IBIS
BOU international journal of avian science

Frontispiece. Adult and immature males of the Satin Berrypecker *Melanocharis citreola* sp. nov. from the Kumawa Mountains, New Guinea. Original artwork by Norman Arlott.

 doi: 10.1111/ibi.12981

A new, undescribed species of *Melanocharis* berrypecker from western New Guinea and the evolutionary history of the family Melanocharitidae

BORJA MILÁ,*[1] JADE BRUXAUX,[2,3] GUILLERMO FRIIS,[1] KATERINA SAM,[4,5] HIDAYAT ASHARI[6] & CHRISTOPHE THÉBAUD[2]

[1]*National Museum of Natural Sciences, Spanish National Research Council (CSIC), Madrid, 28006, Spain*
[2]*Laboratoire Evolution et Diversité Biologique, UMR 5174 CNRS-IRD, Université Paul Sabatier, Toulouse, France*
[3]*Department of Ecology and Environmental Science, UPSC, Umeå University, Umeå, Sweden*
[4]*Biology Centre of Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic*
[5]*Faculty of Sciences, University of South Bohemia, Ceske Budejovice, Czech Republic*
[6]*Museum Zoologicum Bogoriense, Indonesian Institute of Sciences (LIPI), Cibinong, Indonesia*

Western New Guinea remains one of the last biologically underexplored regions of the world, and much remains to be learned regarding the diversity and evolutionary history of its fauna and flora. During a recent ornithological expedition to the Kumawa Mountains in West Papua, we encountered an undescribed species of *Melanocharis* berrypecker (Melanocharitidae) in cloud forest at an elevation of 1200 m asl. Its main characteristics are iridescent blue-black upperparts, satin-white underparts washed lemon yellow, and white outer edges to the external rectrices. Initially thought to represent a close relative of the Mid-mountain Berrypecker *Melanocharis longicauda* based on elevation and plumage colour traits, a complete phylogenetic analysis of the genus based on full mitogenomes and genome-wide nuclear data revealed that the new species, which we name Satin Berrypecker *Melanocharis citreola* sp. nov., is in fact sister to the phenotypically dissimilar Streaked Berrypecker *Melanocharis striativentris*. Phylogenetic relationships within the family Melanocharitidae, including all presently recognized genera (*Toxorhamphus*, *Oedistoma*, *Rhamphocharis* and *Melanocharis*), reveal that this family endemic to the island of New Guinea diversified during the main uplift of New Guinea in the Middle and Late Miocene (14.6 Mya), and represents an evolutionary radiation with high disparity in bill morphology and signalling traits across species. *Rhamphocharis* berrypeckers fall within the *Melanocharis* clade despite their larger beaks and should be included in the latter genus. Interspecific genetic distances in *Melanocharis* are pronounced (average interspecific distance: 8.8% in COI, 12.4% in ND2), suggesting a long history of independent evolution of all lineages corresponding to currently recognized species, including the Satin Berrypecker, which shares a most recent common ancestor with its sister species in the early Pleistocene (~ 2.0 Mya).

Keywords: endemism, expedition, island, Passerides, speciation, West Papua.

*Corresponding author.
Email: b.mila@csic.es
Twitter: @borjamila

The discovery and description of avian diversity across the world remains a major challenge in ornithology (Rheindt *et al.* 2020). Few regions of the world remain as underexplored as the mountainous regions of New Guinea, and the diversity and evolutionary history of its fauna and flora are still poorly known (Diamond 1985, Beehler & Pratt 2016). In 2014 and 2017, we had the opportunity to survey the avifauna in the Bird's Head Isthmus of western New Guinea, including the relatively unexplored Kumawa Mountains. Our work was conducted in the context of two extensive multi-taxa biological expeditions organized by the French Institut de Recherche pour le Développement (IRD) and Indonesia's Museum Zoologicum Bogoriense (MZB) of the Indonesian Institute of Sciences (LIPI) at Cibinong, Indonesia.

The Bird's Head Isthmus, also known as the Bird's Neck, connects the Bird's Head or Vogelkop Peninsula to the rest of New Guinea and harbours a unique landscape of rugged and isolated limestone karst mountains, hosting an impressive range of ecological niches as a result of complex terrain and variable climatic conditions (Marshall & Beehler 2007). This region evolved through a series of complex tectonic movements, with an eastern sector featuring the karstic Lengguru fold belt (< 8 million years (Myr)) that links New Guinea's central cordillera to the moderately high mountains of the eastern coast of the Bird's Head, and a western sector with a vast low-lying sedimentary basin (Bintuni basin) flanked by a broad anticlinal ridge along the southwestern coast (Fakfak and Kumawa Mts) that rose above water less than 5 million years ago (Mya) (Bailly *et al.* 2009, Sapin *et al.* 2009, Baldwin *et al.* 2012). The region is particularly poorly studied from a biological standpoint (Marshall & Beehler 2007, Beehler 2020), in part due to its treacherous karst terrain, steep slopes, and complete lack of streams and other surface water at high elevations, which makes ornithological exploration very difficult (Diamond & Bishop 2015). The Kumawa Mountains are uninhabited by humans and, apart from coastal areas, have probably been so since the first humans arrived on the island. No access roads or trails exist and most of the forest landscapes are still intact (Global Forest Watch 2014). Located in the Bomberai Peninsula, on the southwestern tip of the Bird's Neck, the Kumawa Mountains are separated by 80 km of lowland rainforest habitat from the Fakfak Mountains to the west, 90 km from the Lengguru region highlands north of Triton Bay, 260 km from the Arfak Mountains in the Vogelkop Peninsula, and 250 km from the Weyland Mountains of New Guinea's main cordillera to the east (all measured at 800 m asl; Fig. 1).

We first explored the Kumawa Mountains during a short visit in November 2014, during which we were able to survey birds at 1100–1200 m asl in a mid-montane forest habitat for 4 days, using mist-nets and visual observations. During the last day of our stay, at an elevation of 1200 m asl, we observed and captured a male bird that we identified as a member of an undescribed taxon in the genus *Melanocharis* Sclater 1858 that seemed to only match previous observations by Gibbs (1994) in the Fakfak Mountains. To explore this finding further and obtain additional specimens, we returned to the Kumawas for a longer expedition in October–November 2017. This time we brought equipment to collect rainwater and organized proper food supply, which allowed our team to stay above 1000 m asl for 22 days. During this second expedition we captured three more individuals of the undescribed *Melanocharis* berrypecker: another adult male at 1100 m asl and two immature males at 1200 m asl. Subsequent inspection of other *Melanocharis* specimens at the MZB and the extensive phylogenetic analyses based on genomic data presented here confirmed that the Kumawa specimens represent a new, previously undescribed species in this genus endemic to New Guinea.

The genus *Melanocharis* is currently composed of five species (Fig. 2) and includes the Black Berrypecker *Melanocharis nigra*, which is common and widespread in the lowlands and up to about 1200 m asl, and shows considerable geographical variation in plumage colour; the Mid-mountain Berrypecker *Melanocharis longicauda*, found at elevations between 700 and 1900 m asl; the Streaked Berrypecker *Melanocharis striativentris* also found at mid-elevations between 1150 and 2300 m asl; the Fan-tailed Berrypecker *Melanocharis versteri*, restricted to high elevations between 1750 m and the timberline; and the Obscure Berrypecker *Melanocharis arfakiana*, a very local species known from a few localities between 680 and 1100 m asl (Beehler & Pratt 2016). *Melanocharis striativentris* and *M. arfakiana* are olive overall, whereas the other members of the genus show sexual dichromatism and reverse sexual size dimorphism, with

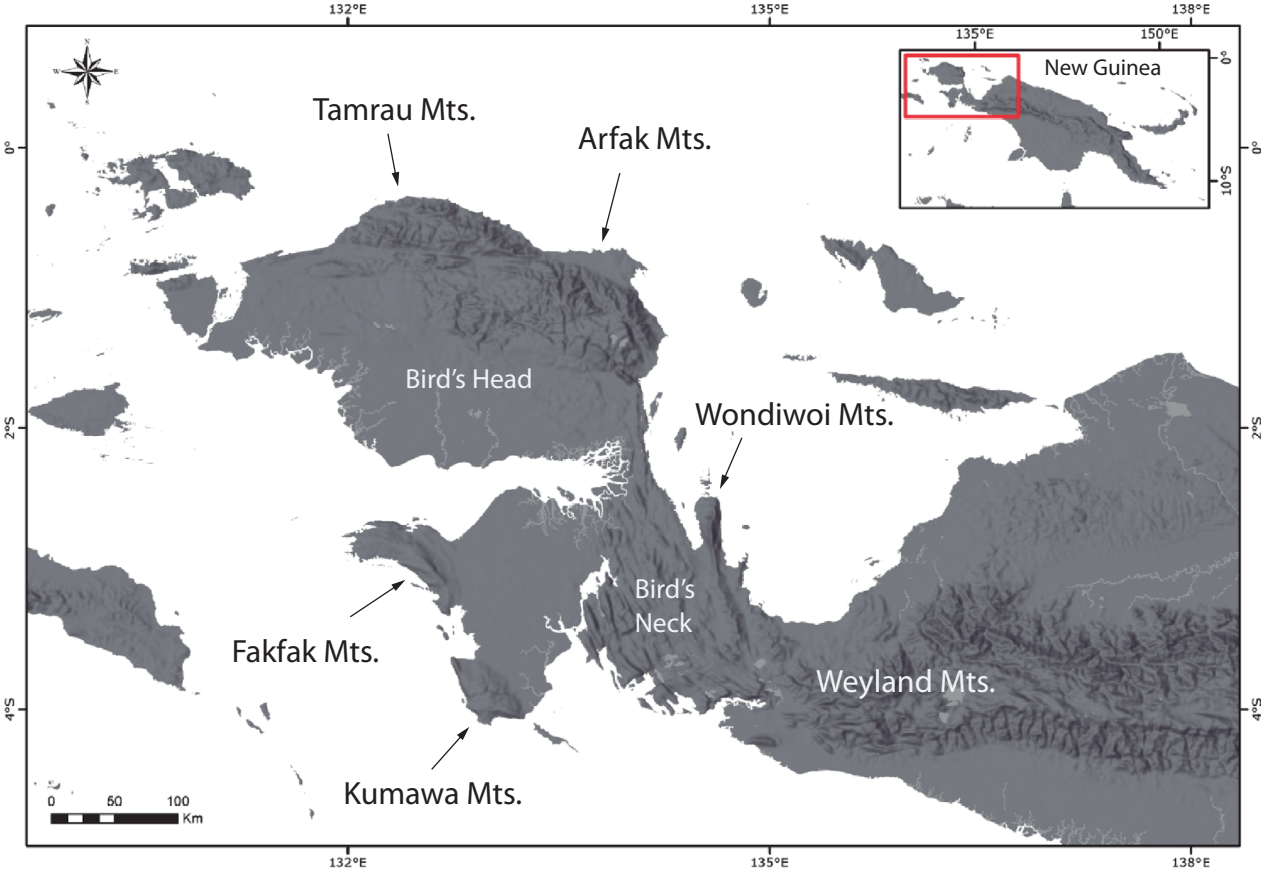

Figure 1. Geographical map of the Bird's Head and Bird's Neck regions of New Guinea, showing the main mountain ranges.

males showing blue-black upperparts, grey to olive underparts and varying amounts of white on the tail, and being smaller than females, which are olive green overall (Mayr & Amadon 1947, Salomonsen 1960, Pratt & Beehler 2014, Beehler & Pratt 2016) (Fig. 2).

