Short Communication

The systematic affinity of the enigmatic *Lamprolia victoriae* (Aves: Passeriformes)—An example of avian dispersal between New Guinea and Fiji over Miocene intermittent land bridges?

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1. Introduction

Lamprolia victoriae (silktail) is a distinctive bird endemic to the Fiji Islands, where two well-marked subspecies inhabit humid forest undergrowth and subcanopy on the islands of Taveuni (*L. v. victoriae*) and Vanua Levu (*L. v. kleinschmidtii*). It is a sparrow-sized, insectivorous passerine with a short rounded tail and velvety black plumage. Iridescent metallic blue spangles on large parts of the body and a large silky white patch on rump and much of the tail are prominent characters. Ernst Mayr (1945) describes *Lamprolia* as "one of the most puzzling birds of the world". More than 60 years later, the systematic affinity of the monotypic Fijian *Lamprolia* remains an enigma. It has been proposed that *Lamprolia* may be related to the birds-of-paradise (Paradisaeidae), based on plumage and structural similarities between *Lamprolia* and birds-of-paradise of the genera *Ptiloris* and *Manucodia* (Cottrell, 1966; Heather, 1977). It has also been associated with for example Australian robins (Petroicidae) and fairy-wrens (Maluridae) (Coates et al., 2006; Beecher, 1953). A detailed review of the earlier systematic and taxonomic history is presented in Cottrell (1966). Olson (1980) argued against relationships with Paradisaeidae and Maluridae, and instead suggested that *Lamprolia* could be an aberrant monarch-flycatcher (Monarchidae) based on previous (Beecher, 1953; Bock, 1963) and own morphological observations. Olson also argued that a relationship with Monarchidae in regard to zoogeographic interpretations is more reasonable than with Paradisaeidae or Maluridae, as the monarchs have dispersed widely to many isolated oceanic islands, contrary to the Paradisaeidae and Maluridae that are restricted to the Australo-Papuan landmass.

In recent publications (e.g. Coates et al., 2006), *Lamprolia* is placed among the monarch-flycatchers (Monarchidae). However, there is no morphological synapomorphy that unambiguously groups *Lamprolia* with the monarchs, and several other passerine lineages, such as *Aplonis* starlings, *Rhipidura* fantails and *Acrocephalus* warblers, have also managed to disperse extensively to remote Pacific Ocean islands. In this study, we explore the systematic affinities of *Lamprolia* by studying sequences from three nuclear loci. We also present a hypothesis of the biogeographical history of *Lamprolia victoriae*.

2. Materials and methods

2.1. Taxon sampling, amplification, and sequencing

We examined the phylogenetic affinity of *Lamprolia victoriae*, by analyzing DNA sequence data from 35 oscines, broadly covering all major divergences of oscine birds (Jønsson and Fjeldså, 2006), including all families to which *Lamprolia* has been associated. We sampled the "core Corvoidea" clade (Barker et al., 2004) particularly densely as it includes monarch-flycatchers and birds-of-paradise to which *Lamprolia* most often has been associated. In order to conduct molecular time estimates (see below), and to root the trees, 4 suboscines, *Acanthisitta chloris*, a parrot, and a bee-eater have also been included. For the phylogenetic inference three nuclear loci, myoglobin intron 2, ornithine decarboxylase introns 6–7 (ODC), and glyceraldehyde-3-phosphodehydrogenase intron 11 (G3PDH), have been studied. For extractions, amplifications, and sequencing procedures for fresh tissue/blood samples see Irestedt et al. (2001, 2002), Fjeldså et al. (2003), and Allen and Omland (2003), while corresponding procedures for study skins are described in Irestedt et al. (2006) and Jønsson et al. (2007). See

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Table 1
Specimen data and GenBank accession numbers for samples used in the study

