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Diversification and biogeography of an Indo-Pacific bird radiation (Pachycephalidae)

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DIVERSIFICATION AND BIOGEOGRAPHY OF AN INDO-PACFIC BIRD RADIATION (PACHYCEPHALIDAE)

by

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THESIS

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DIVERSIFICATION AND BIOGEOGRPAHY OF AN INDO-PACIFIC BIRD RADIATION (PACHYCEPHALIDAE)

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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. Pachycephalidae is one of the most complex avian radiations spanning the vast archipelagos of the Indo-Pacific, making it an ideal group to study the patterns and processes of diversification on islands. Here, we present a robust phylogenetic hypothesis for all five genera within Pachycephalidae, based on thousands of ultraconserved elements (UCEs) generated with a target-capture approach and high-throughput sequencing. We clarify certain taxonomic relationships within *Pachycephala* and discover that Wallacea plays a much larger role in pachycephalid evolutionary history than previously thought. This work further refines our understanding of one of the regions' most enigmatic bird lineages and adds to our growing knowledge about the patterns and processes of diversification in the Indo-Pacific.

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Chapter 1

Introduction

Islands provide ideal settings to study evolution and biogeography due to their geographic isolation with discrete boundaries and relatively well-known geological histories. Generation of biodiversity on 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). In the Indo-Pacific, true species diversity of birds is masked by decades of over-lumping phenotypically distinct, allopatric island populations (sensu Mayr, 1942). However, recent advances in molecular phylogenetics and in our understanding of the speciation process has 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 from Wallacea and the Greater Sundas to Melanesia and Polynesia. This region has complex geologic histories. Vast archipelagos were created from the Philippines to Melanesia in response to the collision of the Australo-Papuan plate and the Ontong Java plateau near the end of the Miocene (Hall 1998; 2000; 2009). These new islands—for which connectivity has waxed and waned with eustatic sea level fluctuation—provided new opportunities for species to colonize and diversify (Esselstyn et al. 2009; Jønsson et al. 2011). Molecular studies of birds and mammals have shown that current species distributions are influenced by long-distance dispersal and back colonization, geologic processes, and Plio-Pleistocene sea-level changes (Filardi and Moyle 2005; Heaney et al. 2005; Irestedt et al. 2008; Jønsson et al. 2018; Esselstyn et al. 2009). 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 (Jønsson et al. 2011; 2017; Moyle et al. 2016). Although the orogeny of New Guinea is uncertain, it is currently assumed that it emerged during the Miocene (Hall 2005; van Ufford et al. 2005).

The whistlers and allies (Aves: Pachycephalidae) are one of the most biogeographically complex avian radiations in the Indo-Pacific. At present, the family spans five genera, 52 species, and 202 subspecific taxa (Boles, 2019). Conversely, the IOC World Bird List 9.1 recognizes 57 species, and 164 named taxa (Gill and Donsker, 2019). The discrepancy in numbers of species reflect the vague and complex nature of pachycephalid taxonomy. Sibley and Ahlquist (1990)—based on DNA-DNA hybridization—included *Daphoenositta, Mohoua, Oreoica, Falcunculus, Pitohui, Rhagologus, Pachycephala, Colluricincla,* and several monotypic genera, *Pachycare, Hylocitrea, Eulacestoma,* and *Coracornis* within the family. The past three decades of molecular systematics based on DNA sequence data have brought much clarity to whistler taxonomy, especially with respect to genus membership in the family. For example, *Pitohui* was found to be paraphyletic: true *Pitohui* as oriolids (Oriolidae) and other taxa as monotypic lineages within Pachycephalidae. Norman et al. (2009) used DNA sequence data from two nuclear gene regions and the mitochondrial cytochrome *b* gene for 40 species of the core Corvoidea. Their findings supported Dumbacher et al. (2008): the core pachycephaline lineages comprised *Pachycephala, Colluricincla,* some *Pitohui* (now *Pseudorectes* and *Melanorectes*), and *Falcunculus,* but they could not resolve the remaining four divergent lineages (*Daphoenositta, Mohoua, Oreoica, Rhagologus*). Pachycephalidae is sister to Oriolidae and *Falcunculus* is not a whistler, but rather part of a newly defined clade, Falcunculidae and Oreoicidae (Moyle et al. 2016; Oliveros et al. 2019).

Our current understanding is that Pachycephalidae is composed of five genera: *Pseudorectes, Colluricincla, Melanorectes, Coracornis,* and *Pachycephala*. The most species-rich genus is *Pachycephala,* containing about 70% of the taxa within the family. Whistler diversity is centered in New Guinea (four genera, 18 species) and Australia (two genera, 13 species) with taxa spanning from Southeast Asia to Oceania. Given this region's species richness, it is unsurprising that previous biogeographical analyses suggested that the origin of the family is Australo-Papuan (Jønsson et al. 2010; 2014).

To date, no study has leveraged genome-scale data to address the phylogeny and biogeography of whistlers, and all have relied on mitochondrial clocks to calibrate divergence times across the clade (Jønsson et al. 2010; Marki et al. 2018). Furthermore, we are lacking a phylogenetic examination of the entire family while various taxa within the family have been partially examined (Mayr 1963; Sibley and Ahlquist 1982; 1990; Barker et al. 2004). Although these approaches have been sufficient to elucidate certain relationships within the tree, many others remain unresolved. Here, we use ultraconserved elements (UCEs; Faircloth et al. 2012) to infer the whistler phylogeny and estimate divergence times based on secondary fossil-calibrated nodes from the literature. UCEs have phylogenetic resolving power at varying depths within the avian tree of life (McCormack et al. 2013; Smith et al. 2014). We use our tree to reconstruct ancestral areas and study macroevolutionary dynamics of this enigmatic group of birds. This study provides an important contribution to understanding the biogeographical patterns that have occurred in this complex region.

Chapter 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 two species recognized by the International Ornithological Congress 9.1 (*Coracornis sanghirensis* and *Pseudorectes incertus*; Gill and Donsker 2019). For *Pachycephala*, we sampled one individual from every species. Approximately 78% of samples were obtained from fresh muscle tissue with associated museum voucher specimens; 22% of the samples were derived from toepad clippings. We downloaded and incorporated in our dataset UCE data from seven outgroup and 11 ingroup taxa that were sequenced for prior studies (Moyle et al. 2016; Oliveros et al. 2019; Table 1).

Table 1. Samples used in this study. Institutional abbreviations: AMNH, American Museum of Natural History; KUNHM, University of Kansas Biodiversity Institute; ANWC, Australian National Wildlife Collection; LSUMZ, Louisiana State University Museum of Natural Science; YPM, Yale Peabody Museum; UWBM, University of Washington Burke Museum of Natural History and Culture; ANSP, Academy of Natural Science; CAS, California Academy of Science; SNZPTKP, Smithsonian National Zoological Park; WAM, Western Australia Museum; AM, Australian Museum; and DMNH, Delaware Museum of Natural History.