Here we provide a formal description of the newly discovered member of *Melanocharis* from the Kumawa Mountains, which we have named Satin Berrypecker, and we use complete mitogenomes and nuclear DNA sequences obtained through next-generation sequencing to produce a comprehensive phylogenetic hypothesis of the family Melanocharitidae, which *Melanocharis* berrypeckers share with *Rhamphocharis* berrypeckers and *Toxorhamphus* and *Oedistoma* longbills. A robust and complete phylogenetic tree is key to help us understand the evolutionary history of this group and place the new species in the proper evolutionary context. Currently, there is no fully sampled species-level phylogeny available for this family, which is thought to consist of three very distinct lineages recently elevated to subfamily rank (Schodde & Christidis 2014), Melanocharitinae, Toxorhamphinae and Oedistomatinae, and represents one of the four 'transitional' oscine lineages endemic to New Guinea (Jønsson *et al.* 2011), with no close relatives (Fjeldså *et al.* 2020).

METHODS

Fieldwork

Field expeditions to the Kumawa Mountains took place on 12–18 November 2014, and 17 October to 13 November 2017. On both occasions we accessed the highlands from the southern coast, starting at a beach site located 11.1 km east of the small village of Nusa Ulan as the crow flies, a site referred to as 'Fatukama Beach' by J. Diamond, who visited the area in 1983 with A. Irwanto of the Indonesian Environment Department (Diamond & Bishop

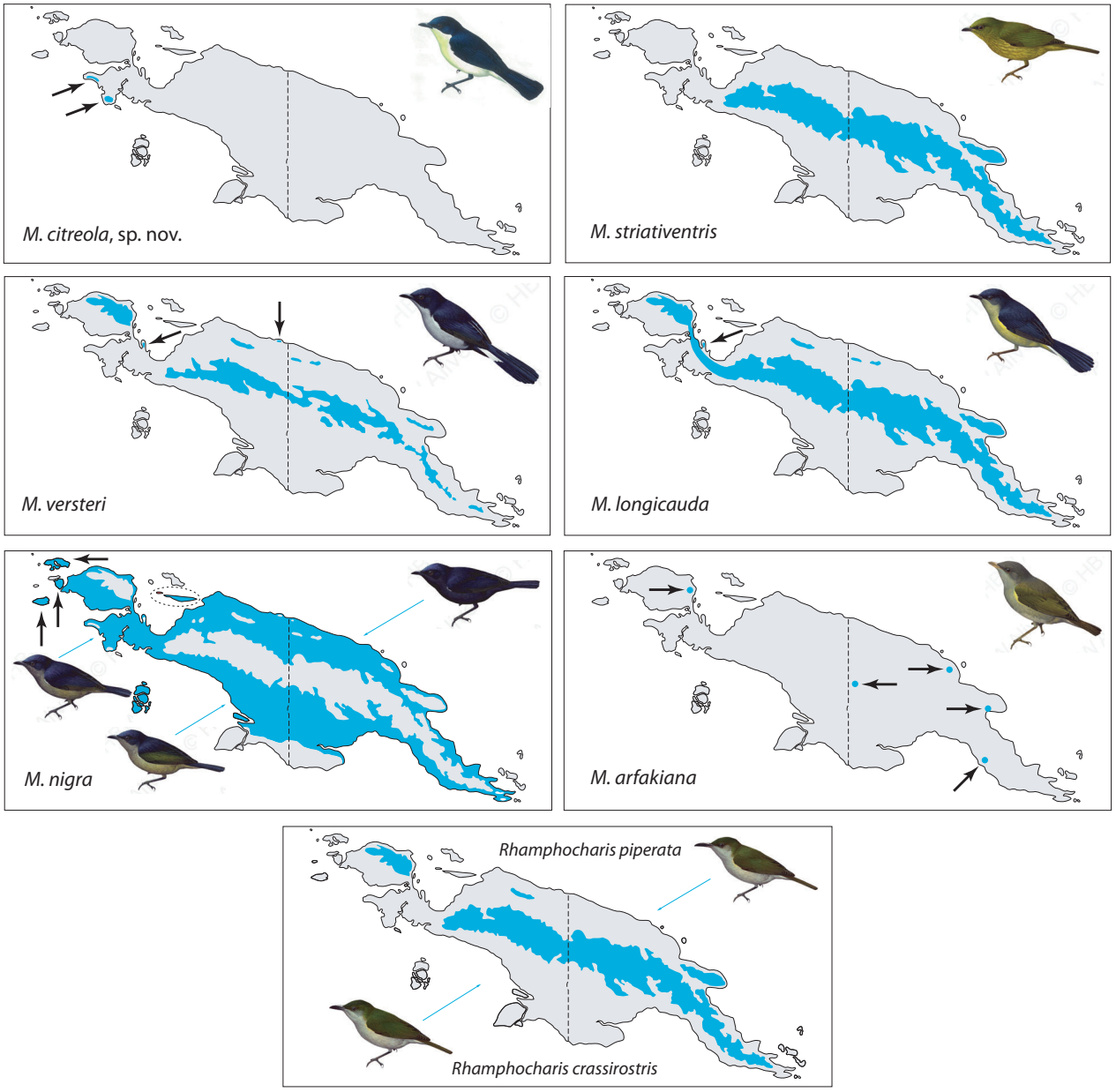

Figure 2. The distribution ranges of all known members of the genus *Melanocharis*. Maps from Pratt and Beehler (2014). The distribution map of *M. longicauda* has been modified from the original to exclude the population in the Fakfak Mountains (Bird's Neck), where *M. citreola* sp. nov. has been reported instead (Gibbs 1994). Male bird illustration of *M. citreola* from an original plate by Norman Arlott. The remaining illustrations, also by Norman Arlott, are used with permission from Lynx Edicions.

2015). We climbed with several porters to a first campsite by a river at 400 m, then the following morning climbed to 1100 m asl, where we established our main camp.

Mist-nets were set up in mid-montane 'cloud' forest habitat in the vicinity of the main camp and on a higher plateau about 0.6 km away to the north, at an elevation of 1200 m asl (4.01134S, 133.08751E). Mist-nets (30–36 mm mesh, 2.5 m tall, and 12 or 9 m in length) were opened just before sunrise (05:30 h) and left open for 5–8 h depending on weather conditions. We operated

between 8 and 14 nets per day, with a daily average of 12.6 nets. Net stations (composed of a single or a double net) were set between 10 and 50 m from each other, overall covering an area of approximately 52 ha, as estimated with the polygon tool in Google Earth Pro™. We moved part of the nets to new locations every day to maximize capture rates. To estimate sampling effort, we summed up the metres of net run every day (e.g. running 10 nets of 12 m, and one net of 9 m, equals 129 m) and multiplied by the number of hours operated that day to obtain a daily number of net hours. We accumulated 3282 net hours during 4 days of netting in 2014 (14–17 November) and 17 339 net hours during 19 days of netting in 2017 (22 October to 9 November), for a total of 20 621 net hours. No playbacks or other attractors were used in the vicinity of the nets.

Birds were identified to species using Pratt and Beehler (2014) and Beehler and Pratt (2016) and we recorded information on age, sex, body condition, reproductive status and moult. We measured unflattened wing chord to the nearest 0.5 mm using a wing rule, and measured tail length, tarsus length, bill length, bill width and bill depth using dial callipers of 0.1 mm precision. We took a small blood sample by venepuncture of the brachial vein. Some birds were prepared as museum skins in the field by LIPI personnel and have been deposited at the MZB ornithological collection.

All fieldwork was conducted according to relevant research and ethical guidelines by the government of the Republic of Indonesia and under research permits issued by RISTEK (Indonesia) (for 2014, 304/SIP/FRP/SM/X/2014; for 2017, 3179/FRP/E5/Dit.KI/IX/2017) and relevant Indonesian government collecting permits.

Genetic sexing of individuals

All four individuals of the new *Melanocharis* species were sexed genetically using two sets of primers P2 and P8 (Griffiths *et al.* 1998) and 2550P and 2718A (Fridolfsson & Ellegren 1999) with the proper positive and negative controls. PCR conditions are available upon request. All four individuals were genetically determined to be males.

Taxonomic sampling

To obtain a good taxonomic and geographical representation of the family Melanocharitidae, with an emphasis on the subfamily Melanocharitinae, we complemented our field sampling with genetic samples from museum collections (Table 1). In addition, we obtained sequence data for one *Melanocharis arfakiana* individual (AMNH 421459) from Knud Jønsson. In total, we obtained sequence data from 24 individuals of 10 of 12 currently recognized species, including all genera in the family Melanocharitidae. Specifically, samples included in phylogenetic analyses included all known *Melanocharis* species (including three subspecies of *M. nigra*, two subspecies of *M. longicauda* and two subspecies of *M. versteri*), one of the two described species of *Rhamphocharis* (*R. piperata*), the two described species of *Oedistoma* (*O. iliolophus* and *O. pygmaeum*), and one of the two described species of *Toxorhamphus* (*T. novaguineae*).

DNA extraction and sequencing

We extracted genomic DNA from blood or tissue samples using a Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Austin, TX, USA) and following the manufacturer's instructions. DNA from dry toe-pad tissue samples from some museum specimens was extracted using the same kit with slight modifications to the protocol (e.g. longer proteinase K digestion) and strict conditions to avoid contamination by modern DNA, as described elsewhere (Bruxaux *et al.* 2018). Libraries were prepared from 54 µL of eluted DNA using the Illumina TruSeq Nano DNA Sample Prep kit following the instructions of the supplier (Illumina Inc., San Diego, CA, USA). Samples were then sequenced with Illumina HiSeq technology to obtain millions of 150-bp-long sequence reads. Library preparation and sequencing were performed at the GeT-PlaGe core facility, hosted by INRAE (Toulouse, France).

Mitogenome reconstruction

We assembled the mitochondrial genomes from the raw reads with the ORGanelle ASeMbler v1.0.3 (https://git.metabarcoding.org/org-asm/org-asm), which removes adapters and takes read quality into account. When sequencing depth did not allow us to obtain a complete circular genome, we mapped reads against one of the mitochondrial genomes obtained for the same species, using the method described below for the nuclear data. To evaluate the quality of our final reconstruction, we

Table 1. Collection and locality data for newly generated sequences in this study. Taxonomy and New Guinea bird regions follow Beehler and Pratt (2016).

