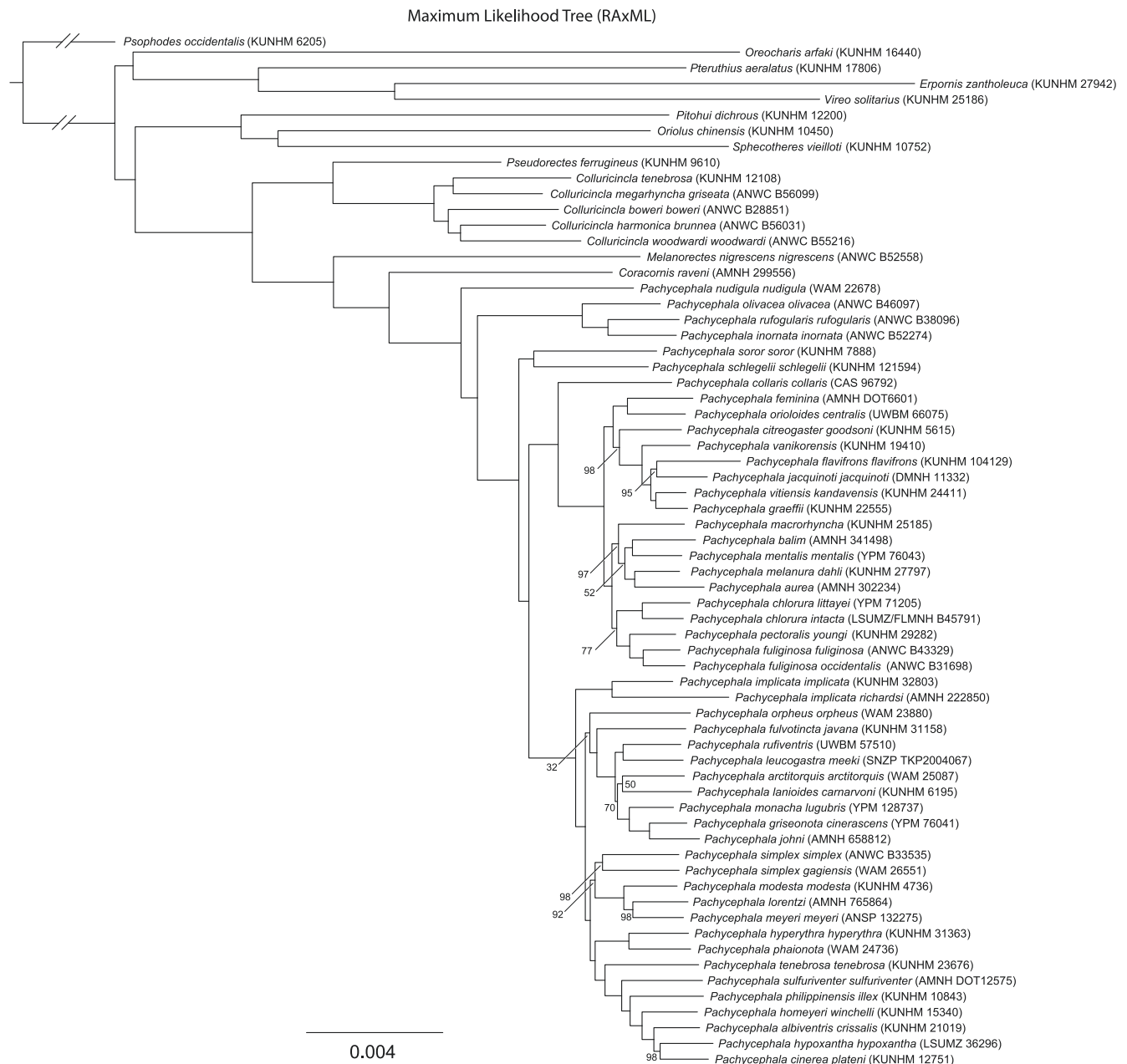


Fig. 1. Maximum likelihood topology from the concatenated, partitioned autoMRE RAxML analysis of the 75%-complete dataset of Pachycephalidae and outgroups with 500 bootstrap replicates. Bootstrap scores are labeled at the nodes for those < 100.

2.4. Time-calibration

We used BEAST v2.5.2 (Bouckaert et al., 2014) to infer a time-calibrated tree. We used a birth-death tree prior, a lognormal, uncorrelated relaxed clock model, and assigned the HKY+G model of sequence evolution to each UCE locus. To reduce computing time, we constrained the topology to our RAxML tree with a multi-monophyletic constraint prior and parsed the 75%-complete data matrix into 20 subsets of 50 loci chosen at random without replacement, following McCullough et al., 2019. We ran MCMC chains for 20 million generations and sampled trees every 10,000 generations. We visualized traces of log files in TRACER v1.7.1 (Rambaut et al., 2018) to assess convergence of individual runs and we ensured ESS values exceeded 200. We used LogCombiner v2.5.2 to combine four replicates from each of the 20 datasets and discarded the first 25% of trees as burn-in. To produce a single maximum clade credibility (MCC) tree, we used TreeAnnotator

v2.5.2 (Bouckaert et al., 2014) and subsampled every 12th tree for a final posterior distribution of 10,000 trees. There are no known fossil whistlers, so we relied on alternative dating methods. Whereas previous time-tree estimates of Pachycephalidae have used mitochondrial clocks (e.g., ca. 2.9%, following Lerner et al., 2011) or island ages (Jonsson et al., 2010; Marki et al., 2018), we used two secondary fossil-calibration points from Oliveros et al. (2019) to date our tree. Oliveros et al. (2019) used 13 fossil calibrations to date their passerine time tree, of which the closest fossil to Pachycephalidae was *Kurrartapu johngnyeni*, a crown artamid that shared a most recent common ancestor with whistlers about 22.9 Ma. The first calibration point we used was for the split between *Psophodes* and the remaining sampled taxa, which we set with a normal distribution, sigma value of 0.5, and a mean date of 22.2 Ma (CI = 21.8–29.6). The second point was the split between Pachycephalidae and outgroups consisting of: *Erpomis*, *Oreocharis*, *Oriolus*, *Pitohui*, *Psophodes*, *Pteruthius*, *Sphecotheres*, and *Vireo* with a normal distribution,