											Areas for BioGeoBEARS							
											A	B	C	D	E	F	G	
	Taxon	Institution	Idenifier	Source	Location	Platform	NCBI Accession	Contigs	Mainland	Sundaland (incl Palawan)	Wallacea	Philippines+Palau	Australia	New Guinea	Oceania
Outgroups	*Vireo solitarius*	KUNHM	25186	-	North America	GenBank	SAMN04301800	4189	X						
	Psaphodes cristatus	KUNHM	6205	-	Australia	GenBank	SAMN10450353	4086					X	X	
	Pteruthius aeralatus	KUNHM	17806	-	Malaysia: Borneo	GenBank	SAMN04301781	4124	X	X					
	Sphecotheres viridis	KUNHM	10752	-	Lesser Sundas	HiSeq 2500	this study; TBD	3990			X		X	X	
	Oreocharis arfaki	KUNHM	16440	-	Papua New Guinea	GenBank	SAMN04301753	4445						X	
	Erpornis zantholeuca	KUNHM	27942	-	Vietnam	GenBank	SAMN10450298	4209	X	X					
	Oriolus chinensis	KUNHM	10450	-	China	GenBank	SAMN04301755	4587	X	X	X	X	X	X	
	Pitohui dichrous	KUNHM	12200	-	Papua New Guinea	GenBank	SAMN10450344	4432						X	
Ingroups	*Colluricincla boweri boweri*	ANWC	B28851	Tissue	Australia	HiSeq 3000	this study; TBD	4373					X		
	Colluricincla harmonica brunnea	ANWC	B56031	Tissue	Australia	HiSeq 3000	this study; TBD	4381					X	X	
	Colluricincla megarhyncha griseata	ANWC	B56099	Tissue	New Guinea	HiSeq 3000	this study; TBD	4277					X	X	
	Colluricincla tenebrosa	KUNHM	12108	Tissue	New Guinea	HiSeq 3000	this study; TBD	4350						X	
	Colluricincla woodwardi woodwardi	ANWC	B55216	Tissue	Australia	HiSeq 3000	this study; TBD	4306					X		
	Coracornis raveni	AMNH	299556	Toepad	Sulawesi	HiSeq 3000	this study; TBD	4447			X				
	Melanorectes nigrescens nigrescens	ANWC	B52558	Tissue	New Guinea	HiSeq 3000	this study; TBD	4375						X	
	Pseudorectes ferrugineus	KUNHM	9610	Tissue	New Guinea	HiSeq 2500	this study; TBD	4134						X	
	Pachycephala albiventris crissalis	KUNHM	21019	Tissue	Philippines	HiSeq 3000	this study; TBD	4161				X			
	Pachycephala arctiorquis arctiorquis	WAM	25087	Tissue	Lesser Sundas	HiSeq 3000	this study; TBD	4275			X				
	Pachycephala aurea	AMNH	302234	Toepad	New Guinea	HiSeq 3000	this study; TBD	4176						X	
	Pachycephala balim	AMNH	341498	Toepad	New Guinea	HiSeq 3000	this study; TBD	4296						X	
	Pachycephala caledonica	ANWC	B45791	Tissue	New Caledonia	HiSeq 2500	this study; TBD	**3601**							X
	Pachycephala chlorura litayei	YPM	71205	Toepad	Vanuatu	HiSeq 3000	this study; TBD	4404							X
	Pachycephala cinerea pluteni	KUNHM	12751	Tissue	Philippines: Palawan	HiSeq 3000	this study; TBD	4126	X	X	X	X			
	Pachycephala citreogaster goodsoni	KUNHM	5615	Tissue	New Guinea	HiSeq 3000	this study; TBD	4283							
	Pachycephala collaris collaris	CAS	96792	Tissue	Louisiade Archpelgo	HiSeq 3000	this study; TBD	4301						X	
	Pachycephala feminina	AMNH	DOT6601	Tissue	Rennell Island	HiSeq 2500	this study; TBD	4271							X
	Pachycephala flavifrons flavifrons	KUHNM	104129	Toepad	Samoa	HiSeq 3000	this study; TBD	2494							X
	Pachycephala fulvotincta javana	KUNHM	31158	Tissue	Lesser Sundas	HiSeq 3000	this study; TBD	4202		X	X				
	Pachycephala graeffii	KUNHM	22555	Tissue	Fiji Islands	HiSeq 2500	this study; TBD	4000							X
	Pachycephala griseonota cinerascens	YPM	76041	Toepad	Moluccas	HiSeq 3000	this study; TBD	3380			X				
	Pachycephala homeyeri winchelli	KUNHM	15340	Tissue	Philippines	HiSeq 3000	this study; TBD	4082				X			
	Pachycephala hyperythra hyperythra	KUNHM	31363	Tissue	New Guinea	HiSeq 3000	this study; TBD	4343						X	
	Pachycephala hypoxantha hypoxantha	LSUMZ	36296	Tissue	Borneo	HiSeq 3000	this study; TBD	4266		X					
	Pachycephala implicata implicata	KUNHM	32803	Tissue	Solomon Islands: Guadalcanal	HiSeq 3000	this study; TBD	4277							X
	Pachycephala implicata richardsi	AMNH	222850	Toepad	Solomon Islands: Bougainville	NovaSeq 6000	this study; TBD	4423							X
	Pachycephala inornata inornata	ANWC	B52274	Tissue	Australia	HiSeq 3000	this study; TBD	4270					X		
	Pachycephala jacquinoti jacquinoti	DMNH	11332	Toepad	Tonga	HiSeq 3000	this study; TBD	4504							X
	Pachycephala johni	AMNH	658812	Toepad	Moluccas	HiSeq 3000	this study; TBD	3694			X				
	Pachycephala lanioides carnarvoni	KUNHM	6195	Tissue	Australia	HiSeq 3000	this study; TBD	4296					X		
	Pachycephala leucogastra meeki	SNZPTKP	TKP2004067	Tissue	New Guinea: Rossel Island	HiSeq 3000	this study; TBD	4305						X	
	Pachycephala lorentzi	AMNH	765964	Toepad	New Guinea	HiSeq 3000	this study; TBD	4355						X	
	Pachycephala macrorhyncha	WAM	25185	Tissue	Lesser Sundas, Moluccas	HiSeq 2500	this study; TBD	4076			X				
	Pachycephala melanura dahli	KUNHM	27797	Tissue	New Guinea	HiSeq 3000	this study; TBD	4393					X	X	X
	Pachycephala mentalis mentalis	YPM	76043	Toepad	Moluccas	HiSeq 3000	this study; TBD	4378			X				
	Pachycephala meyeri meyeri	ANSP	132275	Toepad	New Guinea	HiSeq 3000	this study; TBD	4362						X	
	Pachycephala modesta modesta	KUNHM	4736	Tissue	New Guinea	HiSeq 3000	this study; TBD	4191						X	
	Pachycephala monacha lugubris	YPM	128737	Toepad	New Guinea	HiSeq 3000	this study; TBD	3641						X	
	Pachycephala nudigula nudigula	WAM	22678	Tissue	Lesser Sundas	HiSeq 3000	this study; TBD	4282			X				
	Pachycephala occidentalis occidentalis	ANWC	B31698	Tissue	Australia	HiSeq 3000	this study; TBD	4188					X		
	Pachycephala olivacea olivacea	ANWC	B46097	Tissue	Australia	HiSeq 3000	this study; TBD	4182					X		
	Pachycephala orioloides centralis	UWBM	66075	Tissue	Solomon Islands	HiSeq 3000	this study; TBD	4354							X
	Pachycephala orpheus orpheus	WAM	23880	Tissue	Lesser Sundas	HiSeq 3000	this study; TBD	4318			X				
	Pachycephala pectoralis fuliginosa	ANWC	B43329	Tissue	Australia	HiSeq 3000	this study; TBD	4225					X		
	Pachycephala phaionota	WAM	24736	Tissue	Moluccas	HiSeq 3000	this study; TBD	4329			X			X	
	Pachycephala philippinensis illex	KUNHM	10843	Tissue	Philippines	HiSeq 3000	this study; TBD	3942				X			
	Pachycephala rufiventris	UWBM	57510	Tissue	Australia, New Caledonia	HiSeq 3000	this study; TBD	4073					X		X
	Pachycephala rufogularis rufogularis	ANWC	B38096	Toepad	Australia	HiSeq 3000	this study; TBD	4396					X		
	Pachycephala schlegelii schlegelii	KUNHM	121594	Tissue	New Guinea	NovaSeq 6000	this study; TBD	4027						X	
	Pachycephala simplex gagiensis	WAM	26551	Tissue	Indonesia	HiSeq 3000	this study; TBD	4175			X		X	X	
	Pachycephala simplex simplex	ANWC	B33535	Tissue	Australia	HiSeq 3000	this study; TBD	4254					X		
	Pachycephala soror soror	KUNHM	7888	Tissue	New Guinea	HiSeq 3000	this study; TBD	4289						X	
	Pachycephala sulfuriventer sulfuriventer	AMNH	12575	Tissue	Sulawesi	HiSeq 3000	this study; TBD	4263			X				
	Pachycephala tenebrosa tenebrosa	KUNHM	23676	Tissue	Palau Islands	HiSeq 3000	this study; TBD	4359				X			
	Pachycephala vanikorensis	KUNHM	19410	Tissue	Santa Cruz Islands	HiSeq 2500	this study; TBD	4284							X
	Pachycephala vitiensis kandavensis	KUNHM	24411	Tissue	Fiji Islands	HiSeq 3000	this study; TBD	4393							X
	Pachycephala youngi	ANWC	B29282	Tissue	Australia	HiSeq 3000	this study; TBD	4261					X		