Collection	Catalogue no.	Taxon	Collecting date	Latitude	Longitude	Region	Sample
AMNH	SKIN421459	*Melanocharis arfakiana*	22/11/1933	−8.58	146.93	SE Peninsula	Toepad
USNM	657308	*Melanocharis arfakiana*	19/7/1994	−5.211	141.201	Border Ranges	Fresh tissue
USNM	657309	*Melanocharis arfakiana*	20/7/1994	−5.23	141.18	Border Ranges	Fresh tissue
This study	MZB34796 (LGR167)	*Melanocharis citreola* sp. nov.	14/11/2014	−4.01134	133.08751	Bird's Neck	Fresh tissue
This study	MZB36038 (KUM068)	*Melanocharis citreola* sp. nov.	26/10/2017	−4.01154	133.08754	Bird's Neck	Fresh tissue
This study	MZB36039 (KUM143)	*Melanocharis citreola* sp. nov.	2/11/2017	−4.016247	133.0864	Bird's Neck	Fresh tissue
This study	MZB36040 (KUM201)	*Melanocharis citreola* sp. nov.	8/11/2017	−4.01625	133.08635	Bird's Neck	Fresh tissue
ANWC	B26041	*Melanocharis longicauda captata*	4/11/1973	−6.4583	147.4333	Huon	Toepad
MZB	30618	*Melanocharis longicauda longicauda*[a]	Unknown	−4.09	137.06	Western Ranges	Toepad
This study	LGR-028	*Melanocharis nigra nigra*	26/10/2014	−3.70496	134.06984	Bird's Neck	Fresh tissue
ANWC	B52454	*Melanocharis nigra chloroptera*	5/9/2009	−5.7292	142.2633	Border Ranges	Fresh tissue
ZMUC	150402	*Melanocharis nigra unicolor*	2015	−5.7217	145.2714	Eastern Ranges	Fresh tissue
KSC	9041	*Melanocharis striativentris striativentris*	18/6/2012	−5.7558	145.2364	Eastern Ranges	Fresh tissue
ANWC	B01008	*Melanocharis striativentris striativentris*	28/6/1961	−6.16965	143.66551	Eastern Ranges	Toepad
ANWC	B25717	*Melanocharis striativentris striativentris*[b]	28/10/1973	−6.4583	147.4333	Huon	Toepad
KSC	8943	*Melanocharis versteri maculiceps* De Vis[c]	10/6/2012	−5.7594	145.1803	Eastern Ranges	Fresh tissue
ANWC	B52505	*Melanocharis versteri meeki*	13/9/2009	−5.6566	142.3046	Border Ranges	Fresh tissue
ANWC	B52544	*Melanocharis versteri meeki*	15/9/2009	−5.6566	142.3046	Border Ranges	Fresh tissue
ZMUC	150300	*Rhamphocharis piperata*[d]	2015	−5.7631	145.1974	Eastern Ranges	Fresh tissue
ZMUC	150392	*Oedistoma iliolophus*	2015	−5.7217	145.2714	Eastern Ranges	Fresh tissue
MV	Z44392	*Oedistoma iliolophus*	21/5/1985	−9.16667	147.65	SE Peninsula	Fresh tissue
MV	Z44439	*Oedistoma pygmaeum*	20/7/1987	−8.8833	147.7333	SE Peninsula	Fresh tissue
This study	LGR-144	*Toxorhamphus* n. *novaeguineae*	15/11/2014	−4.01462	133.08696	Bird's Neck	Fresh tissue

AMNH = American Museum of Natural History, New York, USA; ANWC = Australian National Wildlife Collection, Canberra, Australia; KSC = Katerina Sam collection, Czech Republic; MV = Museums Victoria, Australia; MZB = Museum Zoologicum Bogoriense, Cibinong, Indonesia; PNG = Papua New Guinea; USNM = National Museum of Natural History, Smithsonian Institution, Washington DC, USA; ZMUC = Natural History Museum of Denmark, Copenhagen. [a]*Melanocharis longicauda chloris* Streseman & Paludan in HBW; combined into *longicauda* by Beehler and Pratt (2016). [b]*Melanocharis striativentris chrysocome* (Mayr) in HBW; combined into *striativentris* by Beehler and Pratt (2016). [c]*Melanocharis versteri virago* (Streseman) in HBW; combined into *maculiceps* by Beehler and Pratt (2016). [d]Placed in genus *Melanocharis* by Clements (2015) and Gregory (2017); for many years, *Rhamphocharis* was treated as monospecific, but re-examination of specimens from western populations led Beehler and Pratt (2016) to split these populations (*R. crassirostris* Savadori) from the eastern ones (*R. piperata* De Vis).

mapped the reads from each sample against its own mitochondrial genome, again with the method described below. Finally, we annotated each mitochondrial genome with Geneious v.9.1.8 (Biomatters Ltd, Auckland, New Zealand), using *Oedistoma iliolophus* NC_024865 as reference, and checked manually for the reading frame of coding genes. We obtained on average 63.17 million reads per individual (ranging from 6.5 to 467 million; Table S1). We were able to reconstruct a complete circular mitochondrial genome for all individuals except five, for which we recovered > 80% of the estimated full length. The number of reads mapping to the final mitogenome assembly ranged from 217 to 1 million, with an average of 137 114 reads per sample (Table S1). We obtained a final alignment of 17 034 bp, which was used for the phylogenetic analysis.

Nuclear data retrieval

To reconstruct a nuclear DNA dataset, we retrieved low-copy DNA regions using read mapping onto reference sequences, following the strategy presented in Bruxaux *et al.* (2018). Briefly, we used two large sets of independent markers that were assembled recently for large-scale phylogenetic inference in modern birds (McCormack *et al.* 2015, Prum *et al.* 2015). The first set of genes is composed of 259 nuclear loci with an average length of 1501 bp that were defined based on the data obtained in *Corvus albus* (Pied Crow; Corvidae) by Prum *et al.* (2015), for a total sequence length of almost 389 kbp. The second set of markers is composed of 4634 ultra-conserved elements (UCEs) with an average length of 610 bp that were characterized in *Aphelocoma californica* (California Scrub-jay; Corvidae), for a total sequence length of 2.8 Mbp (McCormack *et al.*, 2015).

We first trimmed the raw reads with Trimmomatic v0.38 (Bolger *et al.* 2014) to remove the adapters and the bases at the beginning and the end of low-quality reads (below a value of 3) and kept only the paired-end reads that reached 36 bp after trimming. We then mapped the reads against our reference sequences with BWA MEM v0.7.17 (Li & Durbin 2009), filtered the alignment to skip reads with mapping quality below 30 with SAMTOOLS v1.9 (Li *et al.* 2009), sorted the bam file and removed read duplicates with the same software. We called SNPs with BCFTOOLS v1.10.2 without minimum base quality, normalized indels, and filtered SNPs in the 5-bp vicinity of these indels. Finally, we obtained the consensus sequence for each individual with the BCFTOOLS consensus command and its new option '-a' that deals better with missing data. For the nuclear DNA dataset, we mapped on average 271 360 reads per individual against the reference, ranging from 33 715 to 1 047 251 reads (Table S1). We aligned our Melanocharitidae data with their reference sequence as outgroup with MAFFT v7.313 (Katoh & Standley, 2013) and refined manually the alignment in the region where missing data did not allow a proper automatic alignment.

Phylogenetic analyses

Mitochondrial genome data

In addition to our ingroup sequences, we included the mitochondrial genome data of three other oscine passerines as outgroups to root the tree: Grey Shrikethrush *Colluricincla harmonica* (Pachycephalidae), New Zealand Fantail *Rhipidura fuliginosa* (Rhipiduridae) and Zebra Finch *Taeniopygia guttata* (Estrildidae) (GenBank accessions: KY994582, NC_029145 and NC_007897, respectively). We aligned each protein-coding gene, each transfer RNA gene (tRNA), each ribosomal RNA gene (rRNA) and each non-coding region separately using MAFFT v. 1.3.6 in Geneious v.9.1.8 (Biomatters Ltd.) and concatenated the alignments with SeqCat.pl v1.0 (Bininda-Emonds 2005). To find the best partition schemes and substitution models to describe our data in the phylogenetic analyses, we used PartitionFinder v2.1.1 (Lanfear *et al.* 2017). We used the greedy algorithm, unlinked branch-lengths, and considered 43 potential partitions: the 12S rRNA, the 16S rRNA, all the tRNA together, the control region, and the three codon positions in each of the 13 protein-coding genes. The best-fitting model and partition scheme were selected according to the Bayesian information criterion (BIC). Following PartitionFinder results, we separated our mitochondrial data in four partitions for both the maximum-likelihood (ML) and Bayesian analyses, with mostly GTR+I+G models (Table S2). We used RAxML v8.2.11 (Stamatakis 2014) to perform an ML tree reconstruction, with 20 alternative runs and 1000 replicates of non-parametric bootstrapping. We also used MrBayes v3.2.7 (Ronquist *et al.* 2012) for a Bayesian reconstruction, with eight independent runs of four Metropolis-coupled Markov chains

(MCMC) run for 5 million generations, sampled every 10 000 generations, and a burn-in of 1.25 million generations. We checked the convergence of the chains with Tracer v1.7.1 (Rambaut *et al.* 2018) and ensured that effective sample size (ESS) values were higher than 200 for all parameters, suggestive of proper chain convergence.

Nuclear DNA data

We concatenated the 4893 nuclear DNA markers (3.2 Mbp) for the phylogenetic analysis and used the reference sequences from *Corvus albus* and *Aphelocoma californica* as outgroups in the phylogenetic analysis. We estimated an ML tree with RAxML v8.2.11 (Stamatakis 2014) using the most parameter-rich model of sequence evolution with invariable sites and a gamma distributed rate variation among sites (GTR+I+G model). Due to computing limitations with large datasets, we could not perform nucleotide substitution model selection on the nuclear DNA dataset. We ran the analysis for 20 alternative runs and performed 1000 replicates of non-parametric bootstrapping.

Estimation of divergence times

Because the mitochondrial and nuclear DNA trees were fully congruent at the species level (see Results), and because fossils from members of Melanocharitidae are not available, we estimated divergence times using mitochondrial DNA data only, and secondary calibrations from Oliveros *et al.* (2019). We kept the complete mitochondrial dataset but removed the outgroups, and ran the same analysis as previously described to find the best partition schemes and associated substitution models. We used BEAST v2.5.1 (Bouckaert *et al.* 2014) to estimate divergence times within Melanocharitidae, using a relaxed lognormal uncorrelated evolutionary model for each partition. We assumed either Yule or birth–death branching processes as tree priors, and applied lognormal priors (M = 1, S = 1.25) for the mutation rates, and exponential priors (M = 1) for the mean clock rates. We calibrated the Melanocharitidae crown node with a normal distribution (M = 18.899 Mya, S = 2.95) and the split between *Toxorhamphus* and *Oedistoma* with another normal distribution (M = 17.463 Mya, S = 2.95) to follow Oliveros *et al.* (2019). We ran the analysis for 500 million generations, sampling every 500 000 generations, discarding the first 50 million generations as burn-in, and checking chain convergence with Tracer v1.7.1 (Rambaut *et al.* 2018).