ASTRAL species tree, 75%-complete matrix

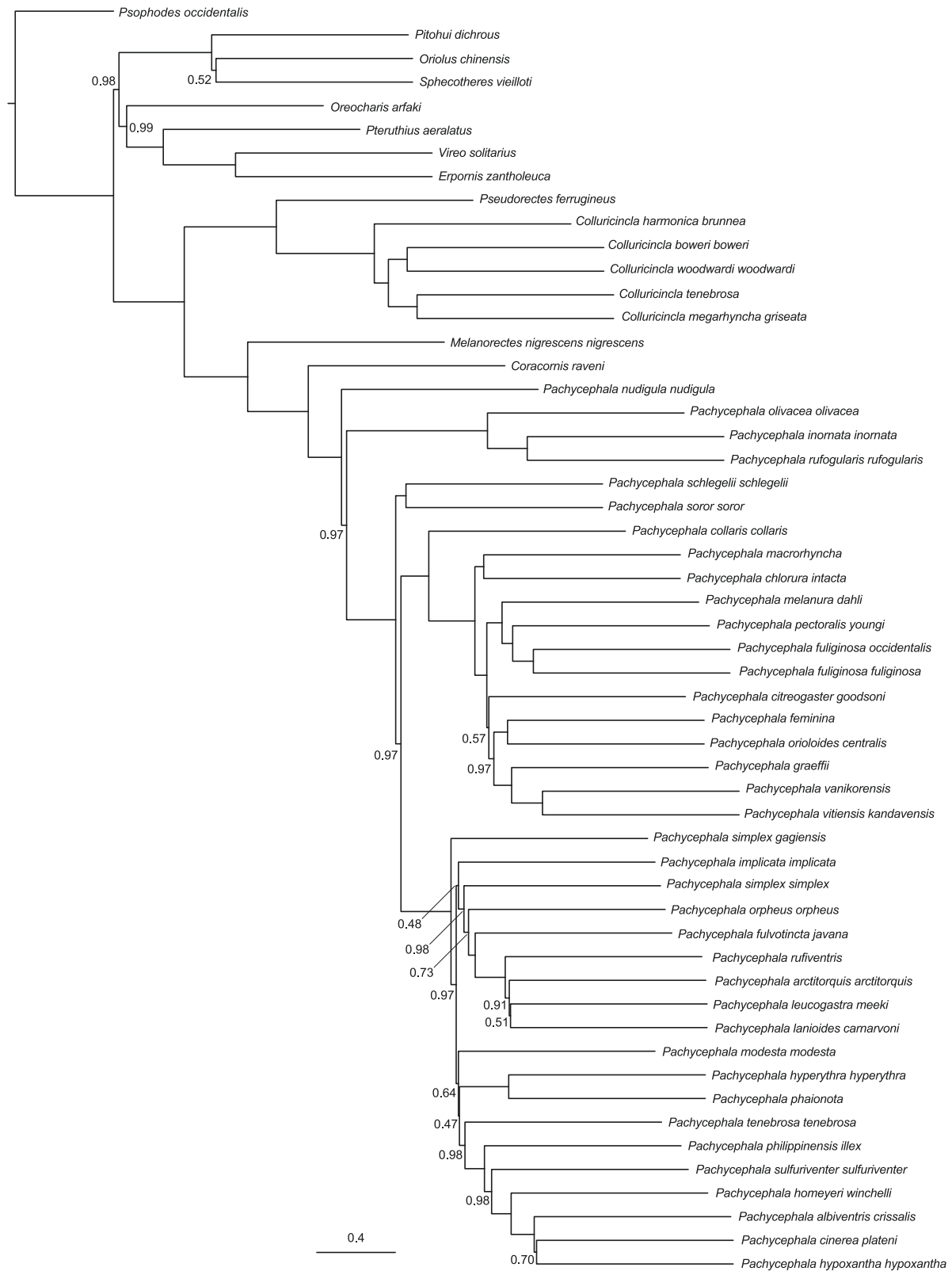


Fig. 2. ASTRAL species tree topology of the 75%-complete, 54-tip phylogeny. Node support was evaluated with 100 multi-locus bootstraps and nodes are labelled for those < 100.

sigma of 0.5, and a mean date of 14.6 Ma (CI = 13.8–15.6). This estimate of the crown-age of Pachycephalidae in the mid-Miocene is consistent with other studies of higher-level oscines (Moyle et al., 2016) and a species-level phylogeny of corvid passerines (Jönsson et al., 2016).

2.5. Biogeographic analysis

Using the R package BioGeoBEARS, we inferred the biogeographic history of whistlers by comparing multiple models within a maximum likelihood framework (Matzke, 2013). We tested three probabilistic models for historical biogeography: DEC, DIVA, and BayArea, each with