Species	Family (Dickinson, 2003)	Source	G3P	ODC	Myo
Batis poensis	Platysteiridae	MNHN CG 1998-783	DQ406665	EU272120	EU529907
Chaetops frenatus	Incerta sedis	PFI uncat.	EF441212	EF441234	AY228289
Chaetorhynchus papuensis	Dicruridae	NRM 569600	EU726206	EU726224	EU726214
Colluricincla harmonica	Colluricinclidae	MV1422	EU273376	EU273356	EU273396
Coracina atriceps	Campephagidae	BMNH1910.12.28.182	EU272091	EU272118	EU272102
Corcorax melanorhamphos	Corcoracidae	AM LAB 1059	EF441214	EF441236	AY064737
Cormobates placens	Climacteridae	MV E309	EF441215	EF441237	AY064731
Corvus corone	Corvidae	MNHN CG 1995-41	DQ406663	EU272116	AY529914
Dicrurus bracteatus	Dicruridae	UWBM 68045	EF052813	EU272113	EF052839
Dicrurus leucophaeus	Dicruridae	MNHN 14-30	EU726204		
Dicrurus leucophaeus	Dicruridae	MNHN 33-8C*		EU726222	EF449727
Eopsaltria australis	Petroicidae	MV 1390	EF441216	EF441238	AY064732
Epimachus albertsii	Paradisaeidae	MV C148	EU380475	EU380436	AY064735
Eupetes macrocerus	Eupetidae	NHMT 1936.4.12.58	EF441217	EF441239	EF441257
Gymnorhina tibicen	Cracticidae	MV AC78	DQ406669	EU27119	AY064741
Hypothymis azurea	Monarchidae	MNHN 4-10B	EU726205	EU726223	EF052768
Lamprolia victoriae	Monarchidae	NRM 569556	EU726207	EU726225	EU726215
Lanius collaris	Laniidae	MNHN 2-26*	DQ406662	EU272112	AY529925
Malurus amabalis	Maluridae	MV C803	EF441219	EF441241	AY064729
Manucodia ater	Paradisaeidae	NRM 566764	EU726210	EU726228	EU726218
Melampitta lugubris	Incerta sedis	NRM 543910	EU726203	EU726221	EU726213
Menura novaehollandiae	Menuridae	MV F722	EF441220	EF441242	AY064744
Monarcha melanopsis	Monarchidae	MV B541	EU272089	EU272114	DQ084110
Oriolus xanthornus	Oriolidae	MNHN 4-10D	DQ406645	EU272111	AY529929
Pachycephala albiventris	Pachycephalidae	ZMUC 117176*	EF441223	EF441245	EF441259
Pericrocotus cinnamomeus	Campephagidae	USNM B6146	EF052753	EU272117	EF052764
Picathartes gymnocephalus	Picathartidae	LSUMZ B-19213	EF441225	EF441247	AY228314
Prunella modularis	Prunellidae	NRM 976138	EF441227	EF441249	AY228318
Ptiloris magnificus	Paradisaeidae	NRM 569616	EU726211	EU726229	EU726219
Ptilorrhoa leucosticta	Eupetidae	NRM 84405	EF441233	EF441255	EF441265
Rhipidura cyaniceps	Rhipiduridae	ZMUC 121493*	EU726208	EU726226	EU726216
Rhipidura fuliginosa	Rhipiduridae	ZMUC 133944*	EU726209	EU726227	EU726217
Rhipidura rufifrons	Rhipiduridae	CEF 239			DQ084100
Rhipidura rufifrons	Rhipiduridae	MV C733	EU272090	EU272115	
Sturnus vulgaris	Sturnidae	NRM 966615	EF441231	EF441253	AY228322
Terpsiphone viridis	Monarchidae	MNHN 2-20*	DQ406641	EF273374	AY529939
Vireo olivaceus	Vireonidae	NRM 976766*	EU272088	EU272110	EU272101
Conopophaga aurita	Conopophagidae	ZMUC 125796	AY336577	DQ435478	AY065784
Elaenia flavogaster	Tyrannidae	NRM 966970	DQ435464	DQ435480	AY064254
Philepitta castanea	Philepittidae	ZMUC 125009*	AY336591	DQ785938	AY065790
Pitta sordida	Pittidae	UWBM 67452	DQ785922	DQ785961	DQ785997
Acanthisitta chloris	Acanthisittidae	NRM 569989	EU726202	EU726220	EU726212
Merops viridis	Meropidae	ZMUC 114337*	AY600498	DQ881752	AY165815
Psittacidae (Amazona aestiva)	Psittacidae	uncat*	AY194432		
Psittacidae (Pyrrhura frontalis)	Psittacidae	NRM 966989		DQ881775	AY233367