RESULTS

A new species of *Melanocharis* berrypecker

The undescribed taxon is distinct from other members of the genus in plumage coloration (Figs 3 & 4), morphological measurements (Table 2) and genetic markers (Figs 5 & 6). We hereby designate it as a new species of berrypecker of the genus *Melanocharis*, and we propose the following names:

Melanocharis citreola, sp. nov. Milá, Ashari & Thébaud

Satin Berrypecker
Burungbuah Satin
Picabayas Satinado
Piquebaie Satiné

Holotype

Museum Zoologicum Bogoriense (MZB), Cibinong, West Java, Indonesia, MZB catalogue number 34796, male, Kumawa Mountains, Bomberai Peninsula, West Papua province, Indonesia, elevation 1191 m asl, 4.01134°S, 133.08751°W, mist-netted on 17 November 2014; prepared by Suparno (MZB-LIPI). GenBank accession number for the mitochondrial genome is MW323040, nuclear DNA is deposited in the NCBI BioSample database under accession SAMN16987481 (BioProject PRJNA682312), and Zoobank registration number is http://zoobank.org/urn:lsid:zoobank.org:act:E52D826A-00F8-4CDF-BBEA-EA9AE2068F9E.

Diagnosis

The new species can be readily assigned to *Melanocharis* by the stout black bill and iridescent blue-black upper parts contrasting with lighter underparts. It can be distinguished from all other members of the genus by the satin-white underparts, washed lemon yellow. It has a white outer vane of the outermost rectrix, compared to the two outermost rectrices in *M. longicauda*, which is also smaller and has yellowish-grey underparts. *M. versteri* has a longer tail with more extensive white patches on several external rectrices, and grey underparts.

Description of holotype

Adult male (Fig. 3A, B, Table 3). Bill and legs black. Iris dark brown. Plumage coloration: crown,

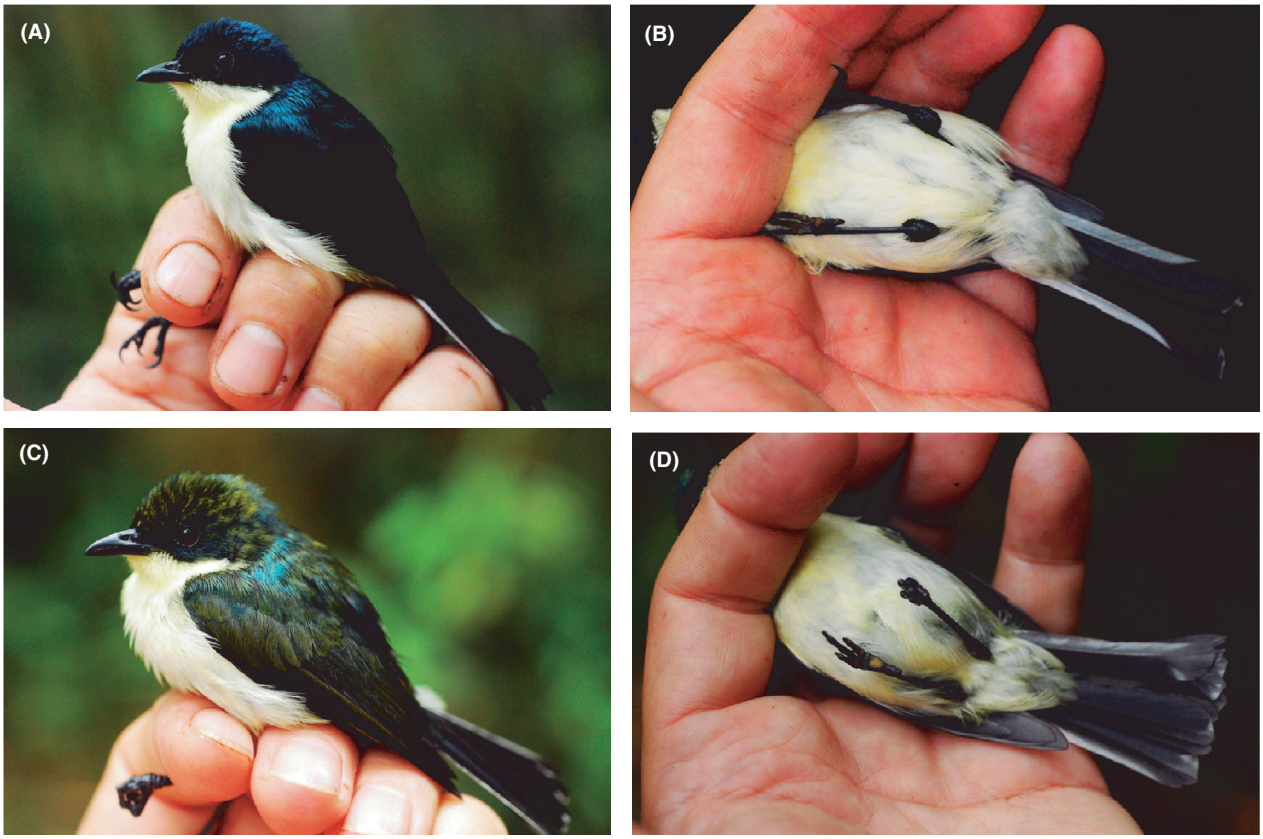

Figure 3. Live specimens of *Melanocharis citreola* sp. nov. in the hand. A and B. Adult male (MZB 36040). C and D. Immature male (MZB 36039). Photographs by B.M.

back and rump iridescent blue-black; throat, breast, belly and vent bright satiny white washed lemon yellow, with lemon wash especially pronounced in the throat, breast and belly, lighter on flanks; underwing feathers white; sharp malar line separating blue-black face from white throat; thigh feathers black, contrasting with white belly; wing feathers black, with white internal edges on primaries and secondaries; tail feathers entirely iridescent blue-black, except for the outermost rectrices, which have the proximal 80% of the outer vane coloured white (including the feather rachis), with the distal 3–4 mm of the white patch tapering off diagonally towards the external edge of the vane (Fig. 3B). Testes enlarged.

Measurements of holotype

Wing chord (unflattened): 62.0 mm; tarsus length: 19.4 mm; tail length: 49.5 mm; bill from base of skull: 11.2 mm; bill from distal end of nostril: 7.3 mm; bill width (at distal end of nostril): 4.1 mm; bill depth (at distal end of nostril): 3.5 mm. Measurements taken in the field by B.M.

Specimens examined

In addition to the holotype, one apparently adult male individual and two apparently immature males were captured in mist-nets between 1100 and 1200 m asl in 2017. They were prepared by H.A. in the field and are also held at the MZB in Cibinong, Indonesia, as paratypes. Mature male from 2017 similar to the holotype. Immature males (Fig. 3C, D) share the satin-white underparts washed yellow of the adult birds, but the upperparts are iridescent olive green with interspersed blue-black feathers; wing feathers (primaries, secondaries, tertiaries and wing coverts) blackish, with yellowish-olive outer edges; central tail feathers washed olive; four outer rectrices with distal white or light grey spots; white patch on outer vane of outermost rectrix as in adult, but washed grey internally, and not including the

Figure 4. Specimens of *Melanocharis citreola* sp. nov. compared to other members of the genus. From left to right: *Melanocharis versteri* (specimens 30755 and 30758), *M. citreola* sp. nov. (specimens 34796 and 36040), *M. longicauda* (specimens 30617 and 30618), and *M. nigra* (*M. n. unicolor* specimen 26047 and *M. n. nigra* specimen 34797). All specimens belong to the ornithological collection at the Museum Zoologicum Bogoriense, Cibinong, Indonesia. Photograph by H.A.

Table 2. Morphological measurements (means in mm and SD) of male specimens of four *Melanocharis* berrypecker species deposited at the Museum Zoologicum Bogoriense. Measurements taken by H.A.

Species	*N*	Wing	Tail	Tarsus	Bill length	Bill culmen	Bill width	Bill depth
M. citreola sp. nov.	4	61.75 (0.5)	50.75 (1.5)	19.18 (0.12)	12.04 (0.15)	7.48 (0.18)	4.51 (0.12)	3.85 (0.12)
M. versteri	6	63.33 (3.33)	71.33 (4.41)	22.13 (0.91)	13.79 (1.02)	7.66 (0.52)	4.45 (0.52)	4.00 (0.28)
M. nigra	6	63.17 (2.79)	42.00 (4.29)	15.72 (0.59)	13.80 (1.25)	7.04 (1.14)	3.80 (0.16)	3.97 (0.24)
M. longicauda	3	63.00 (1.00)	48.33 (5.51)	16.65 (0.51)	12.99 (1.09)	6.78 (0.27)	4.07 (0.25)	3.94 (0.59)

feather rachis (Fig. 3D); legs, bill and iris like adult male. Female: we did not capture nor observe females of the species during fieldwork. Diamond and Bishop (2015) reported sightings of a female putatively assigned to this taxon, which they described as having 'olive upperparts and pale, slightly yellowish, obscurely streaky underparts' (p. 319). Unfortunately, no specimens or photographs are available.

Moult

The two immature individuals (MZB 36038, MZB 36039) were moulting a few body feathers on the breast and back, presumably as part of a