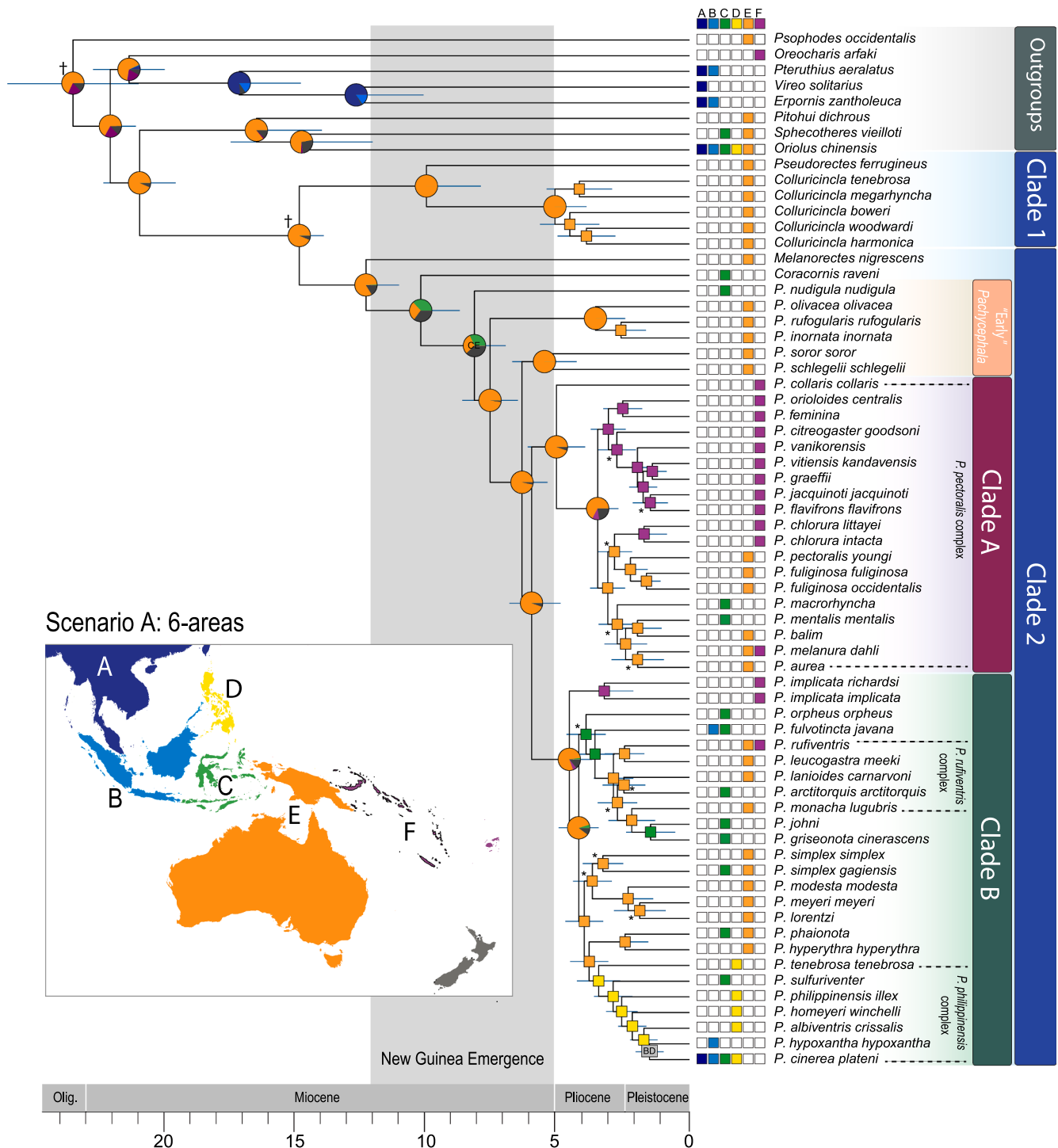


Fig. 3. Biogeographical analysis using six areas, without a time constraint (Scenario A). Maximum clade credibility (MCC) tree of BEAST2 analysis of 500 ultra-conserved loci from the 75% complete dataset with the fixed ML topology. 95% HPD bars are plotted on the nodes as indicated by dark gray bars and asterisks at nodes indicate maximum likelihood bootstrap values for nodes < 100. Nodes are labelled either with a pie chart (deeper nodes) or solid squares (shallower nodes) that denote inferred ancestral ranges from analysis in BioGeoBEARS. Colors correspond to regions A-F on the map; gray nodes and pie wedges indicate equivocal ancestral areas. Colored squares at the tips indicate current species' distributions that were used as biogeographic codings. Dark gray rectangle indicates the estimated time of the emergence of New Guinea, approximately 5–12 Ma.

and without the +j parameter, which allows for long distance dispersal and founder-event speciation, and assessed model fitness with Akaike information criterion (AIC; Akaike, 1974). The DEC +j model tends to explain all biogeographic variation through the jump parameter (Ree and Sanmartín, 2018); however, we justify our use of the +j parameter as relevant to our study because many whistler species are known for

long-distance dispersal to oceanic island archipelagos.

We coded biogeographic regions for all tips according to their modern-day distributions (Winkler et al., 2020). We geologically delineated seven areas: A) Mainland Asia (including New World for outgroup *Vireo*), B) Sundaland (including Palawan), C) Wallacea (Sulawesi, Moluccas, Lesser Sundas), D) Philippines and Palau, E)

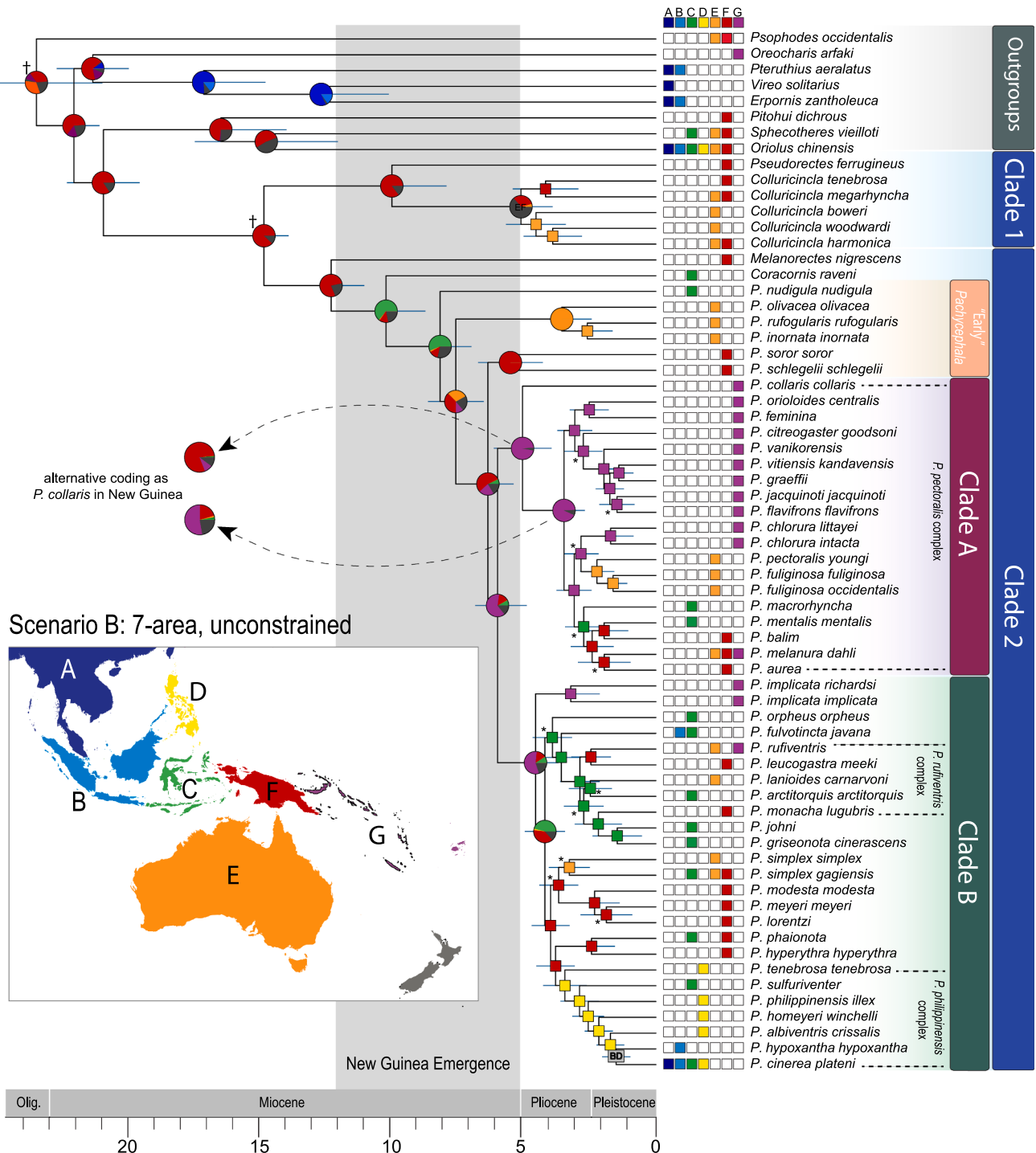


Fig. 4. Biogeographical analysis using seven areas, without a time constraint (Scenario B). Maximum clade credibility (MCC) tree of BEAST2 analysis of 500 ultraconserved loci from the 75% complete dataset with the fixed ML topology. 95% HPD bars are plotted on the nodes as indicated by dark gray bars and asterisks at nodes indicate maximum likelihood bootstrap values for nodes < 100. Nodes are labelled either with a pie chart (deeper nodes) or solid squares (shallower nodes) that denote inferred ancestral ranges from analysis in BioGeoBEARS. Colors correspond to regions on the map; gray nodes and pie wedges indicate equivocal ancestral areas. Colored squares at the tips indicate current species' distributions that were used as biogeographic codings. Dark gray rectangle indicates the estimated time of the emergence of New Guinea, approximately 5–12 Ma. Inset piechart represents the result of the analysis in which *Pachycephala collaris* was coded as New Guinea.