Acronyms: AM = Australian Museum, Sydney; BMNH = British Museum of Natural History, London; LSUMZ = Louisiana State University, Museum of Natural Science; MNHN = Muséum National dHistoire Naturelle, Paris; MV = Museum Victoria, Melbourne; NHMT = Natural History Museum, Tring; NRM = Swedish Museum of Natural History, Stockholm; PFI = Percy Fitzpatrick Institute, Cape Town; USNM = National Museum of Natural History, Smithsonian Institution, Washington; UWBM = University of Washington, Burke Museum; ZMUC = Zoological Museum of the University of Copenhagen. Family level taxonomy follows Dickinson (2003). All samples except those marked with an asterisk * are from vouchered specimens. Taxa without physical vouchers are in most cases documented with photographs of the individual sampled.

Table 1 for the complete taxon sampling and GenBank Accession numbers.

2.2. Phylogenetic inference and model selection

We used Bayesian inference to estimate the phylogenetic relationships. The models for nucleotide substitutions used in the analyses were selected for each gene individually by applying the Akaike Information Criterion using the program MrModeltest 2.2 (Nylander, 2005) in conjunction with PAUP* (Swofford, 1998). Due to a rather low number of insertions in the studied genes/introns, the sequences could easily be aligned by eye. All gaps were treated as missing data in the analyses.

Posterior probabilities of trees and parameters in the substitution models were approximated with MCMC and Metropolis coupling using the program MrBayes 3.1.1 (Ronquist and Huelsenbeck, 2003). Analyses were performed for all the individual genes separately and for a concatenated data set. In the analysis of concatenated data set, the models selected for the individual gene partition were used, but the topology was constrained to be the same. We used an unconstrained, exponential branch length prior. All chains were run for 5 million generations, with trees sampled every 100th generations. The standard deviation of split frequencies was used to estimate the burn-in phase (i.e., before the chain had reached its apparent target distribution). The trees sampled during the burn-in phase (i.e., before the chain had reached its apparent target distribution) were then discarded in the final inferences.

2.3. Divergence date estimates

Bayesian approaches for divergence time estimates were performed using the Multidistribute software package (Kishino et al., 2001; Thorne and Kishino, 2002). We estimated different branch length variance–covariance matrices for our three partitions using Estbranches, after estimating the parameters values of the F84 + Γ model with the assistance of Paml (Yang, 1997). As a calibration point we used the split between *Acanthisitta* and

all remaining passerines. We performed the dating analyses using two time constraints for that split: (1) 82–85 mya, which corresponds to the drift of New Zealand from Gondwanaland (an often used avian primary calibration point to address divergence times within Passeriformes e.g. Barker et al., 2004; Ericson et al., 2002) and (2) 84.8–106.9 mya, which corresponds to the lower and upper bounds of the 95% credibility interval obtained by Pereira and Baker (2006) for that split. The latter estimate is based on the analysis of complete mitochondrial genomes of vertebrates and on the use of several fossil calibration points using the same dating method as in the present study. The primary assumptions on these two estimates are fully independent. We set the prior distribution for the distance between the tip and the root (rttm ± rttmsd) to 100 ± 45 mya. As mean and standard deviation for the prior distribution of the rate at the root node, we used 0.00055 ± 0.00055 substitutions per site per million 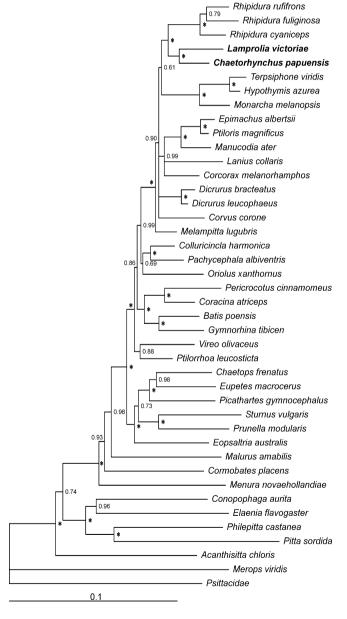years (estimated using the procedure described in Wiegmann et al., 2003). For all the dating analyses, the parameters 'brownmean ± brownmeansd' (which affect the variation of rates of molecular evolution over time) were set to 0.02 ± 0.02, so as the product between 'brownmean' and rttm is around 2 (Wiegmann et al., 2003). We used the topology obtained from the Bayesian mixed-model analyses (Fig. 1) as a template for all the dating analyses. The Markov Chain Monte Carlo analyses were run twice for 1,100,000 generations (burn-in period: 100,000 generations) and parameters were sampled every 100 generations.