2.2 Genetic Analysis and Genomic Preparation

We extracted genomic DNA from tissue samples following the Qiagen Dneasy extraction kit manufactures protocol. For toepad samples, we used a modified protocol adapted from McCormack et al. (2016). We rinsed toepad clippings with 250 uL of 100% ethanol and rehydrated with UV-ed molecular grade water. To ensure full digestion, we finely cut toepads and added 30 uL of Protinase K and Dithiothreitol (DTT; 0.1 g in 1000 uL ddH20) to each sample. We monitored for contamination with the use of a negative control and all samples were quantified for DNA concentrations using a Qubit 3.0 Flourometer (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. Samples were washed with AMPure XP beads, indexed using the iTruStub dual indexing system (Glenn et al. 2019), amplified via PCR, and enriched resulting in equal concentrations for each sample. We used the Mycroarray Mybaits probe kit to target 5,060 UCE loci and pooled six to eight dual-indexed tissue libraries (4–6 toepad libraries), which were amplified and bioanalyzed prior to sequencing. Sequencing was performed at the University of Oklahoma Medical Research Foundation on an Illumina HiSeq 3000 and 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 2015). We trimmed low-quality bases and adaptor sequences from raw sequence

reads using illumiprocessor 1 (Faircloth 2013; Bolger et al. 2014). We assembled contigs from cleaned reads with trinity 2.0.6 (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 0.91 (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 that had at least 50 of 66 taxa present to produce our maximum likelihood tree (Figure 1).