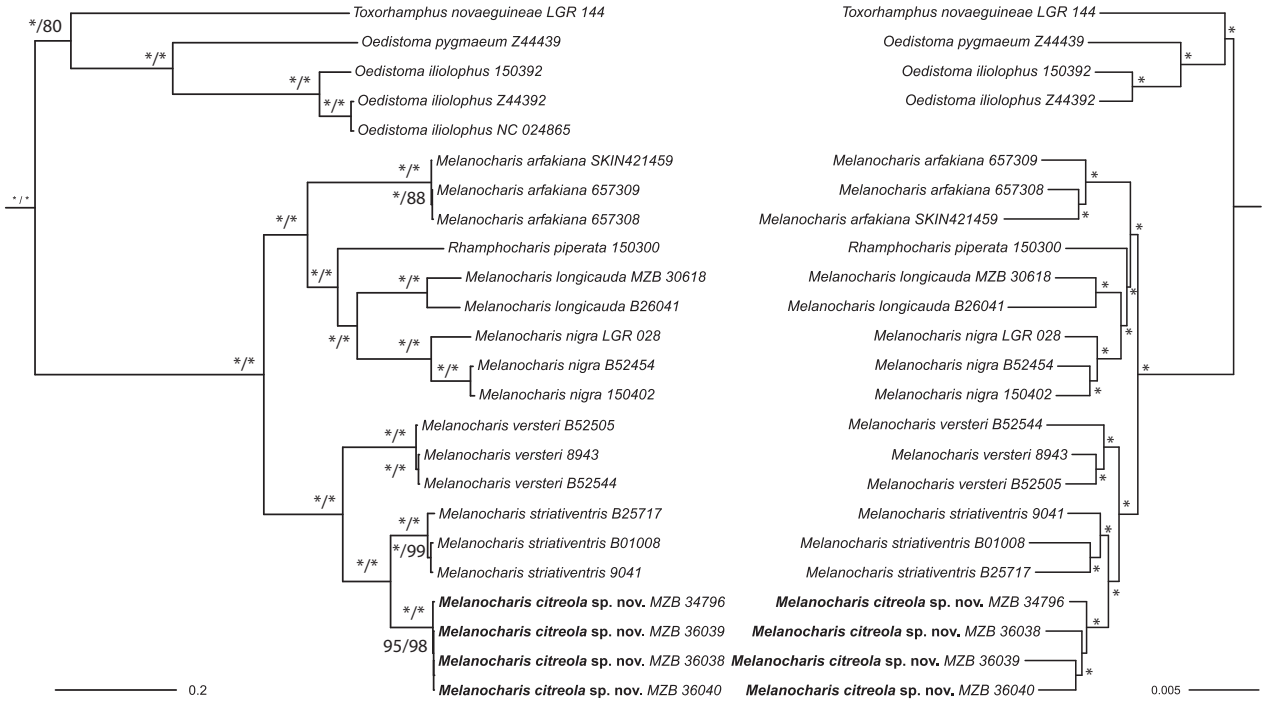

Figure 5. Phylogenetic trees of the family Melanocharitidae based on mtDNA (left) and genome-wide nuclear DNA (right), showing species-level topological concordance between the two datasets. On the left, Bayesian tree based on full mitogenomes, with support values on nodes corresponding to Bayesian posterior probability values on the left and ML bootstrap values on the right. Asterisks correspond to a probability of 1 or 100%, respectively, and values below 0.9 and 75%, respectively, are not shown. On the right, nuclear DNA tree based on ML analysis, with bootstrap values of 100% shown by an asterisk, and values below 75% are not shown. Outgroups are removed for clarity, and are shown in Figure S1.

postnatal moult. No moult was detected in the adult specimens.

Distribution, ecology and behaviour

Kumawa Mountains, Bomberai Peninsula, so far recorded at elevations of 1100-1200 m asl; Fakfak Mountains, Onin Peninsula, at an elevation between 1200 and 1500 m asl (see Gibbs 1994 and Discussion); both in western New Guinea (West Papua province, Indonesia). In the Kumawa Mountains the species was observed and captured in mid-montane cloud forest, with a canopy height of 10–30 m and an abundance of terrestrial and epiphytic ferns, mosses, and lichens where it seems to prefer relatively open areas with sparser trees and more abundant tree ferns (Fig. 7). The only individual observed in the field (other than those captured in the nets) was a silent and solitary adult male, observed for a few seconds perched on a horizontal branch 2 m above the ground.

Vocalizations

One of the captured individuals (adult male captured on 8 November 2017) vocalized on several occasions while being handled, giving high-pitched calls that can be described as rather similar to the contact calls of *M. versteri* (Avian Vocalizations Center, catalogue no. AV#3624). We note that the calls given by this single individual may be distress calls and thus not be representative of its usual vocalizations. These recordings have been uploaded to Xeno-canto (accession: XC560281).

Etymology

Melanocharis Sclater 1858 means black beauty. The specific epithet *citreola* refers to the lemon-yellow wash on the satiny-white underparts of males. The vernacular names Satin Berrypecker, Burungbuah Satin, Picabayas Satinado and Piquebaie Satiné, in English, Indonesian, Spanish and French, respectively, highlight the most striking characteristic of the new species.

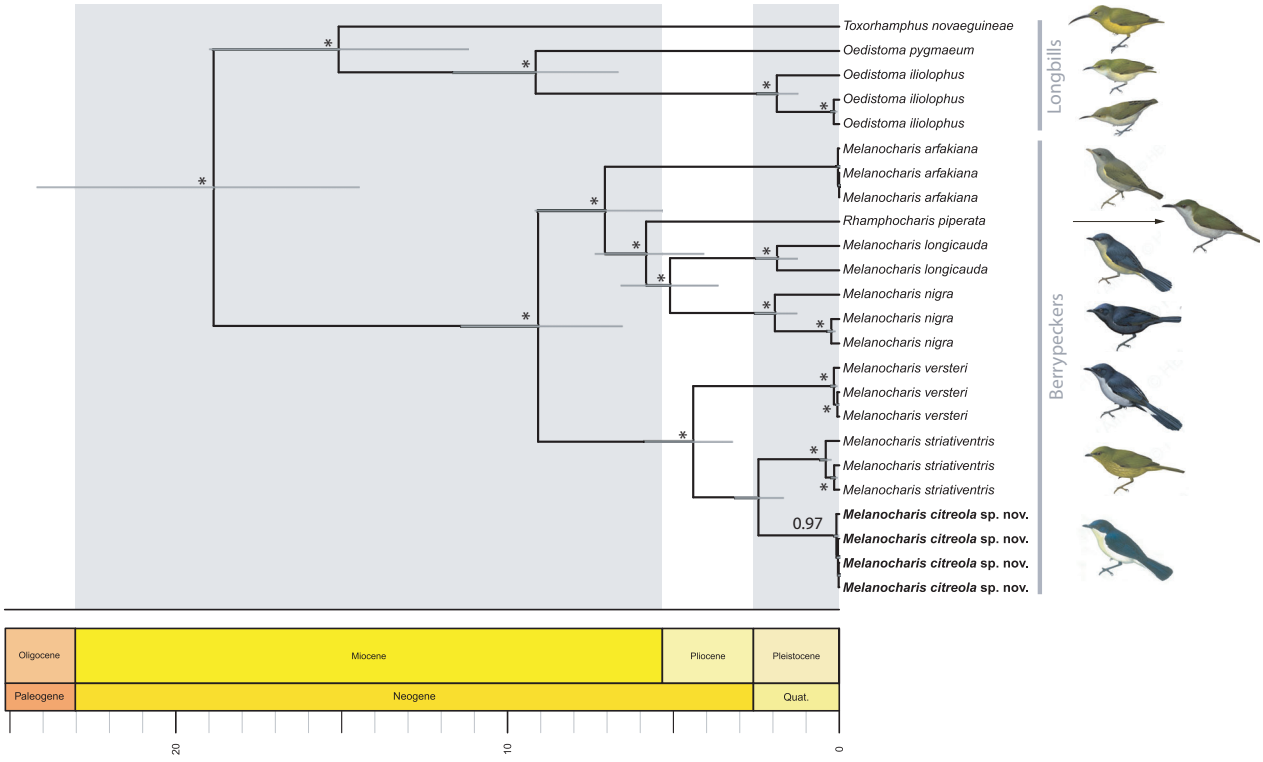

Figure 6. Dated Bayesian phylogenetic tree of the Melanocharitidae based on mitochondrial DNA data, using a Yule model and secondary calibrations from Oliveros *et al.* (2019) at the crown node (normal distribution; M = 18.899 Ma, S = 2.95) and the split between *Toxorhamphus* and *Oedistoma* (normal distribution; M = 17.463 Ma, S = 2.95). Asterisks correspond to a Bayesian posterior probability of 1.0. Nodes correspond to the mean age, with 95% Highest Probability Density (HPD) values shown as grey bars. For specific node dates see Table S3. The male bird illustration of *M. citreola* is from an original plate by Norman Arlott. The remaining illustrations, also by Norman Arlott, are used with permission from Lynx Edicions.

Table 3. Morphological measurements (in mm) and weight (in g) of *Melanocharis citreola* individuals taken in the field on live birds by B.M.

ID	Age	Sex	Mass	Wing	Tail	Tarsus	Bill culmen	Bill length	Bill width	Bill depth
MZB 34796	Adult	M	–	62.0	49.5	19.4	7.3	11.2	4.1	3.5
MZB 36040	Adult	M	9.2	61.0	50.5	19.6	7.3	11.9	4.0	3.6
MZB 36038	Imm.	M	11.7	59.0	48.0	19.7	6.9	11.4	3.8	3.7
MZB 36039	Imm.	M	11.1	62.5	46.5	19.8	6.8	11.3	3.7	3.9

Relative abundance in the Kumawa Mountains

During our 23 days of netting at the Kumawas, we captured 259 birds belonging to 26 different species. Details on the species captured, combined with observations and recordings obtained during the two expeditions, will be presented elsewhere. Relative to other species captured in our nets, *M. citreola* was in the central part of the distribution, with four captures in 23 days, which represents 0.019 captures per 100 net hours. The four individuals were captured in different days and locations, and therefore seem to represent independent captures. The species was uncommon in the area of the Kumawas where we worked, at least during the period of time we spent there, but could be more common in other localities or seasons, as

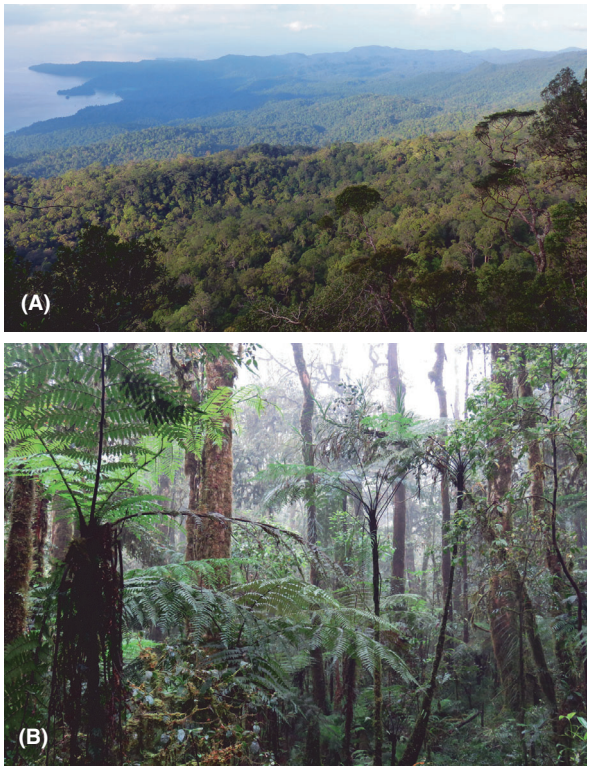

Figure 7. Cloud forest habitat at the sites where the specimens of *Melanocharis citreola* sp. nov. were captured in the Kumawa Mountains, New Guinea. A. View of the Kumawa Mountains from the 1100 m asl campsite (photograph by C.T.). B. Forest interior at 1200 m asl (photograph by B.M.).

suggested by other reports (Gibbs 1994, Diamond & Bishop 2015).

Genetic distances and phylogenetic relationships

Genetic data revealed that the four individuals sequenced are markedly divergent from other species in the genus, with average interspecific percentage divergence of 8.80% for COI (Table 4), 10.33% for Cyt*b* and 12.35% for ND2 (Table S3). Genetic distance between *M. citreola* and its closest relative *M. striativentris* was 3.27% for COI, 4.61% for Cyt*b* and 5.48% for ND2, indicating that *M. citreola* is highly genetically divergent from all currently recognized congeners (Table 4, Table S3).

