FRONTISPIECE. Adult and immature males of the Satin Berryecker *Melanocharis citreola* sp. nov. from the Kumawa Mountains, New Guinea. Original artwork by Norman Arlott.
A new, undescribed species of *Melanocharis* berrypecker from western New Guinea and the evolutionary history of the family Melanocharitidae

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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.

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

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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

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.
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/ES/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-asmb/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 Ranges | Fresh tissue |
| MZB        | 30618 | Melanocharis longicauda Melanocharis longicauda longicauda | Unknown | -4.09 | 137.06 | Western Ranges | Fresh tissue |
| 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 | Fresh tissue |
| ANWC       | B25717       | Melanocharis striativentris striativentris | 28/10/1973 | -6.4583  | 147.4333  | Huon Toepad | Fresh tissue |
| KSC        | 8943         | Melanocharis versteri maculiceps De Vис | 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 | 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 pygmaeae | 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. aMelanocharis longicauda choris Streseman & Paludan in HBW; combined into longicauda by Beehler and Pratt (2016). bMelanocharis striativentris chrysocome (Mayr) in HBW; combined into striativentris by Beehler and Pratt (2016). cMelanocharis versteri virago (Streseman) in HBW; combined into maculiceps by Beehler and Pratt (2016). dPlaced 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 Vис).
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 Trimomatic 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 Colluricinclia 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 using MAFFT v. 1.3.6 in Geneious v.9.1.8 (Biomatters Ltd.). 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](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,
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, secondaries 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

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*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.*

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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

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) |
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 Pique-baie Satiné, in English, Indonesian, Spanish and French, respectively, highlight the most striking characteristic of the new species.
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
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 Cytb 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 Cytb 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,
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

### 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    |         |

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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 Melanocharis 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 Passeridae (Moyle et al. 2016, Oliveros et al. 2019), and emerged shortly after the split between the ancestral Australasian crow-like Corvids 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 immediately 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, Jonsson 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 same. The complex 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.

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**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 Fris:** Formal analysis (equal); Investigation (equal); Methodology (equal); Data curation (equal); Writing-review & editing (equal).
(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-C19/C23

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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 Cytb 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.