Australia, F) New Guinea, and G) Oceania (Bismarcks, Melanesia, Polynesia; Table 1 and Fig. 3). We allowed the maximum range size of any given taxon to be five to account for the widespread outgroup *Oriolus*, although no modern ingroup taxon occurs in more than four areas (*P. cinerea*).

We explored multiple biogeographic scenarios to account for the

geologic complexity of the Indo-Pacific and uncertainty in the timing of the emergence of New Guinea as a biogeographically relevant landmass. First, we ran a biogeographic analysis with six areas, treating New Guinea and Australia as one combined range known as Sahul (Scenario A; Fig. 3). These regions are closely linked biogeographically since New Guinea and Australia have shared connectivity across the Sahul Shelf

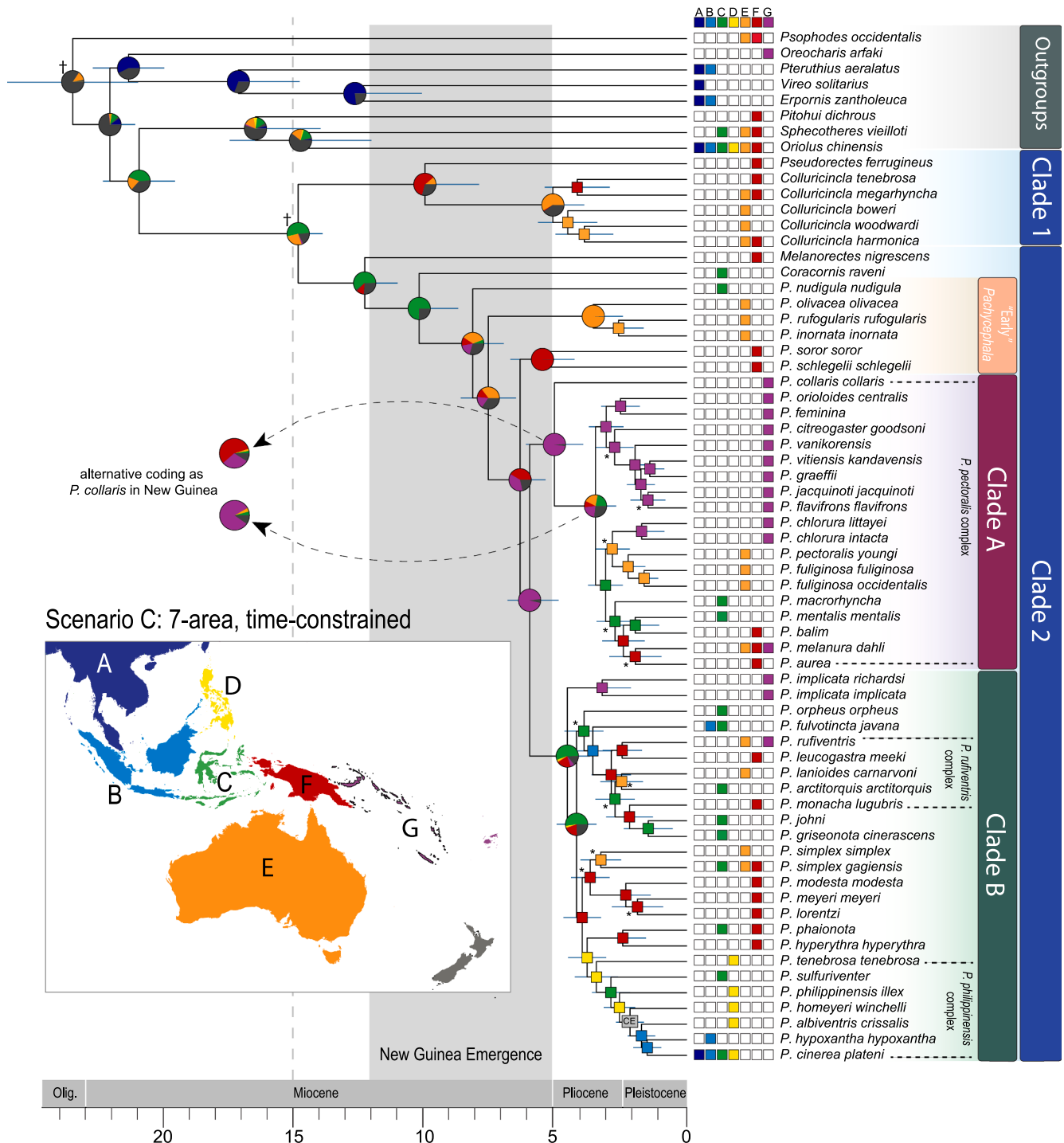


Fig. 5. Biogeographical analysis using seven areas and time constraint (Scenario C). Maximum clade credibility (MCC) tree of BEAST2 analysis of 500 ultraconserved loci from the 75% complete dataset with the fixed ML topology and a 15-Ma time constraint (dashed vertical line). 95% HPD bars are plotted on the nodes as indicated by dark gray bars and asterisks at nodes indicate maximum likelihood bootstrap values for nodes < 100. Nodes are labelled either with a pie chart (deeper nodes) or solid squares (shallower nodes) that denote inferred ancestral ranges from analysis in BioGeoBEARS. Colors correspond to regions on the map; gray nodes and pie wedges indicate equivocal ancestral areas. Colored squares at the tips indicate current species' distributions that were used as biogeographic codings. Dark gray rectangle indicates the estimated time of the emergence of New Guinea, approximately 5–12 Ma; dotted line represents our constraint of New Guinea's emergence at 15 Ma. Inset piechart represents the result of the analysis in which *Pachycephala collaris* was coded as New Guinea.

during glacial maxima (Voris, 2000; Heinsohn and Hope, 2006; Joseph et al., 2019; Peñalba et al., 2019). We then ran two analyses with seven areas, thus treating New Guinea and Australia as separate ranges. These analyses were run with and without a geological constraint model for the emergence of New Guinea some 5–12 Ma (van Ufford and Cloos, 2005; Hill and Hall, 2003). We therefore took a conservative approach and did not allow for ancestral ranges to occupy New Guinea before 15 Ma, following the approach used by Moyle et al. (2016). We refer to these as Scenario B (unconstrained; Fig. 4) and Scenario C (time-constrained; Fig. 5), respectively. Finally, we reran Scenarios B and C and changed the coding of *Pachycephala collaris*, found in the Louisiade Archipelago, from Oceania to New Guinea to account for the Louisiades' proximity to mainland New Guinea (see insets in Figs. 4 and 5). We paid particular attention to this taxon because of its potentially influential placement as sister to the rest of the *P. pectoralis* complex.

3. Results

3.1. Dataset

We recovered an average of 7.87 million reads per individual after cleaning raw reads (6.76 million reads per individual from the HiSeq 3000 and 41.98 million reads per individual from the NovaSeq 6000; Table 1). We recovered an average of 4207 loci (range: 2494–4587) with a mean contig length of 851 base pairs (bp; Table 1). Our 75%-complete matrix had 4226 loci and 3,486,406 bp, of which 484,700 bp were variable characters and 153,149 bp were parsimony-informative characters. Our 75%-complete, 54-tip matrix used for species-tree inference in ASTRAL had 4283 loci and 4,120,898 bp.