The phylogenetic tree of all genera in the family Melanocharitidae based on mitogenomes was fully resolved, with all major nodes showing full support in both ML and Bayesian analyses (Fig. 5, Fig. S1). The topology of the tree based on nuclear data is fully congruent with that of the mtDNA tree, for both ML and Bayesian analyses, and all major nodes are also strongly supported (Fig. 5). Yule and Birth–Death models produced very similar topologies and node dates (Table S4), so only Yule trees are shown.

Divergence times in Melanocharitidae

According to the best available estimates based on fossil-calibrated molecular phylogenies, the diversification of the Melanocharitidae family started in the early Miocene, around 19 Mya (Oliveros *et al.* 2019, Stervander *et al.* 2020). The family is divided into two main clades, one corresponding to longbills (*Toxorhamphus* and *Oedistoma*), and the other to berrypeckers (*Melanocharis* and *Rhamphocharis*) (Fig. 6, Table S4). The two longbill clades are highly divergent and date back to the middle Miocene, with the two *Oedistoma* taxa diverging in the late Miocene. The *Melanocharis*/*Rhamphocharis* clade is divided into two well-supported subclades that diverged in the late Miocene, about 9.08 Mya (95% HPD: 6.57–11.38). In the first subclade, *M. citreola* and *M. striativentris* are found to be sister to *M. versteri*. In the second subclade, *Rhamphocharis* falls as sister to *M. longicauda* and *M. nigra*, which are each other's closest relatives, and this clade is sister to *M. arfakiana*. Intraspecific divergence in both *Oedistoma* and *Melanocharis* is of Pleistocene origin. In *Melanocharis*, divergence among subspecies seems to be low in *M. versteri* (between subspecies *M. v. maculiceps* and *M. v. meeki*) and *M. arfakiana* (between central and eastern localities), yet it is marked in *M. longicauda* and *M. nigra*. In the latter, the *M. n. nigra* individual from the Bird's Neck shows marked divergence from representatives of the other two subspecies (*M. n. chloroptera* and *M. n. unicolor*) from the Border and Eastern Ranges of New Guinea, respectively. The two individuals of *M. longicauda*, one a member of *M. l. longicauda* from the Western Ranges and the other a member of *M. l. captata* from the Huon Peninsula, showed marked differentiation as well.

DISCUSSION

A new species of *Melanocharis* berrypecker

Melanocharis citreola is only the second species to be described in New Guinea in the last 80 years,

Table 4. Sequence divergence in the COI mitochondrial gene among and within species in the genus *Melanocharis* and one species of *Rhamphocharis*. Below diagonal, *p*-distances among species; along diagonal (in italics), *p*-distances within species. Sample sizes for this analysis are as follows: *M. citreola* ($n = 3$), *M. striativentris* ($n = 3$), *M. longicauda* ($n = 2$), *M. nigra* ($n = 3$), *M. arfakiana* ($n = 3$), *R. piperata* ($n = 1$). Similar distance matrices for Cyt *b* and ND2 genes are available in Table S3.

	citreola	*striativentris*	*versteri*	*longicauda*	*nigra*	*arfakiana*	*piperata*
citreola	*0.00*						
striativentris	0.0327	*0.01*					
versteri	0.0727	0.0682	*0.00*				
longicauda	0.1033	0.1028	0.0960	*0.03*			
nigra	0.1173	0.1151	0.1095	0.0893	*0.03*		
arfakiana	0.0965	0.0957	0.1015	0.1005	0.1011	*0.00*	
piperata	0.1054	0.1083	0.1051	0.0946	0.0951	0.0957	–

and represents the first recognized endemic species to the Bird's Neck region (Beehler *et al.* 2007, Pratt & Beehler 2014, Beehler & Pratt 2016). This suggests that very few other species-level undescribed bird taxa may remain to be found on the island, and is a reflection of the thorough surveys that ornithologists before us have carried out across the region with much effort over the last several decades (Mayr 1941, Rand & Gilliard 1967, Diamond 1972, Coates 1985, 1990, Beehler *et al.* 1986, Beehler & Pratt 2016, Gregory 2017, Joseph *et al.* 2019, Freeman *et al.* 2013). This is in contrast to the taxonomic situation of other animal and plant groups, where a large proportion of species and higher taxonomic categories in New Guinea remain to be described and classified (Marshall & Beehler, 2007). However, that does not mean that New Guinea's avifauna is well known, and many aspects of geographical variation, distribution, biogeography and natural history remain poorly known for most species (Mack & Dumbacher 2007, Pratt & Beehler 2014, Beehler & Pratt 2016), even though some major advances have been achieved recently in some groups (e.g. Deiner *et al.* 2011, Jønsson *et al.* 2011, Irestedt *et al.* 2016, Jønsson *et al.* 2017, Marki *et al.* 2017, Norman *et al.* 2018, Garg *et al.* 2019, Joseph *et al.* 2019).

The designation of *M. citreola* as a valid species is consistent with most current species concepts, as both phenotypic and genetic data reveal that it represents an independent evolutionary lineage highly differentiated from its congeners by a degree of divergence similar or superior to that found among other members of the genus (Padial *et al.* 2010). A robust molecular phylogeny of the genus has proven instrumental in revealing true relationships among taxa, and provides important information on the evolutionary history of the genus. Several traits such as tail length, the white patch on the outer rectrices and the elevation at which it was observed suggested a close relationship of *M. citreola* with *M. longicauda*, yet our phylogeny revealed that the sister species is actually *M. striativentris*, which is entirely olive green with streaky breast and belly instead of black and white, and lacks sexual dichromatism. The white tail patch is therefore the result of convergent evolution or, alternatively, the trait has been lost in other members of the genus, such as *M. striativentris* (although *M. s. albicauda* from the SE Peninsula shows white spots on the tips of outer rectrices, Beehler & Pratt 2016), *M. arfakiana* and *M. nigra*. A similar but more prominent white patch is present in the tail of *M. versteri*, where it includes the more proximal sections of not one but three outer rectrices.

Previous sightings of *M. citreola* in the Kumawa and Fakfak Mountains

The only other biologists to have visited the upper range of the Kumawa Mountains before us are J. Diamond and D. Bishop, who conducted expeditions in 1983 (J.D. only) and 2013 (J.D. & D.B.), spending 12 and 7 days above 1000 m asl on each one, respectively. During his 1983 expedition, Diamond collected, described and named three new subspecific taxa from the Kumawas (*Peneothello cryptoleucus maximus*, *Pachycephala soror octogenarii* and *Melipotes fumigatus kumawa*) and proposed several other potential new taxa in

need of further study, as reported in his thorough account of the expedition (Diamond 1985). Although no mention of the *Melanocharis* berrypecker was made in that publication, in a recent article summarizing information on species recorded in their four surveys of the Fakfaks and Kumawas, Diamond and Bishop (2015) do report seeing in 2013 several individuals that fit the general description of *M. citreola*, which they refer to as *Melanocharis longicauda*. Moreover, they report capturing six individuals of unspecified sex back in 1983, which were apparently released without being described or photographed (Diamond & Bishop 2015). They further report the female being green overall, with streaked underparts and a black bill. Unfortunately, since we did not capture any females in our two visits to Kumawa, a formal and definitive description of the female is pending.

Gibbs (1994) visited the Fakfak mountains in 1992 and reported seeing several individuals of a *Melanocharis* berrypecker that he identified as *M. longicauda* and described succinctly as follows: 'Underparts satiny-white rather than grey, more or less washed with lemon-yellow on throat and breast and with lemon-yellow pectoral tufts'. Upon inspection of our photographs of *M. citreola*, he did not notice any differences between what he saw in the Fakfaks and what we collected in the Kumawas (Gibbs, *in litt.*). Given the similarities between the faunas in the two mountain ranges (Diamond & Bishop 2015), largely due to their geographical proximity (being separated by just 80 km of lowland forest), we think it is reasonable to consider the Fakfak population as belonging to the same taxon, pending confirmation with proper specimens and photographs.

According to our capture data in the Kumawas, the species appears to be uncommon, but probably not rare, and was captured at the same rate as other species known to be common in the forest despite moderate capture rates in mist-nets, such as Drongo Fantail *Chaetorhynchus papuensis* or Chestnut-breasted Cuckoo *Cacomantis castaneiventris*. Diamond and Bishop (2015) reported the new species as common in their 1983 South Kumawa transect (abundance category 3 out of 4) in August–September, as fairly common in their 2013 Central Kumawa transect (category 2 out of 4) in February–March, and as uncommon in their 1983 North Kumawa transect (category 1 out of 4) in February–March.

Diversification of the family Melanocharitidae

The Melanocharitidae is an old family that originated in the Oligocene, about 28 Mya (Oliveros *et al.* 2019, Stervander *et al.* 2020), long before the island of New Guinea as we know it today was available for dispersal and colonization by terrestrial organisms (Hill & Hall, 2003, van Ufford & Cloos 2005). Recent phylogenetic results indicate that the Melanocharitidae represents an early lineage of Passerides (Moyle *et al.* 2016, Oliveros *et al.* 2019), and emerged shortly after the split between the ancestral Australasian crow-like Corvides and the primarily extra-Australasian Passerides. The Melanocharitidae lineage must have originated either on an emerging proto-Papuan archipelago (Jønsson *et al.* 2011, 2017, Aggerbeck *et al.* 2014, Toussaint *et al.* 2014) or, as more recently proposed for songbirds (Moyle *et al.* 2016), in rainforests of Australia from which it colonized New Guinea around the middle Miocene when the island had become a substantial landmass (Hall & Sevastjanova 2012, Hall, 2012). Its absence from Australia is thus somewhat surprising, as noted by Mayr and Amadon (1947), and suggests that it is a relictual group whose current diversity and distribution may have been shaped by extinction (Heinsohn & Hope 2006, Schodde 2006). The diversification of genera such as *Melanocharis* and *Oedistoma*, which took place during the main uplift of New Guinea in the Middle and Late Miocene, was more likely to have taken place on New Guinea itself, similarly to what has been described in other bird groups, such as lories and lorikeets (Schweizer *et al.* 2015), woodland kingfishers and kookaburras (Andersen *et al.* 2018), or crowned pigeons (Bruxaux *et al.* 2018). Our phylogenetic reconstruction also confirms that longbill genera *Oedistoma* and *Toxorhamphus* are very old lineages, and despite their phenotypic similarity, the evolutionary distance between them is as large as that between them and *Melanocharis* berrypeckers (Barker *et al.* 2004, Irestedt & Ohlson 2008, Jønsson *et al.* 2011).