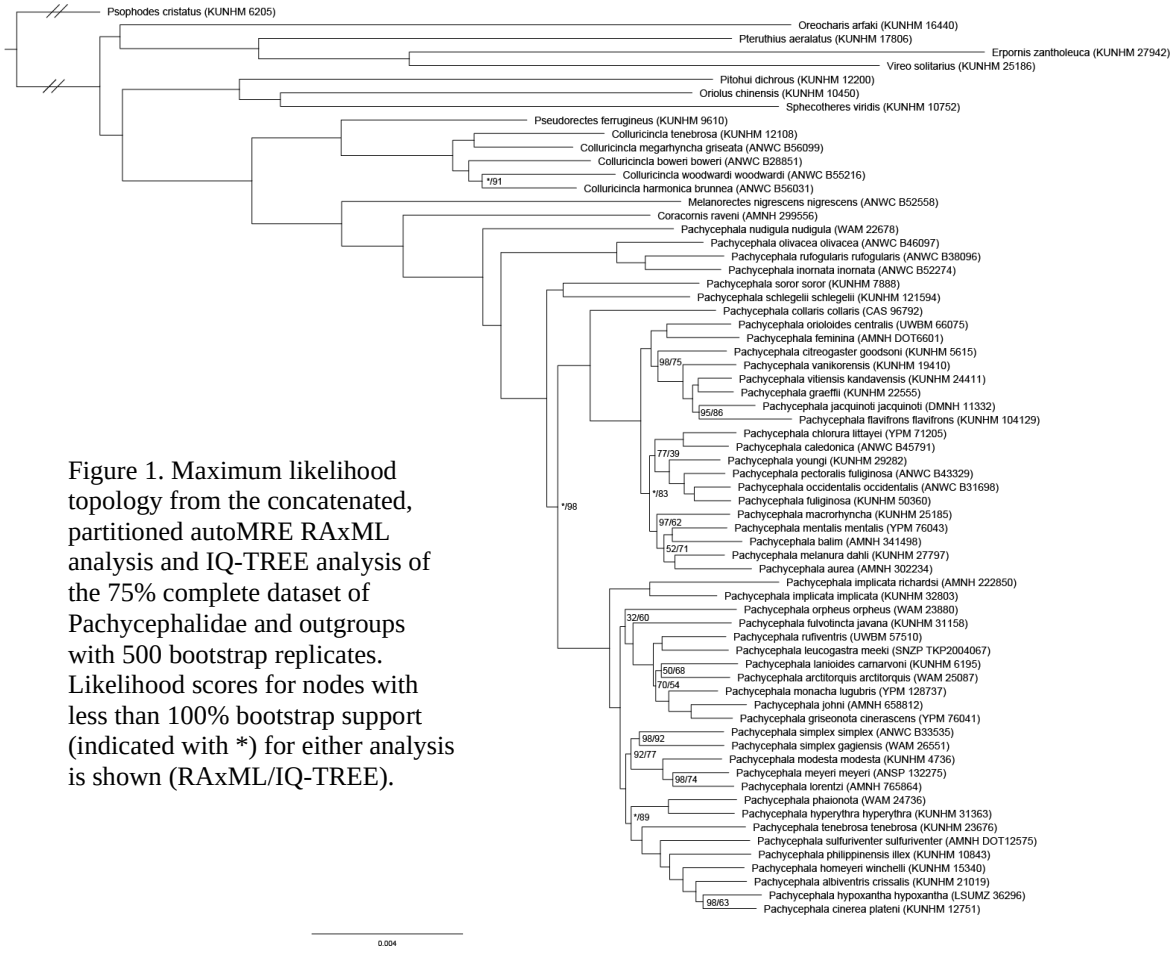


Figure 1. Maximum likelihood topology from the concatenated, partitioned autoMRE RAxML analysis and IQ-TREE analysis of the 75% complete dataset of Pachycephalidae and outgroups with 500 bootstrap replicates. Likelihood scores for nodes with less than 100% bootstrap support (indicated with *) for either analysis is shown (RAxML/IQ-TREE).

Using PartitionFinder 2.1.1 (Lanfear 2014), the best fit partitioning scheme for the concatenated dataset was determined to be a general time reversible model of nucleotide rate substitutions with gamma distributed rates among sites (GTR+G). We then performed

maximum likelihood tree searches of the partitioned, concatenated data matrices using RaxML 8.2.10 (Stamatakis 2006) and IQ-TREE 1.6.10 (L.-T. Nguyen et al. 2015) on the CIPRES gateway. IQ-TREE often achieves higher likelihood scores with less computing time than RaxML and uses the best priors determined by PartitionFinder for each set of loci (L-T Nguyen et al. 2015). The topologies produced from both methods were identical, therefore we present a single tree with each methods likelihood score, respectively (Figure 1).

Gene trees and species trees have been known to differ in topology due to missing data, masking potential issues within concatenated datasets. Therefore, we estimated species trees from independent gene trees in ASTRAL-III (Mirarab et al. 2014; Zhang et al. 2018) using PHYLUCE scripts for both matrices (Figure 2). This program constrains the search space by using a set of bipartitions and is statistically consistent under the multi-species coalescent model (Mirarab et al. 2014). Additionally, ASTRAL-III can run on very large datasets with a higher degree of accuracy than SVDQuartets (Chou et al. 2015).

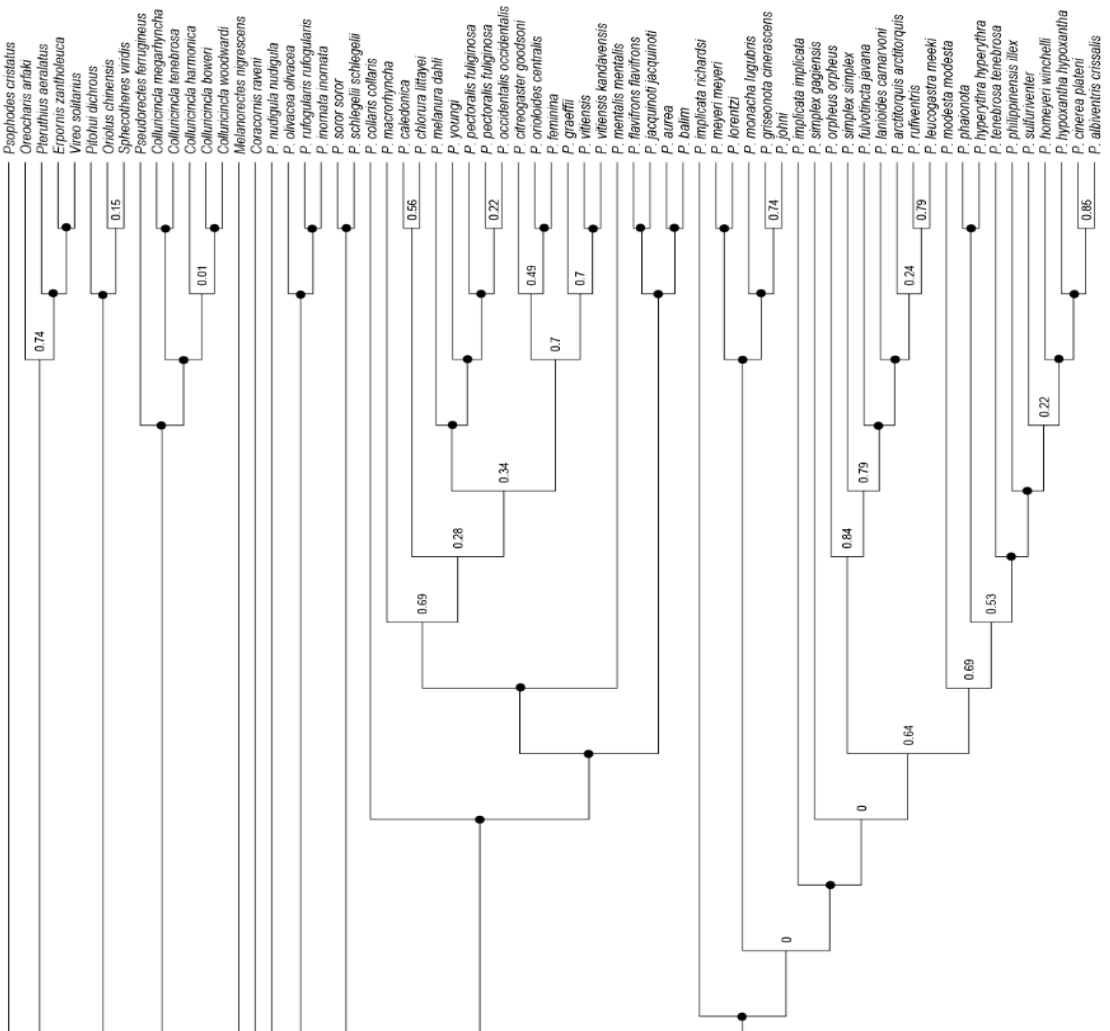


Figure 2. ASTRAL-III species tree topology of the 75% complete phylogeny. Evaluated with 100 bootstraps; black circles indicate 100% bootstrap support.

