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# Dynamic colonization exchanges between continents and islands drive diversification in paradise-flycatchers (*Terpsiphone*, Monarchidae)

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## ABSTRACT

**Aim** We use parametric biogeographical reconstruction based on an extensive DNA sequence dataset to characterize the spatio-temporal pattern of colonization of the Old World monarch flycatchers (Monarchidae). We then use this framework to examine the role of dispersal and colonization in their evolutionary diversification and to compare plumages between island and continental *Terpsiphone* species.

**Location** Africa, Asia and the Indian Ocean.

**Methods** We generate a DNA sequence dataset of 2300 bp comprising one nuclear and three mitochondrial markers for 89% (17/19) of the Old World Monarchidae species and 70% of the *Terpsiphone* subspecies. By applying maximum likelihood and Bayesian phylogenetic methods and implementing a Bayesian molecular clock to provide a temporal framework, we reveal the evolutionary history of the group. Furthermore, we employ both LAGRANGE and Bayes-LAGRANGE analyses to assess ancestral areas at each node of the phylogeny. By combining the ancestral area reconstruction with information on plumage traits we are able to compare patterns of plumage evolution on islands and continents.

**Results** We provide the first comprehensive molecular phylogenetic reconstruction for the Old World Monarchidae. Our phylogenetic results reveal a relatively recent diversification associated with several dispersal events within this group. Moreover, ancestral area analyses reveal an Asian origin of the Indian Ocean and African clades. Ancestral state reconstruction analyses of plumage characters provide an interpretation of the plumage differentiation on islands and continents. Ancestral plumage traits are inferred to be close to those of the Asian paradise-flycatcher (*Terpsiphone paradisi*), and island species display a high degree of plumage autapomorphy compared with continental species.

**Main conclusions** *Terpsiphone paradisi* is polyphyletic and comprises populations that have retained the ancestral plumage of the widespread *Terpsiphone* genus. The genus appears to have colonized south-west Asia, the Indian Ocean and Africa from eastern Asia. The phylogeny and divergence time estimates indicate multiple simultaneous colonizations of the western Old World by *Terpsiphone*. These results reinforce a hypothesis of range expansions of a *Terpsiphone paradisi*-like ancestor into eastern Asia and the western Old World.

## Keywords

Africa, Asia, biogeography, colonization, dispersal, Indo-Pacific, island, Monarchidae, plumage, speciation.

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## INTRODUCTION

Dispersal to, and colonization of, new land is widely accepted to be amongst the key drivers of speciation, and these processes have contributed to the diversification of many organisms (Simpson, 1953; Mayr, 1963). Indeed, these non-ecological mechanisms of divergence may have played a prominent role in some of the most remarkable evolutionary and adaptive radiations (Rosenzweig, 1995; Groth, 1998; Moore & Donoghue, 2007, 2009; Grant & Grant, 2008; Losos, 2010; Jönsson *et al.*, 2011), and there is now considerable evidence that many lineages that have successfully colonized new land have also undergone numerous speciation events (Steppan *et al.*, 2004; Moyle *et al.*, 2009; Van Bocxlaer *et al.*, 2010; Fritz *et al.*, 2011; Purvis *et al.*, 2011). In these non-adaptive radiations, speciation precedes ecological diversification, and geographical isolation by allo/parapatric barriers is the main factor underlying these speciation events (Rundell & Price, 2009). Therefore, geographical isolation on newly available land is likely to be the principal driver of diversification in diverse groups without ecological differentiation (e.g. Cameron *et al.*, 1996; Comes *et al.*, 2008; Phillimore & Price, 2008; Price, 2008).

Speciation by geographical isolation appears to be particularly common amongst oscine passerine birds, for example in many families within the Passerida (Price, 2008) and the core Corvoidea (Jönsson *et al.*, 2011) radiations, in which large numbers of similarly coloured species replace each other in different geographical regions. Within the core Corvoidea, there are many examples (Fritz *et al.*, 2011) where colonizations of newly formed islands or archipelagos have led to a substantial increase in species diversity, for instance the island radiations of highly dispersive birds such as the Pachycephalidae (Jönsson *et al.*, 2010a), the Campephagidae (Jönsson *et al.*, 2010b) and the Monarchidae (Cibois *et al.*, 2004; Filardi & Moyle, 2005; Filardi & Smith, 2005). The core Corvoidea have recently been shown to have originated within an island setting, and all members of this large radiation seem to be well adapted to persisting in archipelagos and to dispersing (Jönsson *et al.*, 2011). Indeed, a number of studies of the core corvid families have revealed complex colonization histories for several families, reflecting their great abilities to disperse and to adapt within insular regions. Members of the Monarchidae (90 species; Clements, 2007) belong to the corvid passerines (Barker *et al.*, 2002). They are widely distributed from the Old World to Australia and Oceania, and high species diversity is associated with a multitude of island allospecies (Filardi & Smith, 2005; Uy *et al.*, 2009) and even with 'upstream' colonization, whereby the direction of dispersal is from islands to the mainland (Filardi & Moyle, 2005; Bellemain & Ricklefs, 2008; Cibois *et al.*, 2011). The family Monarchidae is divided into two groups (Pasquet *et al.*, 2002; Filardi & Moyle, 2005): (1) the Old World Monarchidae (19 species; *Eutrichomyias*, *Hypothymis*, *Terpsiphone*, *Trochocercus*), and (2) the Australasian Monarchidae (71 species; *Arses*, *Chasiempis*, *Clytorhynchus*, *Grallina*, *Mayrornis*, *Metabolus*, *Monarcha*, *Myiagra*, *Neolalage*, *Pomarea*). Amongst the Old