3. Results

3.1. Variation in the molecular data set, model selection, and phylogenetic relationships

The alignments of the non-coding intron regions were 416 bp for G3PDH, 737 bp for myoglobin and 769 bp for ODC. Most indels were found to be short (one exception is the ODC sequences from *Rhipidura* that has an 83 bp long insertion) and autapomorphic. However, several indels congruent with the tree topology from the combined phylogeny were found in all loci. Interesting for this study is a deletion of 1 bp in the ODC shared between *Lamprolia victoriae* and *Chaetorhynchus papuensis*. A few indels were also found to be incongruent with the combined phylogeny, but these were all found in the most variable regions of the studied loci, and none concerns the taxa closely related to *Lamprolia victoriae*. The observed uncorrected sequence divergences for the data sets ranged between 1.0 and 17.8 in myoglobin, 0.7 and 34.5 in G3PDH, and 0.9 and 28.4 in ODC. The observed sequence divergence between *Lamprolia* and *Chaetorhynchus* ranged between 3.5 in myoglobin, 4.0 in ODC and 5.6 in G3PDH.

The a priori selection of substitution models supported that the GTR + Γ model had the best fit for myoglobin and G3PDH and the GTR + Γ + I for ODC. We applied a partitioned analysis of the combined data set, as the nucleotide state frequencies, as well as the gamma distribution, differed between the three gene regions. After discarding the burn-in phase the inference was based on a total of 35,000–40,000 samples from the posterior for the individual genes and the combined data sets. For the phylogenetic inference, the mode of the posterior distribution of topologies was presented as a majority-rule consensus tree from each analysis.

The trees obtained from the Bayesian analyses of the individual gene partitions (not shown) all have more or less similar topologies. Conflicting nodes are almost exclusively found at short internodes with low (<0.95) posterior probability value. Importantly for the aim of this study, there is no topological conflict between the gene trees concerning the affinity of *Lamprolia*. Both the myoglobin and the ODC tree support a sister relationship between *Lamprolia* and *Chaetorhynchus* (0.85 and 1.00, respectively), while *Lamprolia* in the G3PDH tree is positioned at an unresolved polytomy that includes several "core Corvoidea" taxa, including *Chaetorhynchus*. There is also good support (1.00) for *Lamprolia* and *Chaetorhynchus* forming a sister clade to *Rhipidura* in the myoglobin tree (this affinity is neither supported nor in conflict with the other two genes). Deeper nodes in the tree are obtained from the combined analyses (Fig. 1) are overall well resolved while several terminal relationships within "core Corvoidea" are unresolved or poorly supported. However, important for this study is the strong support (1.00) for a sister relationship between *Lamprolia* and *Chaetorhynchus*, and that they in turn are sister to *Rhipidura* (1.00).

3.2. Divergence date estimates

Our molecular dating performed under a relaxed-clock hypothesis in a Bayesian framework indicates that *Lamprolia* diverged

Fig. 1. The majority rule consensus trees obtained from the Bayesian analyses of combined data sets (myoglobin, G3PDH, and ODC). Posterior probability values are indicated at the node, posterior probability values of 1.00 are indicated with an asterisk.

from *Chaetorhynchus* about 20–23 mya (82–85 calibration point: 20.8 Myrs, 95% CI 14.2–28.8; 84.8–106.9 calibration point: 23.7 mya 95% CI 15.7–33.3). The latter clade diverged from the *Rhipidura* clade around 24–28 mya (82–85 calibration point: 24.7 Myrs, 95% CI 17.9–32.6; 84.8–106.9 calibration point: 28.0 mya 95% CI 19.7–38.10).