2.4 Time-calibration

We used BEAST2 2.5.2 (Bouckaert R. et al. 2014) to infer a time-calibrated tree. We used a birth-death tree prior, a relaxed clock log normal 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. We ran MCMC chains for 20 million generations and sampled trees every 10,000 generations. We visualized traces of log files in TRACER 1.7.1 (Rambaut A, Drummond AJ. 2007) to assess convergence of individual runs and we ensured ESS values exceeded 200. We used LogCombiner 2.5.2 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 2.5.2 (Bouckaert R. 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 used two secondary calibration points from the literature to estimate divergence time (Oliveros et al. 2019). The first dated split was between *Psophodes* and the remaining sampled taxa, 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: *Erpornis, Oreocharis, Oriolus, Pitohui, Psophodes, Pteruthius, Sphecotheres*, and *Vireo* with a normal distribution, sigma of 0.5, and a mean date of 14.6 Ma (CI = 13.8–15.6).

2.5 Biogeographic and Macroevolutionary Analysis

Using the R package BioGeoBEARS, we inferred the biogeographic history of phylogenies 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 and without the +j parameter, which allows for long distance dispersal and founder-event speciation and assessed model fitness with AIC. The DEC +j model has a tendency to explain all biogeographical variation through the jump parameter (Ree and Sanmartín 2018); however, we believe the +j parameter is relevant to Pachycephalidae, and thus we justify our use of it, because many whistlers are known for long-distance dispersal to oceanic island archipelagos.

We coded biogeographic regions for all tips according to their modern-day distributions (Boles 2019). We delineated seven geologically informed 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) Australia, F) New Guinea, and G) Oceania (Bismarcks, Melanesia, Polynesia; Table 1 and Figure 3). The maximum range size of an outgroup taxa was six, accounting for the widespread outgroup *Oriolus*, for which there is a single, vagrant record from Oceania (New Britain; Dutson 2011). The maximum range size of the ingroup taxa was four, accounting for *Pachycephala cinerea*. We ran two biogeographic analyses—following methods described by Moyle et al. (2016)—with and without a geological constraint model for the emergence of New Guinea at 15 Ma (van Ufford et al. 2005; Hill et al. 2003). Additionally, we ran the time-constrained analysis with *Pachycephala collaris*, found in the Louisiade Archipelago, coded for Oceania as well as for New Guinea.

We estimated evolutionary rate regimes and calculated speciation rates across the whistler tree using Bayesian analysis of macroevolutionary mixtures, BAMM 2.5 (Rabosky 2014). BAMM detects and quantifies heterogeneity in evolutionary rates by using reversible

jump MCMC to explore candidate models of lineage diversification and trait evolution (Rabosky 2014). We visualized evolutionary rate regime shifts and diversification rates through time using 'Bammtools' 2.1 (Rabosky et al. 2014). Because posterior estimates of the number of diversification-rate shifts are sensitive to the choice of prior (Mitchell and Rabosky 2016; Moore et al. 2016), we explored a range of prior values in our analyses (expectedNumberOfShifts = 0.1, 0.5, 1.0, 2.0, 5.0). We followed additional guidelines for conducting and interpreting BAMM analyses (http://bamm-project.org), including assessing MCMC convergence, exploring the credible set of shift configurations, and computing marginal odds ratios (Shi and Rabosky 2015). We refer readers to the ongoing debate over BAMM for further information (Moore et al. 2016; Rabosky et al. 2017).

Chapter 3

Results

3.1 Dataset

We recovered an average of 7.87 million reads per individual after cleaning raw reads. We recovered an average of 4207 loci (range: 2494–4587) with a mean contig length of 851 bp (Table 1). Our 75% complete matrix (i.e., where the percentage represented the number of taxa present per UCE alignment) had 4226 loci and 3,486,406 bp, of which 484,700 bp were variable characters and 153,149 bp were parsimony-informative characters. UCE raw reads are registered as NCBI BioProject ID (TBD).

3.2 Phylogenetic relationships

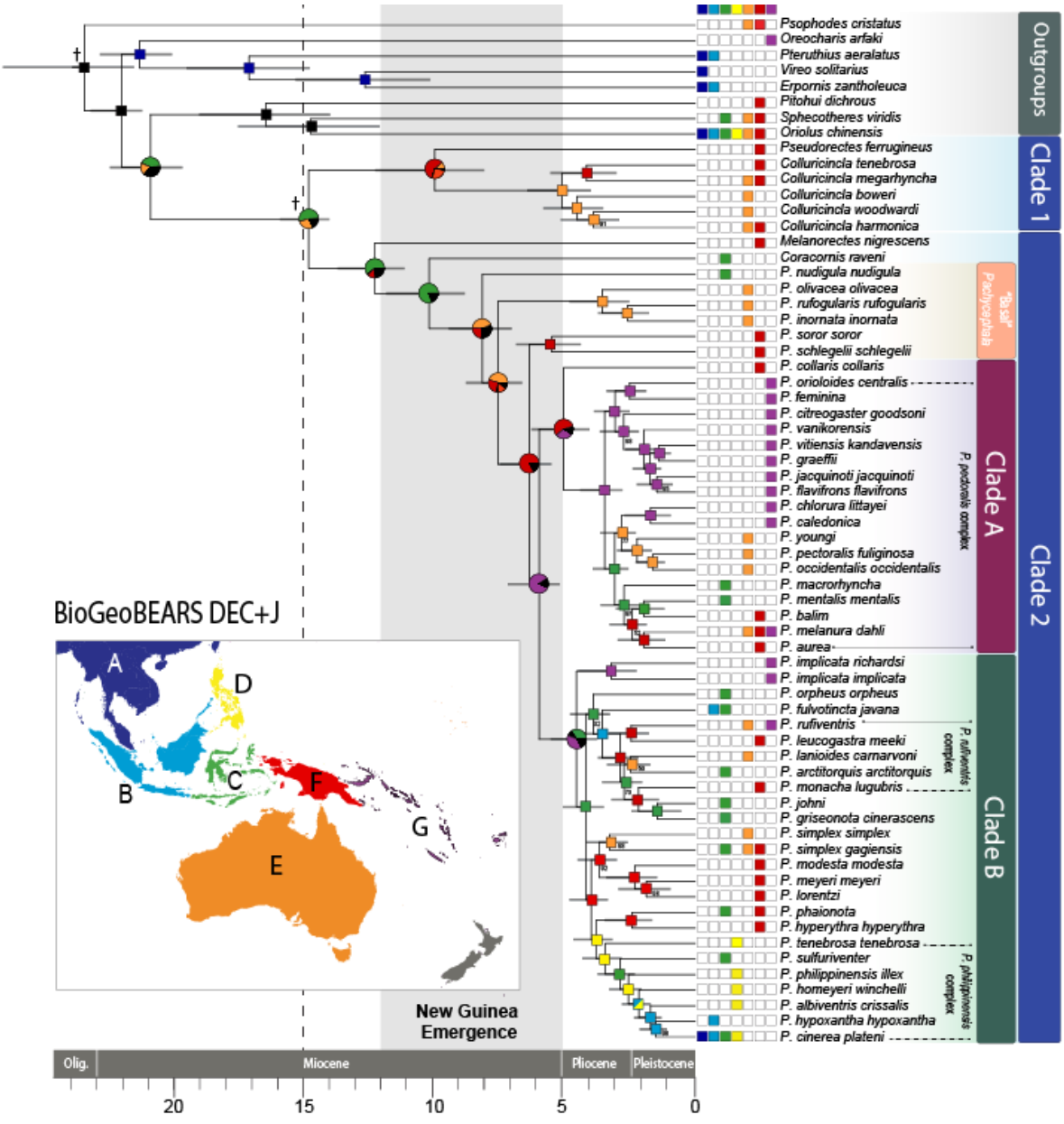
We recovered a well-resolved, dated phylogeny of Pachycephalidae. Most nodes had 100% bootstrap support in both the autoMRE RaxML and IQ-TREE (Figure 1). Additionally, most relationships were corroborated in our ASTRAL species tree, with varying levels of support (Figure 2). With our dataset, we were able to resolve some previously uncertain nodes deeper in the tree; conversely, the node support for the rapid radiations at the tips remain equivocal.