The family Melanocharitidae underwent a striking phenotypic diversification associated primarily with foraging traits, and represents an excellent example of evolutionary radiation with additional divergence along axes of habitat and signalling, implying a role for both natural and sexual selection (Streelman & Danley 2003). A range of bill

shapes has evolved within the family, from the stout bills of the primarily frugivorous *Melanocharis* berrypeckers to the slender, decurved bills of primarily nectarivorous *Toxorhamphus* and *Oedistoma* longbills, and the intermediately elongated beaks of *Rhamphocharis* berrypeckers, which appear to feed on berries and small fruits (Pratt & Beehler 2014, Gregory & Bonan, 2020). Our phylogenetic results reveal that *Rhamphocharis* berrypeckers (*R. piperata* and *R. crassirostris*, the latter not included in our study) are nested within *Melanocharis*, as sister to the clade formed by *M. longicauda* and *M. nigra*, rendering *Melanocharis* paraphyletic. Given these results, we recommend that the two species currently in *Rhamphocharis* be included in the genus *Melanocharis*, as originally proposed by Sibley and Monroe (1990) and already implemented by some authors (Freeman *et al.* 2013, Gregory *et al.* 2020).

According to our results, and well in line with recent findings on other New Guinean passerine birds (Deiner *et al.* 2011, Irestedt *et al.* 2016, 2017, Marki *et al.* 2018, Jønsson *et al.* 2019), considerable diversity within species in the genus *Melanocharis* remains to be explored and documented. Specifically, we show that at least three of the four subspecies of Black Berrypecker *M. nigra*, which are quite distinct according to phenotype (Salomonsen 1960), are genetically divergent and may represent independent evolutionary lineages perhaps deserving species status. Further phylogeographical analyses including sampling at contact zones among these intraspecific taxa will be necessary to resolve the systematics of the complex. The same can be said about the Mid-mountain Berrypecker *M. longicauda*, as suggested by the high genetic differentiation among individuals of the two subspecies included in our study out of the five currently recognized across the island. Finally, *M. striativentris*, the sister species to *M. citreola*, also shows considerable variation across its range, including two main subspecies corresponding to western and eastern sections of the main cordillera (*M. s. axillaris* and *M. s. striativentris*, respectively) and including the form *albicauda* from the South East Peninsula of New Guinea, synonymized with *M. s. striativentris* by Beehler and Pratt (2016), which shows white spots on the tips of the outer rectrices, a character shared with immatures of *M. citreola*.

We thank Thane Pratt, Bruce Beehler, Phil Gregory, Knud Jønsson, the Associated Editor Gary Voelker, Editor Rauri Bowie and two anonymous reviewers for providing constructive comments on the manuscript. We are grateful to the villagers of Nusa Ulan, and to their chief Asamai, for permission to access the Kumawa Mts and for providing excellent guidance and field assistance during our 2014 and 2017 expeditions. Suparno and Hadi, from MZB, helped prepare specimens in the field. Bruno Fromento provided essential logistical support during the 2017 expedition. Jared Diamond provided information on local contacts at Nusa Ulan and the access point along the coast to access the highlands. Robert Kirk provided us with an advance copy of the Pratt and Beehler 2014 field guide. Bruce Beehler and Thane Pratt made available to us their yet unpublished checklist and appended materials. Uxue Sescun assisted with DNA extractions, Sophie Manzi prepared sequencing libraries, and Pablo Valencia run analyses in the molecular laboratory at MNCN to determine the sex of *Melanocharis citreola* individuals. María Victoria González Cascón made the map for Figure 1. We are grateful to Kadarusman, Laurent Pouyaud and Régis Hocdé for encouraging us to conduct these expeditions and facilitating many logistical aspects. We thank the National Museum of Natural History in Washington, DC, USA, for loaning us tissue samples of the two *Melanocharis arfakiana* specimens collected by Bret Whitney, Leo Joseph of the Australian National Wildlife Collection, Joanna Sumner of Museums Victoria, and Knud Jønsson of the Natural History Museum of Denmark, who kindly processed loans of many specimens. Knud Jønsson kindly provided sequence data of the AMNH 1933 Matsika sample of *Melanocharis arfakiana*. Fieldwork was supported by the Lengguru Project (www.lengguru.org) conducted by the French Institut de Recherche pour le Développement (IRD), the Indonesian Institute of Sciences (LIPI) with the Research Center for Biology (RCB) and the Research Center for Oceanography (RCO), the University of Papua (UNIPA), the University of Cendrawasih (UNCEN), the University of Musamus (UNMUS), and the Polytechnic KP Sorong with corporate sponsorship from COLAS and TIPCO groups, Veolia Water and the Total Foundation. High-throughput sequencing was supported by the 'Laboratoire d'Excellence' TULIP (ANR-10-LABX-41). K.S. acknowledges GACR grant 18-23794Y.

AUTHOR CONTRIBUTION

Borja Milá: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Methodology (equal); Supervision (equal); Writing-original draft (lead); Writing-review & editing (lead). **Jade Bruxaux:** Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing-review & editing (equal). **Guillermo Friis:** Formal analysis (equal); Investigation (equal); Methodology

(equal). **Katerina Sam:** Data curation (equal); Investigation (equal); Writing-review & editing (equal). **Hidayat Ashari:** Data curation (equal); Investigation (equal); Methodology (equal). **Christophe Thébaud:** Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Project administration (equal); Supervision (equal); Writing-review & editing (equal).

Data Availability Statement

Mitochondrial genomes have been deposited in GenBank under accessions MW323029-MW323051. Nuclear DNA data have been deposited in the Sequence Read Archive (SRA) of the National Center for Biotechnology Information (NCBI) under BioProject PRJNA682312. Nuclear data alignments have been deposited in Dryad (https://doi.org/10.5061/dryad.fbg79cnsv). This paper describing the new species of berrypecker is registered on ZooBank under LSID urn:lsid:zoobank.org:act:E52D826A-00F8-4CDF-BBEA-EA9AE2068F9E.

REFERENCES

Aggerbeck, M., Fjeldså, J., Christidis, L., Fabre, P.-H. & Jønsson, K.A. 2014. Resolving deep lineage divergences in core corvoid passerine birds supports a proto-Papuan island origin. *Mol. Phyl. Evol.* **70**: 272–285.

Andersen, M.J., McCullough, J.M., Mauck, W.M. III, Smith, B.T. & Moyle, R.G. 2018. A phylogeny of kingfishers reveals an Indomalayan origin and elevated rates of diversification on oceanic islands. *J. Biogeogr.* **45**: 269–281.

Bailly, V., Pubellier, M., Ringenbach, J.C., De Sigoyer, J. & Sapin, F. 2009. Deformation zone 'jumps' in a young convergent setting; the Lengguru fold-and-thrust belt. *New Guinea Island. Lithos* **113**: 306–317.

Baldwin, S.L., Fitzgerald, P.G. & Webb, L.E. 2012. Tectonics of the New Guinea Region. *Annu. Rev. Earth Planet Sci.* **40**: 495–520.

Barker, F.K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. 2004. Phylogeny and diversification of the largest avian radiation. *Proc. Natl Acad. Sci. USA* **101**: 11040–11045.

Beehler, B. 2020. *New Guinea, nature and culture of Earth's grandest island*. Princeton, NJ: Princeton University Press.

Beehler, B.M., Diamond, J., Kemp, M., Scholes, E., Milensky, C. & Laman, T. 2012. Avifauna of the Foja Mountains of western New Guinea. *Bull. B.O.C.* **132**: 84–101.

Beehler, B.M. & Pratt, T.K. 2016. *Birds of New Guinea. Distribution, taxonomy, and systematics*. Princeton, NJ: Princeton University Press.

Beehler, B.M., Pratt, T.K. & Zimmerman, D.A. 1986. *Birds of New Guinea*. Princeton, NJ: Princeton University Press.

Beehler, B.M., Prawiradilaga, D.M., de Fretes, Y. & Kemp, N. 2007. A new species of smoky honeyeater (Meliphagidae: *Melipotes*) from western New Guinea. *Auk* **124**: 1000–1009.

Bininda-Emonds, O.R.P. 2005. *SeqCat.pl version 1.0. Program distributed by the author*. Oldenburg: AG Systematik und Evolutionsbiologie, IBU - Fakultät V, Carl von Ossietzky Universität.

Bolger, A.M., Lohse, M. & Usadel, B. 2014. Trimmomatic: a flexible trimmer for Illumina sequence data. *Bioinformatics* **30**: 2114–2120.

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A. & Drummond, A.J. 2014. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comp. Biol.* **10**: e1003537.

Bruxaux, J., Gabrielli, M., Ashari, H., Prŷs-Jones, R., Joseph, L., Milá, B., Besnard, G. & Thébaud, C. 2018. Recovering the evolutionary history of crowned pigeons (Columbidae: *Goura*): implications for the biogeography and conservation of New Guinean lowland birds. *Mol. Phyl. Evol.* **120**: 248–258.

Clements, J.F. 2015. *The Clements Checklist of Birds of the World*. 6th ed., with updates to August 2015. Ithaca, NY: Cornell University Press.

Coates, B.J. 1985. *The Birds of Papua New Guinea. Vol. 1. Non-passerines*. Alderley, QLD: Dove Publications.

Coates, B.J. 1990. *The Birds of Papua New Guinea. Vol. 2. Passerines*. Alderley, QLD: Dove Publications.

Deiner, K., Lemmon, A.R., Mack, A.L., Fleischer, R.C. & Dumbacher, J.P. 2011. A passerine bird's evolution corroborates the geologic history of the island of New Guinea. *PLoS One* **6**: e19479.

Diamond, J. 1972. *Avifauna of the Eastern Highlands of New Guinea*. Cambridge, MA: Nuttall Ornithological Club.

Diamond, J. 1985. New distributional records and taxa from the outlying mountain ranges of Irian Jaya. *Emu* **85**: 65–91.

Diamond, J. & Bishop, K.D. 2015. Avifaunas of the Kumawa and Fakfak Mountains, Indonesian New Guinea. *Bull. B.O.C.* **135**: 292–336.

Fjeldså, J., Christidis, L. & Ericson, P.G.P. (eds) 2020. *The Largest Avian Radiation. The Evolution of Perching Birds, or the Order Passeriformes*. Barcelona: Lynx Edicions.

Freeman, B.G., Class, A., Mandeville, J., Tomassi, S. & Beehler, B.M. 2013. Ornithological survey of the mountains of the Huon Peninsula, Papua New Guinea. *Bull. B.O.C.* **133**: 4–18.

Fridolfsson, A.K. & Ellegren, H. 1999. A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.* **30**: 116–121.

Garg, M.K., Sam, K., Chattopadhyay, K., Sadanandan, K.R., Koane, B., Ericson, P.G.P. & Rheindt, F.E. 2019. Gene flow in the Müllerian mimicry ring of a poisonous Papuan songbird clade (*Pitohui*; Aves). *Gen. Biol. Evol.* **11**: 2332–2343.

Gibbs, D. 1994. Undescribed taxa and new records from the Fakfak Mountains, Irian Jaya. *Bull. B.O.C.* **114**: 4–12.

Global Forest Watch. 2014. *World Resources Institute*. Available at: www.globalforestwatch.org (accessed 16 June 2020).

Gregory, P. 2017. *Birds of New Guinea, including Bismarck Archipelago and Bougainville*. Barcelona: Lynx Edicions.

Gregory, P. & Bonan, A. 2020. Berrypeckers and Longbills (Melanocharitidae). In del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds) *Handbook of the Birds of the World Alive*. Barcelona: Lynx Edicions. https://www.hbw.com/node/52347 (accessed 31 March 2020).