We estimated the divergence between the Lyrebird and the remaining Oscines to have occurred between 60 and 72 mya (82–85 calibration point: 62.7 Myrs, 95% CI 54.6–70.6; 84.8–106.9 calibration point: 71.1 mya 95% CI 59.0–84.1). The dating analyses using the geological calibration point, recovered thus the same estimate as Barker et al. (2004) (62–65 mya) and Fuchs et al. (2006) (63.4 mya 95% CI 53.6–72.7) for that split, albeit differences in lineage sampling design. As another comparison point with previous studies, we here estimated the split between *Gymnorhina* and *Batis* to have occurred around 24–28 mya (82–85 calibration point: 24.8 Myrs, 95% CI 17.3–33.5; 84.8–106.9 calibration point: 28.1 mya 95% CI 19.1–38.9). This estimate is very close to the estimate of Barker et al. (2004) (26–29 mya) but only slightly overlapping with the one of Fuchs et al. (2006) (37.7 mya, 95% CI 29.2–47.3).

The reason for the discrepancies between some divergence time estimates in the different studies appears to be the uneven taxonomic sampling in some part of the tree (as all studies relied on the same initial calibration point). Barker et al. (2004) aimed to understand the timing of divergence of major Passeriformes lineages and sampled a few member of each passerine families while Fuchs et al. (2006) focused on the clade composed by the bush-shrikes and allies (represented by *Gymnorhina* and *Batis* here) and sampled all genera known to be included in that clade (with the exception of the Vangidae) along with one representative of most Corvoidea families. Linder et al. (2005) showed that divergence time estimates for some clades increase with the number of included taxa in all dating methods. This effect of lineage sampling may explains why all studies recovered the same divergence date for Lyrebird, as they sampled all major clades around them (Suboscines, Menurae, crown Corvoidea and Passerida), but not for more derived nodes in the Passerifomes, like the bush-shrikes and allies, where sampling among studies is generally more heterogeneous. Given this pitfall associated with the dating analyses we thus regard the divergence dates for the split between *Lamprolia* and *Chaetorhynchus* as minimal estimates, whatever the initial calibration point used as denser sampling among "core Corvoidea" lineages may lead to more ancient divergence date estimates.

4. Discussion

The phylogenetic hypotheses in the present study strongly support a sister relationship between *Lamprolia victoriae* and *Chaetorhynchus papuensis* (Papuan mountain drongo), and that they in turn are sister to the fantails (*Rhipidura*). That *Chaetorhynchus* is related to fantails rather than to the true drongos (*Dicrurus*), has been demonstrated previously (Barker et al., 2004). However, the strongly supported relationship between *Lamprolia* and *Chaetorhynchus* is both novel and unexpected. The position of *Lamprolia* in recent publications among monarch-flycatchers (Monarchidae) (e.g. Coates et al., 2006), is tentative and without any substantial support. Based on the external morphology the relationship suggested herein is as reasonable as any other previously suggested affinities of *Lamprolia* (Cottrell, 1966; Olson, 1980).