3.2. Phylogenetic relationships

We recovered a well-resolved, time-calibrated phylogeny of Pachycephalidae. Most nodes had 100% bootstrap support in the autoMRE RAxML tree (Fig. 1). Additionally, most relationships were in agreement with our ASTRAL species tree, but with varying levels of support (Fig. 2). Our dataset resolved some previously uncertain nodes deeper in the tree (e.g., *P. nudigula* sister to other *Pachycephala*, sister relationship of *P. soror* and *P. schlegelii*; see section 4.2 for details); however, node support for the rapid radiations at the tips remained equivocal.

The family comprised two main clades (Fig. 3): (1) Clade 1: *Pseudorectes* + *Colluricincla* was the sister clade of (2) Clade 2: *Melanorectes* + (*Coracornis* + *Pachycephala*). Within *Pachycephala*, three branches sequentially diverged from the base and subtended lineages that we collectively refer to as “Early *Pachycephala*.” *Pachycephala nudigula* was unequivocally sister to all other members of the genus. Then *Pachycephala olivacea*, *P. inornata*, and *P. rufogularis* constituted a clade that was sister to all remaining *Pachycephala* taxa. The third lineage of Early *Pachycephala* comprised the sister pair of *P. schlegelii* and *P. soror* (BS = 100%). It was sister to the main clades that comprised most *Pachycephala* species diversity, hereafter referred to as the “Core *Pachycephala*.”

Two clades made up the Core *Pachycephala*: Clade A was composed of the *P. pectoralis* species complex and Clade B included all other described taxa, including the *P. rufiventris* and *P. philippinensis* species complexes (Fig. 3). Within Clade A, the Louisiade endemic, *P. collaris*, was sister to the rest of the clade. It is on a long branch separate from the rest of the *P. pectoralis* complex, which was otherwise split roughly into a Pacific clade and an Australo-Papuan clade. The Pacific clade comprised lineages such as *P. orioides* from the Solomon Islands and *P. vitiensis* of Fiji, whereas the Australo-Papuan clade comprised lineages such as *P. pectoralis* from Australia and *P. melanura*, a mangrove and coastal specialist of the region. Clade B was more geographically complex and included lineages from Melanesia (*P. implicata* + *P. richardsi*), New Guinea (*P. lorentzi*), Wallacea (*P. sulfuriventer*), the Philippines (*P. philippinensis*), Palau (*P. tenebrosa*), Sundaland (*P. hypoxantha*), and mangrove forests of mainland Southeast Asia (*P. cinerea*).

3.3. Biogeography and divergence timing

Our biogeographic analysis and model selection found that the dispersal-extinction-cladogenesis model, including founder-event speciation, was the best-supported model for all three biogeographic scenarios (Table 2). When we treated New Guinea and Australia as one region (Scenario A), the results overwhelmingly supported an origin and early diversification of whistlers in the Sahul region during the Mid-Miocene, approximately 13.9–15.7 Ma (mean 14.8 Ma; Fig. 3). The crown group for Clades 1 and 2 was also inferred to have originated there, approximately 7.9–12.1 Ma (mean 9.9 Ma) for Clade 1 and 11.0–13.5 Ma (mean 12.3 Ma) for Clade 2. Furthermore, a majority of the nodes within the family (37 out of 57 nodes) were inferred to be largely Australo-Papuan in origin. Two nodes near the base of Clade 2 were equivocal in their support for Australo-Papua or a Wallacean ancestral area. These nodes led to *Coracornis raveni* and *Pachycephala nudigula*, two Wallacean-endemic lineages in Sulawesi and the Lesser Sundas, respectively. When Australia and New Guinea were treated as separate regions (Scenario B; Fig. 4), New Guinea was supported as the biogeographic origin of whistlers, including the ancestral areas for Clades 1 and 2. In this unconstrained analysis, Clade 1 was inferred to have originated in New Guinea with a higher probability than the constrained analysis (Figs. 4, 5). Furthermore, Clade 2 was inferred to be most likely of New Guinea origin (about 75% probability), whereas in the constrained analysis, <10% of the likely ancestral area of Clade 2 was attributed to New Guinea. Conversely, when we employed a time-constraint on the geologic emergence of New Guinea (Scenario C; Fig. 5), our biogeographic results across the backbone of the family changed dramatically. Most notably, we inferred a Wallacean and Australian origin of Pachycephalidae (~55% for Wallacea, 30% for Australia, and ~15% equivocal; Fig. 5), to the exclusion of New Guinea.

In general, those clades whose origins post-dated our time-constraint were relatively unchanged between these analyses. The crown age of *Pachycephala* is approximately 6.9–9.3 Ma (mean 8.1 Ma) and was inferred to have origins in Sahul (Scenario A) or Wallacea (Scenarios B and C). The inferred ancestral area of the genus *Pachycephala* was less equivocal in the unconstrained analysis than the constrained analysis. In the former, Australia, Oceania, and New Guinea were suggested as possible ancestral areas, whereas in the latter, Wallacea received >50% of the ancestral area likelihood. The next three species after *P. nudigula* form a clade that is endemic to Australia (*P. olivacea*, *P. rufogularis*, and *P. inornata*), followed by a sister pair of *P. soror* and *P. schlegelii* that is endemic to New Guinea. Their ancestral areas were inferred largely to be in Australia and New Guinea, respectively. The Core *Pachycephala* (Clades A + B) diverged approximately 5.1–7.0 Ma (mean 5.9 Ma) and was strongly supported as originating in Oceania in both 7-area analyses (Scenarios B and C), though with less support in the unconstrained analysis. However, the 6-area analysis (Scenario A) strongly inferred a Sahul origin of the Core *Pachycephala*.

Clade A diverged 3.9–6.1 Ma (mean 5.0 Ma) and we inferred a mostly Oceanian origin of this clade. The first branch in Clade A was *P. collaris* of the Louisiade Archipelago. When this taxon was coded as occurring in Oceania, this clade was strongly inferred to have originated there; however, when it was coded in New Guinea, the ancestral area for Clade A was more heavily weighted to New Guinea than Oceania. The rest of Clade A exhibits a pattern consistent with a sweep of diversification into the Pacific with back colonization into Wallacea and Australia (i.e., *P. pectoralis*, *P. fuliginosa*, *P. macrorhyncha*, *P. mentalis*, and *P. balim*). Finally, Clade B originated approximately 3.4–4.9 Ma (mean 4.5 Ma) and reconstruction of its ancestral area was complicated and varied depending on the analysis. For example, Scenario A inferred an origin in Sahul with subsequent colonization of Oceania, Wallacea, and the Philippines. Scenarios B and C supported an origin in Oceania and Wallacea, respectively, but support was equivocal.

Table 2

Biogeographical model selection, analysed with BioGeoBEARS using seven areas and six maximum areas for the time-constrained analysis and unconstrained analyses.