Gregory, P., del Hoyo, J., Christie, D.A. & Collar, N. 2020. Spotted Berrypecker (*Melanocharis crassirostris*), version 1.0. In: Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S. (eds). *Birds of the World*. Ithaca, NY: Cornell Lab of Ornithology.

Griffiths, R., Double, M.C., Orr, K. & Dawson, R.J.G. 1998. A DNA test to sex most birds. *Mol. Ecol.* **7**: 1071–1075.

Hall, R. 2012. Late Jurassic–Cenozoic reconstructions of the Indonesian region and the Indian Ocean. *Tectonophysics* **570–571**: 1–41.

Hall, R. & Sevastjanova, I. 2012. Australian crust in Indonesia. *Aust. J. Earth Sci.* **59**: 827–844.

Heinsohn, T., Hope, G. 2006. The Torresian connections: zoogeography of New Guinea. In Merrick, J.R. et al. (eds) *Evolution and Biogeography of Australasian Vertebrates*. Oatlands, NSW: Auscipub.

Hill, K.C. & Hall, R. 2003. Mesozoic–Cenozoic evolution of Australia's New Guinea margin in a west Pacific context. *Geol. Soc. Am. Spec.* **372**: 265–290.

Irestedt, M., Batalha-Filho, H., Ericson, P.G.P., Christidis, L. & Schodde, R. 2017. Phylogeny, biogeography and taxonomic consequences in a bird-of-paradise species complex, *Lophorina–Ptiloris* (Aves: Paradisaeidae). *Zool. J. Linn. Soc.* **181**: 439–470.

Irestedt, M., Batalha-Filho, H., Roselaar, C.S., Christidis, L. & Ericson, P.G.P. 2016. Contrasting phylogeographic signaturs in two Austrao-Papuan bowerbird species complexes (Aves: *Ailuroedus*). *Zool. Scr.* **45**: 365–379.

Irestedt, M. & Ohlson, J.I. 2008. The division of the major songbird radiation into Passerida and 'core Corvoidea' (Aves: Passeriformes) – the species tree vs. gene trees. *Zool. Scr.* **37**: 305–313.

Jønsson, K.A., Borregaard, M.K., Carstensen, D.W., Hansen, L.A., Kennedy, J.D., Machac, A., Marki, P.Z., Fjeldså, J. & Rahbek, C. 2017. Biogeography and biotic assembly of Indo-Pacific corvoid passerine birds. *Ann. Rev. Ecol. Evol. Syst.* **48**: 231–253.

Jønsson, K.A., Fabre, P.-H., Ricklefs, R.E. & Fjeldså, J. 2011. Major global radiation of corvoid birds originated in the proto-Papuan archipelago. *Proc. Natl Acad. Sci. USA* **108**: 2328–2333.

Jønsson, K.A., Reeve, A.H., Mozes, A.H., Blom, P.K., Irestedt, M. & Marki, P.Z. 2019. Unrecognised (species) diversity in New Guinean passerine birds. *Emu* **119**: 191–195.

Joseph, L., Heinsohn, R. & Mack, A. 2019. Ornithology of New Guinea and the Indo-Pacific Islands: introduction to the special issue of Emu-Austral Ornithology and a dedication to Paul Igag. *Emu* **119**: 191–195.

Katoh, K. & Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* **30**: 772–780.

Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B. 2017. PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Mol. Biol. Evol.* **34**: 772–773.

Li, H. & Durbin, R. 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics* **25**: 1754–1760.

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., Marth, G., Abecasis, G. & Durbin, R. 2009. The sequence alignment/map format and SAMtools. *Bioinformatics* **25**: 2078–2079.

Mack, A.L. & Dumbacher, J.P. 2007. Birds of Papua. In Marshall, A.J. & Beehler, B.M. (eds) *The Ecology of Papua*: 654–688. Singapore: Periplus Editions.

Marki, P.Z., Fjeldså, J., Irestedt, M. & Jønsson, K.A. 2018. Molecular phylogenetics and species limits in a cryptically coloured radiation of Australo-Papuan passerine birds (Pachycephalidae: *Colluricincla*). *Mol. Phyl. Evol.* **124**: 100–105.

Marki, P.Z., Jønsson, K.A., Irestedt, M., Nguyen, J.M.T., Rahbek, C. & Fjeldså, J. 2017. Supermatrix phylogeny and biogeography of the Australasian Meliphagides radiation (Aves: Passeriformes). *Mol. Phyl. Evol.* **107**: 516–529.

Marshall, A.J. & Beehler, B.M. 2007. *The Ecology of Papua*. Singapore: Periplus Editions.

Mayr, E. 1941. *List of New Guinea Birds. A Systematic and faunal list of the birds of New Guinea and adjacent islands*. New York: The American Museum of Natural History.

Mayr, E. & Amadon, D. 1947. A review of the Dicadeidae. *Am. Mus. Novit.* **1360**: 1–32.

McCormack, J.E., Tsai, W.L.E. & Faircloth, B.C. 2015. Sequence capture of ultraconserved elements from bird museum specimens. *Mol. Ecol. Res.* **16**: 1189–1203.

Moyle, R.G., Oliveros, C.H., Andersen, M.J., Hosner, P.A., Benz, B.W., Manthey, J.D., Travers, S.L., Brown, R.M. & Faircloth, B.C. 2016. Tectonic collision and uplift of Wallacea triggered the global songbird radiation. *Nat. Commun.* **7**: 12709.

Norman, J.A., Christidis, L. & Schodde, R. 2018. Ecological and evolutionary diversification in the Australo-Papuan scrubwrens (*Sericornis*) and mouse-warblers (*Crateroscelis*), with a revision of the subfamily Sericornithinae (Aves: Passeriformes: Acanthizidae). *Org. Div. Evol.* **18**: 241–259.

Oliveros, C.H., Field, D.J., Ksepka, D.T., Barker, F.K. et al 2019. Earth history and the passerine superradiation. *Proc. Natl Acad. Sci. USA* **116**: 7916–7925.

Padial, J.M., Miralles, A., De la Riva, I. & Vences, M. 2010. The integrative future of taxonomy. *Front. Zool.* **7**: 16.

Pratt, T.K. & Beehler, B.M. 2014. *Birds of New Guinea*, 2nd ed. Princeton, NJ: Princeton University Press.

Prum, R.O., Berv, J.S., Dornburg, A., Field, D.J., Townsend, J.P., Moriarty Lemmon, E. & Lemmon, A.R. 2015. A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**: 569–573.

Rambaut, A., Drummond, A., Xie, D., Baele, G. & Suchard, M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Syst. Bio.* **67**: 901.

Rand, A.L. & Gilliard, E.T. 1967. *Handbook of New Guinea Birds*. London: Weidenfeld and Nicolson.

Rheindt, F.E., Prawiradilaga, D.M., Ashari, H., Suparno, Lee, G.W.X., Wu, M.Y. & Ng, N.S.R. 2020. A lost world in Wallacea: description of a montane archipelagic avifauna. *Science* **367**: 167–170.

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Bio.* **61**: 539–542.

Salomonsen, F. 1960. Notes on Flowerpeckers (Aves, Dicaeidae) 1. The Genera *Melanocharis*, *Rhamphocharis*, and *Prionochilus*. American MUSEUM NOVITATES No. 1990.

Sapin, F., Pubellier, M., Ringenbach, J.C. & Bailly, V. 2009. Alternating thin versus thick-skinned decollements, example in a fast tectonic setting: the Misool–Onin–Kumawa Ridge (West Papua). *J. Struct. Geol.* **31**: 444–459.

Schodde, R. 2006. Australasia's bird fauna today–origins and evolutionary development. In Merrick, J.R. et al. (eds) *Evolution and Biogeography of Australasian Vertebrates*: 413–458. Oatlands, NSW: Auscipub.

Schodde, R. & Christidis, L. 2014. Relicts from Tertiary Australasia: undescribed families and subfamilies of songbirds (Passeriformes) and their zoogeographic signal. *Zootaxa* **3786**: 501–522.

Schweizer, M., Wright, T.F., Peñalba, J.V., Schirtzinger, E.E. & Joseph, L. 2015. Molecular phylogenetics suggests a New Guinean origin and frequent episodes of founder-event speciation in the nectarivorous lories and lorikeets (Aves: Psittaciformes). *Mol. Phylogenet. Evol.* **90**: 34–48.

Sibley, C.G. & Monroe, B.L. 1990. *Distribution and taxonomy of birds of the world*. New Haven, CT: Yale University Press.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.

Stervander, M., Fjeldså, J., Christidis, L., Ericson, P.G.P., Ohlson, J.I. & Alström, P. 2020. Appendix 2. An updated chronology of passerine birds. In Fjeldså, J., Christidis, L. & Ericson, P.G.P. (eds) *The Largest Avian Radiation. The Evolution of Perching Birds, or the Order Passeriformes*: 387–396. Barcelona: Lynx Edicions.

Streelman, J.T. & Danley, P.D. 2003. The stages of vertebrate evolutionary radiation. *Trends Evol. Evol.* **18**: 126–131.

Toussaint, E.F.A., Hall, R., Monaghan, M.T., Sagata, K., Ibalim, S., Shaverdo, H.V., Vogler, A.P., Pons, J. & Balke, M. 2014. The towering orogeny of New Guinea as a trigger for arthropod megadiversity. *Nat. Commun.* **5**: 1–10.

Van Ufford, A.Q. & Cloos, M. 2005. Cenozoic tectonics of New Guinea. *AAPG bulletin* **89**: 119–140.

Received 16 June 2020;
Revision 30 November 2020;
revision accepted 31 May 2021.
Associate Editor: Gary Voelker

SUPPORTING INFORMATION

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

Figure S1. Phylogenetic trees of the family Melanocharitidae including outgroups.

Figure S2. Dated Melanocharitidae Bayesian tree based on the whole mitogenome, a Birth-Death model, and secondary calibrations from Oliveros *et al.* (2019) at the crown node (normal distribution; M=18.899 Ma, S=2.95) and the split between *Toxorhamphus* sp. and *Oedistoma* sp. (normal distribution; M=17.463 Ma, S=2.95).

Table S1. Number of Illumina reads sequenced and mapped against reference genomes for the different taxa in the study.

Table S2. Partitions and substitution models proposed by PartitionFinder and used in the mitochondrial phylogenies built with RAxML, MrBayes, and BEAST.

Table S3. Sequence divergence in Cyt*b* and ND2 mitochondrial genes among and within species in the genus *Melanocharis* and one species of *Rhamphocharis*.

Table S4. Node ages in the mtDNA phylogenetic tree according to secondary calibrations from Oliveros *et al.* (2019) at the crown node 1 (normal distribution; M=18.899 Ma, S=2.95) and the split between *Toxorhamphus* sp. and *Oedistoma* sp. (node 20; normal distribution; M=17.463 Ma, S=2.95), using Yule and Bird-Death (BD) models of sequence evolution for each one.