The family comprises two main clades: (1) *Pseudorectes* + *Colluricincla* is the sister clade of (2) *Melanorectes* + (*Coracornis* + *Pachycephala*; Figure 3). Within *Pachycephala*, there were several early branching lineages (hereafter dubbed "Basal *Pachycephala*"). *Pachycephala nudigula* was unequivocally the first branch of *Pachycephala* and therefore sister to all other members of the genus. *Pachycephala olivacea*, *P. inornata*, and *P. rufogularis* comprise a clade that was sister to all remaining *Pachycephala* taxa. The next

lineage comprised the sister pair of *P. schlegelii* and *P. soror* (BS=100%), which was in turn, 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 *pectoralis* species complex and Clade B comprised all other described taxa, including the *rufiventris* and *philippinensis* species complexes (Figure 3). Within Clade A, the Louisiade endemic, *Pachycephala collaris*, was the first lineage. It sat on a long branch separate from the rest of the *pectoralis* complex, which was otherwise split roughly into a Pacific clade and an Australo-Papuan clade. The Pacific clade comprised lineages such as *P. orioloides* 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 perhaps 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 mangroves of mainland Southeast Asia (*P. feminina*).

Figure 3. Maximum clade credibility (MCC) tree of BEAST2 analysis of 500 ultraconserved loci from the 75% complete dataset with the fixed ML topology and a time-constraint (Figure 1). Confidence intervals (95%) of divergence times are indicated by dark grey bars. This tree is a combination of the inferred ancestral ranges with BioGeoBEARS with solid coloured nodes and pie charts that account biogeographic uncertainty at each node, conditional on this node to occur; black nodes indicate equivocal nodes. The colours of the pie charts reflect the probability of the area of origin according to the geographical delimitations in the map. Coloured squares at the tips indicate current species' distributions. Dark grey rectangle indicates the estimated time of the emergence of New Guinea; dotted line represents our constraint of New Guinea emergence (couldn't emerge before 14.6 Ma).



3.3 Biogeography

Our biogeographical analysis and model selection found the dispersal-extinction-cladogenesis model, including founder-event speciation, was the best supported model (DEC+j, AIC weight = 0.81, Table 2).

Model	**LnL**	**parameters**	***d***	***e***	***j***	**AIC**	**AIC weight**
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

Table 2. Biogeographical model selection, analysed with BioGeoBEARS using seven areas.

We inferred a Wallacean and Australian origin of Pachycephalidae with the time-constrained analysis (~55% for Wallacea, 30% for Australia, and ~15% equivocal; Figure 3, Figure S1). We inferred a New Guinean and Australian origin of Clade 1 (*Pseudorectes* and *Colluricincla*) approximately 10 Ma; New Guinea was represented by ~60%, Australia by ~13%, and ~27% equivocal. For Clade 2, we inferred a largely Wallacean origin, despite the first branch being a New Guinean endemic (*Melanorectes*) and that node being inside the 15-Ma time constraint, although ~15% was inferred as New Guinea. The subsequent two branches after *Melanorectes* are endemic lineages of Sulawesi and Lesser Sundas, respectively (*Coracornis* and *Pachycephala nudigula*). We inferred a Wallacean origin of the node leading to *Coracornis* + *Pachycephala* about 10 Ma, whereas the origin of *Pachycephala* was inferred to have origins in Australia (~38%), New Guinea (~13%), and Oceania (~20%) approximately 8.1 Ma. The next three clades inside of *P. nudigula* are endemic to Australia (*P. olivacea*, *P. rufogularis*, and *P. inornata*) and New Guinea (*P. soror* and *P. schlegelii*), respectively, and their ancestral areas were inferred largely to be in Australia and New Guinea. The Core *Pachycephala* (Clades A and B) were strongly inferred

to have an origin in Oceania dating to around 5.9 Ma (Figure 3). Clade A diverges around 5.0 Ma and we inferred a mostly Oceania origin. The first branch of Clade A, *P. collaris*, inhabiting the Louisiade Archipelago, was coded to inhabit Oceania (Figure 3) or New Guinea (Supplemental Figure 3). When *P. collaris* is coded as inhabiting New Guinea, the node for Clade A is inferred to be more New Guinea in origin. There was then a sweep of diversification into the Pacific and a back colonization into Wallacea and Australia. Clade B shows a signal from both Wallacea and New Guinea approximately 4.5 Ma (Figure 3). Once again, we have basal lineages originating in Oceania (*P. implicata and P. richardsi*) with subsequent diversification into Wallacea, New Guinea, and then the Philippines.

When we removed the 15-Ma time constraint of New Guinea's emergence, our results were more equivocal with regards to the biogeographic patterns of the family. In this analysis, Pachycephalidae was inferred to have its origins in New Guinea with much higher confidence (Figure S2). Clade 1 was inferred to be New Guinea in origin, regardless of the analysis. Clade 2 was inferred to be mostly New Guinea in origin, whereas in the constrained analysis only a small percentage was attributed to New Guinea. Notably, the node at which *P. soror* and *P. schlegelii* diverge from the rest of *Pachycephala* had a strong New Guinea origin regardless of the constraint. The genus *Pachycephala* had equivocal nodes in both analyses: in the constrained analysis, it is more Australia and New Guinea, whereas in the unconstrained analysis, it was approximately 50% Wallacean. The Core *Pachycephala* (Clades A+B) had a strong New Guinea origin, whereas in our time-constrained tree this node had a strong Oceania signal.

3.4 Macroevolutionary dynamics

According to our BAMM results, there is a single rate regime shift within Pachycephalidae. This single shift is supported along the branch leading to *Pachycephala* for both the best and second-best rate shift placements (Figure 4). These results were corroborated by testing a range of rate-shift priors (expectedNumerOfShifts) from 0.1 to 5.0. The mean evolutionary rate for the family is λ = 0.249 (95% CI: 0.196 – 0.311) with an increase in speciation rate after 10 Ma. When we removed the genus *Pachycephala* the rest of the family had a speciation rate of λ = 0.101 (Figure 4). Conversely, *Pachycephala* alone had a mean speciation rate of λ = 0.318 (Figure 4).