Scenario	Model	LnL	parameters	d	e	j	AIC	AIC weight
A	DEC	-132.2	2	0.011	1.00E-12	0	268.4	3.70E-05
	DEC+J	-121.3	3	0.0079	2.20E-09	0.028	248.5	0.75
	DIVALIKE	-141.6	2	0.015	1.00E-12	0	287.3	2.90E-09
	DIVALIKE+J	-122.6	3	0.0082	1.00E-12	0.029	251.3	0.19
	BAYAREALIKE	-159.5	2	0.01	0.095	0	322.9	5.30E-17
	BAYAREALIKE+J	-123.8	3	0.0071	1.00E-07	0.032	253.6	0.059
B _{OC}	DEC	-172	2	0.012	2.00E-08	0	348.1	1.30E-07
	DEC+J	-155.3	3	0.0088	1.00E-12	0.037	316.6	0.91
	DIVALIKE	-180.9	2	0.016	1.00E-12	0	365.8	1.90E-11
	DIVALIKE+J	-157.7	3	0.0096	1.00E-12	0.037	321.4	0.084
	BAYAREALIKE	-200.6	2	0.015	0.12	0	405.2	5.20E-20
	BAYAREALIKE+J	-160	3	0.0082	1.00E-07	0.041	326.1	0.0079
B _{NG}	DEC	-173.3	2	0.012	2.00E-08	0	350.6	9.30E-08
	DEC+J	-156.2	3	0.0088	1.00E-12	0.037	318.4	0.91
	DIVALIKE	-180.5	2	0.016	4.00E-09	0	365	7.00E-11
	DIVALIKE+J	-158.5	3	0.0097	1.00E-12	0.037	323.1	0.087
	BAYAREALIKE	-200.7	2	0.015	0.12	0	405.4	1.20E-19
	BAYAREALIKE+J	-161	3	0.0082	1.00E-07	0.041	328	0.0075
C _{OC}	DEC	-184.4	2	0.014	0.012	0	372.8	4.90E-07
	DEC+J	-169.1	3	0.01	0.0073	0.041	344.1	0.82
	DIVALIKE	-191.8	2	0.019	0.02	0	387.6	2.90E-10
	DIVALIKE+J	-170.6	3	0.011	0.0074	0.041	347.2	0.18
	BAYAREALIKE	-205.7	2	0.019	0.13	0	415.4	2.70E-16
	BAYAREALIKE+J	-174.5	3	0.0095	0.011	0.048	355	0.0035
C _{NG}	DEC	-185.7	2	0.014	0.013	0	375.3	3.70E-07
	DEC+J	-170	3	0.01	0.0073	0.042	346.1	0.82
	DIVALIKE	-191.6	2	0.019	0.02	0	387.2	9.60E-10
	DIVALIKE+J	-171.5	3	0.011	0.0074	0.041	349.1	0.18
	BAYAREALIKE	-205.9	2	0.018	0.13	0	415.8	6.00E-16
	BAYAREALIKE+J	-175.5	3	0.0095	0.011	0.049	357.1	0.0033

4. Discussion

4.1. Overview

We used ultraconserved elements (UCEs) to examine the systematics and biogeography of one of the most biogeographically complex avian radiations, the whistlers and their allies (Aves: Pachycephalidae). Our study represents the first genome-wide dataset for the family. Although our phylogenetic analyses support the overall genus-level topology of previous studies (Norman et al., 2009b; Jönsson et al., 2010), we resolved key phylogenetic relationships within the early branching lineages of *Pachycephala*.

We found conflicting support for whether New Guinea, Australia, or Wallacea played the most significant roles as ancestral biogeographic areas during the origin of the family approximately 13.9–15.7 Ma (mean 14.8 Ma). The results of our ancestral area reconstruction were dependent on whether we treated New Guinea and Australia as one area or two, and whether we implemented a time constraint in the model. Our results highlight the difficulty in revealing the ancestral origin of crown-group whistlers because they likely originated in a geologically complex region at a time of upheaval and uncertainty. We discuss these results in light of recent biogeographic analyses within this group specifically, and higher-level passerines generally. We do not assert that our results conflict with prior studies, but we suggest that differences are the result of taxon sampling and assumptions of the biogeographic models.

4.2. Systematics

Higher-level relationships of whistlers based on Sanger data are well-supported (Jönsson et al., 2016) and our study corroborates this topology for the first time with genome-wide data. Whistlers comprise two main clades that we refer to as Clades 1 and 2. Clade 1 comprised the two species of *Pseudorectes* of New Guinea, which are sister to *Colluricincla*, whose five species are distributed widely throughout New Guinea and

Australia. Our analyses suggest that the traditionally recognized five species of *Colluricincla* are structured phylogenetically into two clades. The first clade comprises *C. tenebrosa* and *C. megarhyncha*, whereas the second clade comprises *C. boweri*, *C. woodwardi*, and *C. harmonica*. Recent phylogeographic analysis of *Colluricincla* recognized upwards of 11 species in this genus due to elevation of subspecies to species rank in *Colluricincla megarhyncha* sensu lato (Marki et al., 2018), which we did not sample densely. Our estimates of divergence times differ markedly from previous studies. For example, we estimated that Clade 1 diverged approximately 7.9–12.1 Ma (mean 9.9 Ma), and we estimated the crown age of *Colluricincla* as 5 Ma. This estimate is dramatically more recent than the 11.5 Ma crown age of *Colluricincla* estimated by Marki et al. (2018). We attribute the difference to our use of secondary fossil calibrations derived from Oliveros et al. (2019) versus mtDNA clock rates (Marki et al., 2018), as well as to the different sources of sequence data (UCEs versus mtDNA). We suspect that the true age of *Colluricincla* is closer to our estimated 5 Ma because recent studies on passerine birds that used fossil calibrations have coalesced on a more recent crown age of Passeriformes (Moyle et al., 2016; Oliveros et al., 2019).

Clade 2 comprised *Melanorectes*, *Coracornis*, and the hyper-diverse *Pachycephala*, and we estimated its crown age at approximately 11.0–13.5 Ma (mean 12.3 Ma), slightly older than our estimate of the crown age of Clade 1. The monotypic genus *Melanorectes* is sister to *Coracornis* + *Pachycephala*. We estimated the crown age of *Pachycephala* as approximately 8.2 Ma. *Pachycephala* was divided into three groups, which we have referred to as Early *Pachycephala*, and two clades comprising the Core *Pachycephala* (Clades A and B; Fig. 3). We found strong support in our likelihood and species trees that *P. nudigula* is sister to all other *Pachycephala* and that three Australian species from temperate southern Australian rainforests (*P. olivacea*) and semi-arid vegetation systems (*P. inornata*, *P. rufogularis*) comprised the next oldest clade within the genus. *Pachycephala nudigula* has long-been suspected of not having close extant relatives within *Pachycephala*; however, previous studies differ in its phylogenetic placement due to

low bootstrap support. Jönsson et al. (2010; 2014) found support for *P. olivacea* and *P. inornata* as the first branching lineages of *Pachycephala*, followed by *P. nudigula* as sister to all remaining taxa. Conversely, Andersen et al. (2014) found *P. nudigula* to be within the same clade as *P. olivacea* and *P. inornata*, and this clade was sister to all other *Pachycephala*. Indeed, our ASTRAL tree also suggested a level of uncertainty for the placement of *P. nudigula* (Fig. 2) given that the internode distance separating it from the rest of *Pachycephala* was short and that node support value was 97, warranting some caution about this result. Our results are the first to complete relevant taxon sampling with the inclusion of the restricted range *P. rufogularis* and confidently place these lineages within a well-supported phylogenetic framework.