From a biogeographic point of view, the sister relationship between *Lamprolia* and *Chaetorhynchus* is quite intriguing, as they occur in widely disjunct regions (Fiji and the highlands of New Guinea, respectively). Many recent studies have presented evidence of long-distance dispersal from continents to other continents, from continents to oceanic islands and among oceanic islands (Cowie and Holland, 2006; Filardi and Moyle, 2005; Gillespie and Roderick, 2002; Glor et al., 2005; Jansa et al., 2006; de Queiroz, 2005; Rocha et al., 2006). The land birds of the tropical Pacific islands are mostly members of lineages with a wide distribution in the Australasian and southwestern Pacific regions, e.g. *Ptilinopus*, *Aplonis*, *Zosterops* and Monarchidae. Long-distance dispersal and recent diversification have generally been suggested as the main characteristics of the land bird faunas of the tropical Pacific, as in the case of Monarchidae, where dispersal is suggested to be of Plio-/Pleistocene age (Filardi and Moyle, 2005). The old age of the split between *Lamprolia* and *Chaetorhynchus* at ca. 20 Mya does not in itself preclude a recent dispersal event. However, contrary to the above-mentioned groups, neither *Lamprolia* nor *Chaetorhynchus* shows any behavioral or morphological traits suggesting any significant abilities for long-distance dispersal. Both are sedentary inhabitants of humid forest interior, as opposed to the forest edge and semi-open habitats typical of most of the widely distributed land bird groups of the Pacific. Differences in habitat preferences have been shown to have a strong correlation to the capacity for long-distance dispersal in bats (Heaney, 2007, and references therein). The fact that both *Lamprolia* and *Chaetorhynchus* occupy the interior of humid forest suggests that an explanation of the distribution of these taxa may need to involve the geological history of the southwest Pacific in a more explicit way.

Three scenarios are possible to explain the distributional pattern of *Lamprolia* and *Chaetorhynchus*. The first two involve long-distance dispersal, either by the ancestor of *Lamprolia* to Fiji from the Australo-Papuan region, or by the ancestor of *Chaetorhynchus* to New Guinea from an ancestral area in the tropical Pacific. A third scenario takes into account the highly dynamic nature of island arcs at subduction zones, where islands form and disappear continuously. Although the individual islands are ephemeral, taxa can survive in the region as long there is a sufficient area of land present, and in many cases taxa on a specific island could accordingly be older than the island they occupy (Heads, 2005). In a situation like that, *Lamprolia* and *Chaetorhynchus* may be the sole survivors of a lineage once widely distributed in the region. They may have spread by short-distance dispersal over intermittent land bridges or island chains in a dynamic arc system, but the long time span and the dynamics of volcanic arc systems in the tropical Pacific have left these two disjunct species at two geographical areas through the extinction of intervening populations.

The tectonic history of the Wallacean, Papuan, and southwest Pacific region is extremely complex (reviewed by Hall, 2002 and Schellart et al., 2006), and tectonic models for the region (Hall, 1998, 2002; Hall and Holloway, 1998; Schellart et al., 2006) reveal some interesting patterns that could help explain the disjunct distribution of sedentary forest birds in New Guinea and Fiji. According to these reconstructions the Fiji islands, Melanesia (Bismarck, Solomon, Santa Cruz, and Vanuatu islands), and the northern mountain ranges of New Guinea are all part of an island/volcanic arc system at the subduction zone between the Eurasian, Australian, and Pacific plates (Hall, 1998, 2002), stretching from the Philippines to the Fiji Islands. This arc system has had a westward movement relative to the Australian plate since at least 25 Mya and in this process, several terranes were accreted to the northern margin of the Australian plate, forming the coastal ranges of New Guinea (e.g. the Torricelli and Adelbert ranges) (Hall, 2002). Due to the combination of tectonic instability and fluctuations in the global sea level, the extent of land area during different periods is poorly known. However, smaller or greater parts of the Melanesian Arc have no doubt been above water during periods of low sea levels, forming partial and intermittent land connections along the chain that would have facilitated the dispersal of organisms between them. Some birds probably benefited from the plethora of

new islands emerging all the time, not least opportunistic birds like fantails and monarch-flycatchers. Other birds, such as the *Lamprolia* and the *Chaetorhynchus*, dispersed far away but never maintained widespread populations throughout the archipelago.

We are unable to determine the area of origin of the *Lamprolia/Chaetorhynchus* lineage whether it is Australo-Papuan or Pacific, although we consider an Australo-Papuan origin more likely. Regardless, the distributions point towards an interesting dispersal event probably facilitated by the presence of intermittent island connections between Fiji and New Guinea along the Melanesian Arc. A similar scenario of dispersal facilitated by island bridges was recently proposed for birds crossing the Indian Ocean (Jönsson et al., 2008).

Acknowledgments

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