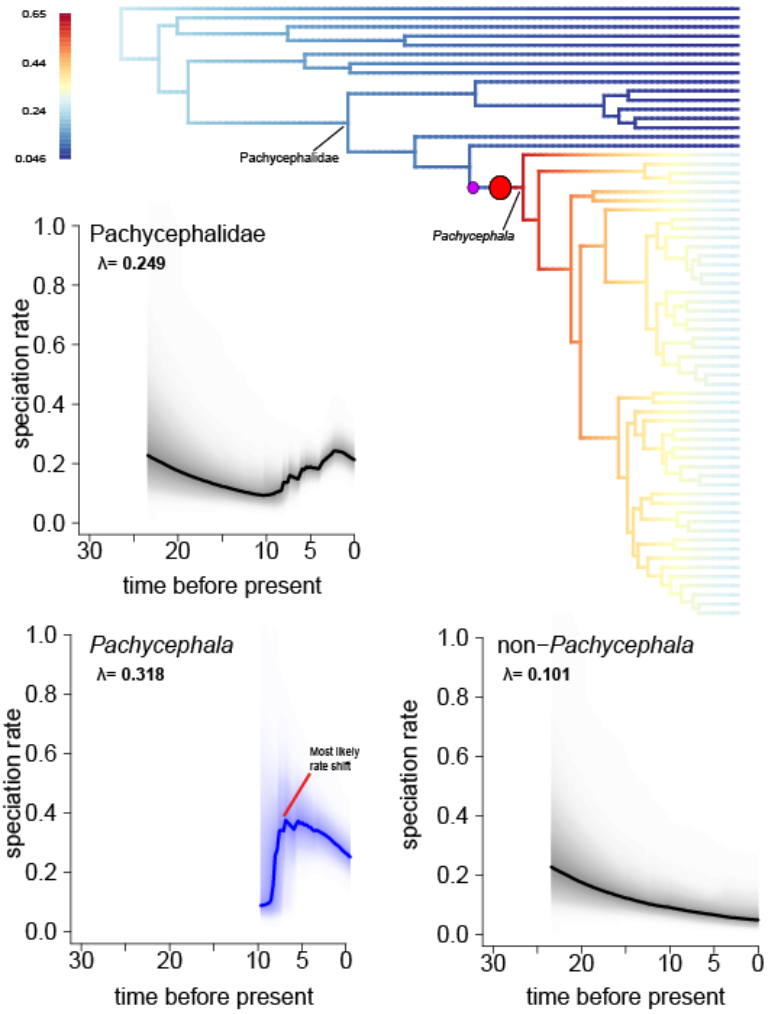


Figure 4. BAMM Results. Plots of diversification rates through time and BAMM phylorate plot of Pachycephala. Cool colors represent slow rates while warm colors represent fast rates. The red dot along the branch leading to Pachycephala denotes the most likely position of an inferred rate shift; smaller circle is the second most likely.

Chapter 4

Discussion

We used ultraconserved elements (UCEs) to examine the systematics and biogeography of one of the most biogeographically complex avian radiations, the whistlers (Aves: Pachycephalidae). Our dataset, the first genome-wide dataset for the whistlers, helped resolve key nodes near the base of the tree and found strong support for Wallacea as a key biogeographic area during the origin of the family approximately 14.8 Ma. Although our phylogenetic analyses support the overall topography of previous studies, we discovered key differences, especially within the early branching lineages of *Pachycephala*. We also find an early burst of diversification and an increased speciation rate in this genus, relative to the background rate across the entire family.

4.1 Systematics

As with previous studies (Norman et al. 2009; Jønsson et al. 2010), we find support for the relationships within Pachycephalidae genera, but we find some novel relationships between species. We corroborate that Clade 2 diversified around 12.2 Ma while Clade 1 diversified around 9.9 Ma, supporting the inference that the crown age of Clade 2 is older than the crown age of Clade 1 (Jønsson et al. 2010; Marki et al. 2018). Additionally, our tree corroborates that C*olluricincla* consists of two clades; the first consists of *C. tenebrosa + C. megarhyncha* and the second contains *C. boweri + C. woodwardia + C. harmonica* (Marki et al. 2018). However, Marki et al. suggest the origin of *Colluricincla* to be in the late Miocene (11.5 Ma), whereas our analyses date *Colluricincla* to around 5.1 Ma. These differences are likely due to their use of mitochondrial clocks versus our use of secondary fossil calibrations.

Clade 2 comprises *Melanorectes, Coracornis,* and the hyper-diverse *Pachycephala*. The monotypic genus *Melanorectes* is sister to *Coracornis* + *Pachycephala*. *Pachycephala* can be divided into three groups, which we refer to here as the "basal" lineages and the Core *Pachycephala*, composed of Clade A and Clade B (Figure 3). *Pachycephala nudigula* has long-been suspected of being an early branching lineage within *Pachycephala*; however, previous studies differ in its phylogenetic placement due to low bootstrap support. Jønsson et al. (2010; 2014) found *P. olivacea* and *P. inornata* to be the most basal lineages of *Pachycephala*, and *P. nudigula* was sister to all remaining taxa. 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*. Our novel findings strongly support *P. nudigula* as the basal-most lineage of the genus and that Australian *P. olivacea*, *P. inornata*, and *P. rufogularis* comprise their own clade.

Pachycephala schlegelii and *Pachycephala soror* live in the highlands of New Guinea and have overlapping elevational ranges (Boles 2019). Although not frequently mentioned in the systematic literature, the certainty of their phylogenetic relationships has been ambiguous. Dumbacher et al. (2008) found *P. schlegelii* sister to *P. lorentzi* with *P. soror* sister to an unidentified *Pachycephala* specimen and these two pairs of taxa were in turn sister to one another; however, dense taxon sampling was not the focus of this study. *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* as the sister clade to all other *Pachycephala* (Jønsson et al. 2010). Our concatenated and species-tree analyses agree with Jønsson et al. (2010) for a sister relationship between *P.*

schlegelii and *P. soror* (BS=100%), which are in turn sister to the Core *Pachycephala* (Figures 1–3).

Clade A contains taxa that have historically belonged to the Golden Whistler species complex. Our data supports that *P. collaris*, distributed throughout the Louisiade Archipelago, is the first branching lineage of this clade. Other systematic studies have shown that early branching lineages, from birds (Andersen et al. 2014; 2015; Kearns et al. 2013; Pedersen et al. 2018) to herpetiles (Oliver, L.A et al. 2013; 2017) are biogeographically unique in the Louisaides. We then have a well-supported node (100% BS) splitting Clade A into two groups, one which contains taxa belonging to a Pacific clade and the other, an Australo-Papuan clade. This differs from previous studies where relationships resembled a "staircase" instead of well-supported branches (Dumbacher et al. 2008; Jønsson et al. 2008). Within the Pacific clade, the Rennell whistler (*P. 21eminine*) resolves as sister to *P. orioloides* of the Solomon Islands. This species' taxonomic relationship to other Pacific taxa has previously remained equivocal (Jønsson et al. 2010; Andersen 2014). Both our concatenated and species tree analyses support *P. 21eminine* as sister to *P. orioloides*. However, node support for the rest of the sub-clades dwindles, thus rendering other individual taxonomic relationships equivocal (Figure 1).