The final clade that lies outside the Core *Pachycephala* comprised *P. schlegelii* and *P. soror*. These two species live in the New Guinea highlands and have overlapping elevational ranges (Beehler and Pratt, 2016), and their phylogenetic relationships are uncertain. Dumbacher et al. (2008) found *P. schlegelii* sister to *P. lorentzi* and these taxa were in turn sister to *P. soror*, but sparse taxon sampling likely obfuscated true relationships. *Pachycephala schlegelii* has been found as sister to the Core *Pachycephala* (Andersen et al., 2014), albeit without strong support, whereas other studies placed *P. schlegelii* sister to *P. soror* (Jönsson et al., 2010). Our concatenated and species-tree analyses agree with Jönsson et al. (2010) that these two taxa are sister species and that this pair represents the sister lineage to our Core *Pachycephala*.

The Core *Pachycephala* is composed of two clades (Clades A and B). Clade A contains taxa that belong to the golden whistler (*P. pectoralis* sensu lato) species complex. Our data support that *P. collaris*, distributed throughout the Louisiades Archipelago, is sister to the rest of this clade, in agreement with previous studies (Andersen et al., 2014; Jönsson et al., 2014). Our study adds to a growing body of literature that supports the Louisiades as a biogeographically unique archipelago. Like our study, others have shown that Louisiades-endemic lineages of birds (Andersen et al., 2014; 2015; Kearns et al., 2013; Pedersen et al., 2018) and squamates (Oliver et al., 2013; 2015) are sister to more widespread and species-rich clades, suggesting that this relatively small archipelago played an outsized role in the biogeographic history of these radiations. Within the sister group of *P. collaris*, two species-rich clades diverged, one with mostly Pacific species and one with mostly Australo-Papuan species. This topology differs from previous studies where relationships resembled a “staircase” instead of this balanced topology (Dumbacher et al., 2008; Jönsson et al., 2008). Within the Pacific clade, the Rennell whistler (*P. feminina*) was sister to *P. orioloides* of the Solomon Islands. The taxonomic relationship of *P. feminina* to other Pacific taxa has previously remained equivocal (Jönsson et al., 2010; Andersen et al., 2014); however, both of our concatenated and species-tree analyses supported *P. feminina* as sister to *P. orioloides*. Nodal support within the rest of the *P. pectoralis* species complex remained equivocal, suggesting that future efforts at resolving these relationships may require denser taxonomic and genomic sampling (Fig. 1).

Clade B comprised the geographically complex cohort of species that ranged from mainland SE Asia to Melanesia. The first branch in Clade B comprised the sister pair of Melanesian highland species, *P. richardsi* and *P. implicata*, which are endemic to the mountains of Bougainville and Guadalcanal islands, respectively. These taxa were reported to be upwards of 8% divergent in ND2 (Andersen et al., 2014) and our UCE data support a similarly deep divergence between these two species, that until recently were considered one species (Mayr and Diamond, 2001). This species pair was strongly supported as sister to all remaining *Pachycephala* species in Clade B. This sharply contrasts with previous studies (Andersen et al., 2014; Jönsson et al., 2014) where these species were well outside of the Core *Pachycephala* based on mtDNA. Clade B also contained the *P. rufiventris* and *P. philippinensis* species groups, as well as several New Guinean endemic species (e.g., *P. modesta*, *P. meyeri*, *P. lorentzi*, and *P. hypertyra*). Finally, *P. simplex* contains several geographically isolated populations that have variably been classified as separate species or one polytypic species (Beehler and Pratt, 2016). We

sampled only two named subspecies (*P. s. simplex* and *P. s. gagiensis*) and thus cannot render judgment on the classification of this group; however, our two samples were deeply diverged, which highlights the need for further investigation into the species limits within this group. Jönsson et al. (2014) also found a relatively deep divergence between three samples from New Guinea, Australia, and the Kai Islands. Clearly, this complex is intriguing and certainly worth further study.

4.3. Biogeography

The origin of Pachycephalidae occurred in the Mid-Miocene. When we coded Sahul as one region (Scenario A), the ancestral origin of Pachycephalidae was unequivocally inferred to occur there (Fig. 3). Sahul was also inferred as the ancestral area for most nodes across the whistler tree, which is unsurprising given present-day species richness of whistlers in this region. The only deviations from this pattern along the tree’s backbone were the nodes subtending two Wallacean endemics, *Coracornis* and *P. nudigula*, in which case the ancestral areas were either Sahul or Wallacea, or a combination of both. This analysis supported three colonizations of Oceania (twice in Clade A, once in Clade B), and independent colonizations of Wallacea (i.e., *P. rufiventris* complex) and the Philippines and Sundaland (i.e., *P. philippinensis* complex) from Sahul.

When we split Sahul into constituent regions (Australia and New Guinea; Scenarios B and C), our results at deeper nodes were equivocal and sensitive to the 15-Ma constraint placed on New Guinea. Conversely, our results at shallower nodes (e.g., Plio-Pleistocene divergences) were more robust to the implementation of a time-constraint. When we ran the analysis unconstrained, the influence of New Guinea was evident across the backbone of the whistler phylogeny (Fig. 4) and matched previous studies that allowed equal opportunity through time for New Guinea as an ancestral area (e.g., Jönsson et al., 2011; 2014). For example, the origin of whistlers was inferred overwhelmingly to be in New Guinea, as were the origins of Clades 1 and 2. Curiously, the Wallacean signal that was apparent in Scenario A was amplified in this analysis, suggesting that Wallacea was influential in the early diversification of Clade 2. This result was again likely owing to the modern distributions of two lineages endemic to Sulawesi (*Coracornis raveni*) and the Lesser Sundas (*P. nudigula*) that sit on long branches with deep nodes early in whistler evolution. The influence of Wallacea in the origin of songbirds was discussed in detail by Moyle et al. (2016), and indeed, we followed their constraints for the timing of the emergence of New Guinea in the subsequent analysis (Scenario C). The relevance of Wallacea in the early diversification of songbirds has also been suggested for honeyeaters, in which the first branch is the Sulawesi endemic genus, *Myza* (Joseph et al., 2014b; Marki et al., 2017; Andersen et al., 2019).