Clade B shows similar taxonomic patterns to Clade A although it is more geographically complex. Our data resolves the old highland relicts of *P. implicata* and *P. richardsi* as the first branching lineages of this clade. We then have 100% bootstrap support for a bifurcating clade sister to *P. implicata* and *P. richardsi* (Figure 1). This is in opposition to Jønsson et al. (2014) findings; they found *P. implicata* + *P. richardsi* sister to *P. caledonica*. This group was then sister to the rest of *Pachycephala*, minus the "basal"

lineages of *P. nidigula*, *P. olivacea, P. inornata*, *P. soror,* and *P. schlegelii* (Jønsson et al. 2014). Within Clade B, there is a group consisting of mostly Wallacean taxa with the remaining taxa circumscribed to New Guinea, Australia, and the Philippines. However, relationships within these groups are poorly supported and they resolved to a polytomy (Figure 1).

4.2 Biogeography

There are no known fossils for Pachycephalidae, thus, dating the origin of crown whistlers is problematic. We used two secondary fossil-calibration points from Oliveros et al. (2019), who used 13 fossil calibrations to date their passerine tree. Other studies of Pachycephalidae used an ND2 divergence rate from Galapagos Mockingbirds and from Hawaiian Honeycreepers to time-calibrate BEAST trees (Jønsson et al. 2010; Marki et el. 2018). These molecular clocks are known to evolve rapidly; conversely UCEs, are conserved regions and thus thought to evolve more slowly; therefore, our geologic estimates are older by comparison. Additionally, because New Guinea is a diversity stronghold for Pachycephalidae, it was important to consider its geological formation in our analyses. The emergence of New Guinea has geological range estimates around 12 Ma to as late as 5 Ma (Moyle et al. 2016). We constrained our analysis to ensure that taxa could not be present on New Guinea before its emergence which we conservatively dated to around 15 Ma. This time-constraint clearly affects our biogeographical interpretation of the origin of Pachycephalidae. According to our time-constrained biogeographic analyses, Wallacea is important during the early stages of whistler diversification. Around the mid-Miocene, the Sula Spur was colliding with proto-Sulawesi, partially causing the uplift of Wallacea; this event created new islands and therefore steppingstones into Sundaland (Hall, 1998; 2013;

Moyle et al. 2016). While Clade 2 has a Wallacea origin, *Pseudorectes* and *Colluricincla* (Clade 1) have a strong New Guinea origin. *Pseudorectes* colonized and remains in New Guinea while *Colluricincla* colonized Australia and then re-colonized New Guinea (Figure 3). Conversely, when examining the unconstrained tree (Figure S2), deep nodes that were strongly Wallacean are inferred to be strongly New Guinean without the constraint. We chose to present and support the time-constrained tree due to the significance of the New Guinea emergence in the evolutionary history of Pachycephalidae.

According to our analysis, there appears to be a jump from a Wallacean node (first and second nodes of Clade 2) to an Australia/New Guinea/Oceania node around 8.1 Ma (Figure 3). We infer an Australian (~38%), New Guinea (~13%) and Oceania (~20%) origin of *Pachycephala* in the late Miocene (7.5 Ma). This divergence estimate is more recent than previous hypotheses, in which the genus is thought to have diversified between 18–12 Ma (Moyle et al. 2016; Oliveros et al. 2019; Marki et al. 2019), but not as recent at 2.9 Ma as inferred by Jønsson et al. (2010). However, previous ancestral range analyses have suggested that the genus originated in Australo-Papua and this is seen in our time-constrained analysis but not the unconstrained. Jønsson et al. (2008) found that the family diverged during the early Pliocene, with the genus *Pachycephala* diverging in the late Pliocene, and the bulk of species diversity in the family diversifying in the Pleistocene. These nodes are all much younger in geologic time than what we discovered. However, they used the ND2 rates of 0.028 substitutions per site per lineage, whereas we used secondary fossil calibrations.

Our analysis corroborates the notion that *Pachycephala* independently colonized disparate geographic areas multiple times, including Oceania, the Philippines, and Sundaland (Galbraith 1956; Jønsson et al. 2014). Three independent dispersal events led to the

colonization of the Pacific, as seen by *P. chlorura* in Vanuatu, *P. caledonica* in New Caledonia, and *P. implicata* and *P. richardsi* in the Solomon Islands, all independently of the first wave of colonization into Oceania (Figure 3). Additionally, when we code *P. collaris* as inhabiting New Guinea, the node for Clade A changes from a distinctly Oceania node (Figure 3) to one with a strong New Guinea signal (Supplemental Figure 3). 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. There appears to have been a wave into Sundaland from the Philippines and New Guinea, bypassing Wallacea (Figure 3). There is a pattern within *Pachycephala* of Oceanic lineages with varying degrees of diversification that are sister to other taxa that are dispersed into Sahul. Clade A diversifies into oceanic islands of the Pacific, while Clade B colonizes and diversifies to oceanic islands west of New Guinea such as Wallacea and the Philippines. Jønsson et al. (2014) hypothesized that the *P. pectoralis* complex (our Clade A) originated in the Pacific and this is confirmed in our analysis. Similarly, in Clade B, Oceania is important early on, as evidenced by the old, highland relicts of *P. implicata* and *P. richardsi*, taxa that are today confined to the uplands of Guadalcanal and Bougainville. There is more of an island effect to the west of Australia/New Guinea, with patterns centered around Wallacea and the Philippines. Our analyses rendered *P. implicata* and *P. richardsi* as sister to one another and a basal lineage to the rest of this clade (Figure 3).

Pachycephalidae is considered a rapidly diversifying and radiating group (Moyle et al. 2009; Fritz et al. 2012), therefore we would expect to see an increase in speciation rates within the family. Our BAMM analyses support an elevated diversification rate within the genus *Pachycephala*. This singular rate shift occurred where *Pachycephala* diverged from

the rest of the family. These data support an early burst of diversification followed by a decreasing rate over the course of the genus' evolutionary history. This slowdown could be an artifact of not fully accounting for species level diversity and with denser sampling, we might expect an uptick in speciation rates.

Chapter 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 use of UCEs, we clarified certain taxonomic relationships and discovered that Wallacea played a much larger role in pachycephalid evolutionary history than previously thought. However, UCEs are not the final nail in the proverbial coffin and several nodes throughout the tree were not fully supported. We are still lacking species-level resolution where lineages diversified rapidly. Future studies should sample more densely at the tips (e.g., subspecies and multiple island populations) to examine population-level dynamics within these clades.

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