When we constrained New Guinea as a possible ancestral area before 15 Ma, we inferred Wallacea as the most probable origin of the Pachycephalidae (Fig. 5). The biogeographic analysis assigned about 50% of the likely ancestral area of crown Pachycephalidae to Wallacea and another 25% to Australia; the remaining 25% were assigned to mixed areas. The first split in Pachycephalidae leads to Clade 1. We inferred this clade to have an origin in New Guinea approximately 9.9 Ma, but with lesser probability in Australia or New Guinea and Australia combined. The lineage that leads to modern *Pseudorectes* appears to have diversified from *Colluricincla* and occupied New Guinea more than 10 Ma where it remains today, whereas *Colluricincla* diversified more broadly across Australia and New Guinea. We inferred Clade 2 to have an origin in Wallacea approximately 12.3 Ma. Wallacea is not thought to be a center of origin for songbirds, but Moyle et al. (2016) offered a new interpretation of the biogeographic importance of this region. Around the mid-Miocene, the Sula Spur was colliding with proto-Sulawesi, partially causing the uplift of Wallacea. This geologic event created new islands and offered stepping-stones from Australia through Wallacea and into Sundaland (Hall, 1998; 2013; Moyle et al., 2016). This new “out of Australia” route offered an explanation that did not invoke New Guinea as a center of origin before that landmass came into prominence,

thus relying on Australia as the geographic origin of songbirds. Here, we find similarities with the evolutionary history of Pachycephalidae to the broader pattern of early songbird diversification. Namely, Wallacea played an important role early in the group's evolution. These results suggest that properly interpreting the geologic history of New Guinea—in particular, the timing of orogeny and subaerial land formation (van Ufford and Cloos, 2005; Toussaint et al., 2014)—is paramount to our understanding of the biogeographic history of birds in this region. This is especially true for a group like whistlers for which New Guinea is a modern-day hotspot of species richness.

We inferred the origin of *Pachycephala* in the late Miocene, about 7.5 Ma. Our divergence estimates suggested that the bulk of *Pachycephala* species diversified in the Plio-Pleistocene. These estimates are about 2.7 times older than one previous estimate, in which the genus was estimated to have diversified in the late Pliocene, approximately 2.8 Ma (Jönsson et al., 2010). Node ages were not reported by Jönsson et al. (2014), despite reporting having estimated divergence times. These differences in node-age estimates highlight the variability in these analyses depending on sampling and choice of divergence time estimation methods (dos Reis and Yang, 2013).

Biogeographically, our inference of the ancestral area of *Pachycephala* was equivocal. Our results from Scenario B assigned approximately 55% of the likely ancestral area to Wallacea and 15% to New Guinea. Our results from Scenario C, on the other hand, assigned about 38% of the probability to Australia, about 13% to New Guinea, and about 20% to Oceania. However, previous ancestral range analyses have suggested that the genus originated in Australo-Papua, for which we found support in our Scenario A with those regions combined.

The biogeographic patterns within Clade 2 were complex. After the early branching lineages diversified into present-day temperate and semi-arid southern Australia (*P. olivacea*, *P. rufogularis*, and *P. inornata*) and New Guinea (*P. soror* and *P. schlegelii*), our time-constrained analysis (Fig. 5) supported a strong influence of Oceania in the early diversification of the ancestral node leading to subclades A and B. In particular, the node leading to these clades, as well as the ancestral node of Clade A, were inferred to have an origin in Oceania. Jönsson et al. (2014) also inferred a Pacific origin of the *P. pectoralis* complex (our Clade A). This pattern, while intriguing, is perhaps unsurprising given the species richness within the *P. pectoralis* species complex (i.e., Clade A) that is distributed across Oceania and Australia. Clearly, there is a Pacific clade of “*pectoralis*” whistlers that is distributed across the Bismarck (*citreogaster*), Solomon (*orioloides*, *feminina*), Fijian (*vitiensis* and *graeffii*), Samoan (*flavifrons*) and Tongan (*jacquinoti*) archipelagos. However, three other lineages within Clade A also occur in Oceania and are worth noting. First, *P. melanura* is a mangrove specialist that occurs in coastal northern Australia, SE New Guinea, and the Bismarcks, and it resides in a clade with other taxa from New Guinea and Wallacea (*macrorhyncha*, *mentalis*, *balim*, and *aurea*). Second, taxa from Vanuatu (*chlorura*) and the Loyalty group (*littayei*) were sister to the Australian *pectoralis* group and not closely related to taxa from elsewhere in Oceania. That the Australian *pectoralis* taxa are embedded deeply within the *pectoralis* complex suggests that the Australian taxa are a product of back-colonization from Oceania. This pattern is also known from at least monarchs (Filardi and Moyle, 2005). Third, *P. collaris* of the Louisiade Archipelago was the sister lineage to the rest of Clade A. Previous studies have shown that the Louisiades are biogeographically unique (Andersen et al., 2014; 2015; Kearns et al., 2013; Pedersen et al., 2018) and therefore we explored both hypotheses. Given its placement in this clade and its curious distribution in an oceanic archipelago that is geographically proximate to mainland New Guinea, we explored two different biogeographic coding schemes (Oceania and New Guinea). In our analysis with this taxon coded as occurring in New Guinea, the probability of the origin of Clade A was assigned to New Guinea with about 80% and 60% probability for Scenarios B and C, respectively, up from <5% when we coded *P. collaris* as occurring in Oceania (see insets of Figs. 4, 5).

Our study corroborates the notion that *Pachycephala* independently

colonized disparate geographic areas, including Oceania, the Philippines, and Sundaland (Galbraith, 1956; Jönsson et al., 2014). At least three independent dispersal events led to the colonization of the Pacific by *Pachycephala* whistlers, at least once and possibly as many as three times in Clade A—including back-colonization to Australia—and twice more in Clade B (*P. implicata* and *P. richardsi*, and *P. rufiventris*). There appears to have been one wave into the Philippines that subsequently invaded Sundaland, bypassing Wallacea. This clade comprises the *P. philippinensis* species complex and warrants more detailed sampling to better assess species limits (Hosner et al., 2018).

5. Conclusions

The complex biogeography of the whistlers has confounded researchers for decades. Their complexity of geographic distributions is ideal for studying processes of colonization and diversification on island systems. With our phylogenetic analysis of UCEs, we clarified certain taxonomic relationships and discovered that Wallacea may have played a larger role in the evolutionary history of whistlers than previously thought. However, our UCE dataset could not fully resolve the whistler tree, nor could we rule out the relative importance of New Guinea as an early influence in whistler diversification. Indeed, the very biogeographic complexity that makes this an exciting group in which to study historical biogeography also makes interpretation difficult. That in turn is because our results were often equivocal due to the region's dynamic and still uncertain geological history. Future studies should focus sampling strategies at the tips of the tree using genome-scale data, including all named subspecies and multiple island populations, to examine population-level dynamics of gene flow within these clades and to better inform phylogenetic resolution across the whistler tree.

CRedit authorship contribution statement

Serina S. Brady: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **Robert G. Moyle:** Resources, Writing – review & editing, Funding acquisition. **Leo Joseph:** Resources, Writing – review & editing. **Michael J. Andersen:** Conceptualization, Formal analysis, Resources, Data curation, Writing – review & editing, Visualization, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data Accessibility

Illumina raw reads are deposited in NCBI Sequence Read Archive under BioProject PRJNA774817. Config files, UCE contigs, sequence alignments in phylip format, and tree files are archived in zip format as a Dryad repository (<https://doi.org/10.5061/dryad.4mw6m90bn>).

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