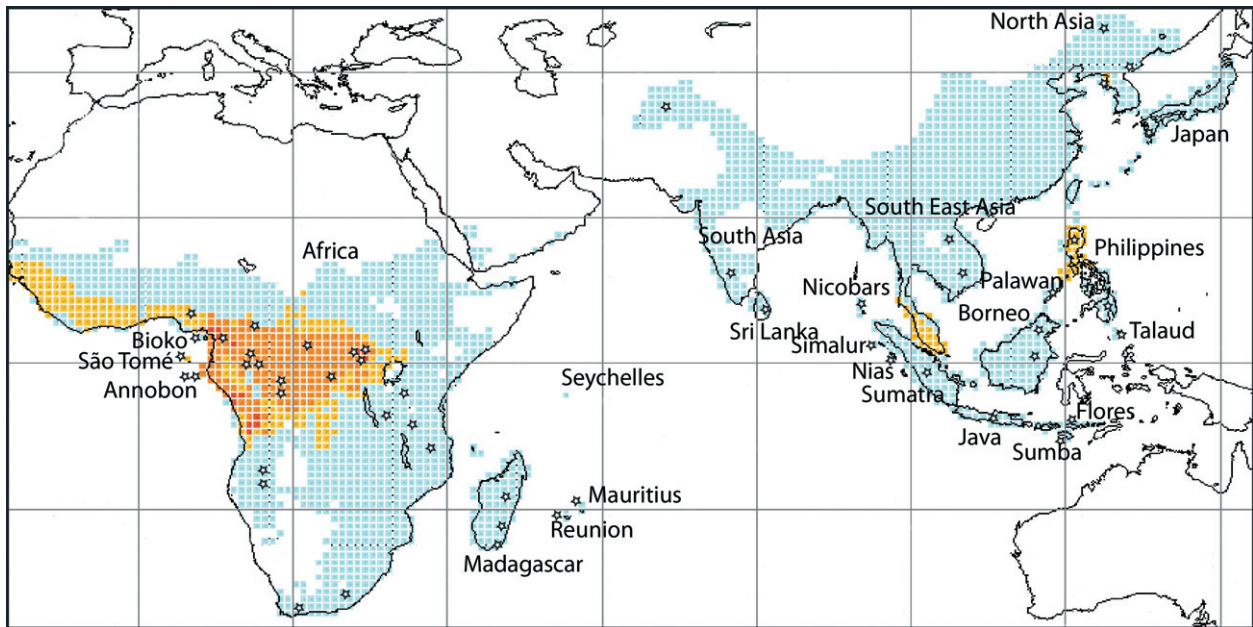
World Monarchidae, the genus *Terpsiphone* constitutes the clearest example of a dispersalist radiation, as evident from its wide distribution and the occurrence of several distinct taxa on remote islands.

The genus *Terpsiphone* Gloger, 1827 (Old World paradise-flycatcher) comprises 13 extant species and is distributed throughout the tropics of the Old World, including the Philippines, the islands of the Indian Ocean and the Gulf of Guinea (Fig. 1). The wide species distribution across a broad range of mesic thicket and forest habitats make this genus an excellent group for studying dispersal and speciation dynamics between islands and continents. Given that the diversification within the Monarchidae took place mainly in the middle/late Miocene (Filardi & Moyle, 2005; Jönsson *et al.*, 2011), vicariance can be reasonably dismissed as a factor contributing to speciation between Africa and Asia. Indian Ocean islands and archipelagos have not been connected to Africa or Asia in the last 50 million years (Myr). Therefore dispersal seems to be the only mechanism by which this island region could have been colonized. Indeed, recent biogeographical studies (see Warren *et al.*, 2010) highlight a number of connections between Asian and Indian Ocean avifaunas.

Among Asian *Terpsiphone*, several *T. paradisi* subspecies have spread across the entire Asian continent, and their relationship with species in the Philippines, Palawan and Japan remains unknown. The geological history of Asia has been very dynamic and complex throughout the Cenozoic (Hall, 2002), and it is likely that the distribution and plumage variation of Asian *Terpsiphone* was shaped by major historical vegetational and climatic changes (Heaney, 1991; Bird *et al.*, 2005; Patou *et al.*, 2010).

The large diversity of plumage phenotypes (Stresemann, 1924; Salomonsen, 1933a,b; Chapin, 1948) in the widely distributed continental species in Asia (the Asian paradise-flycatcher) and Africa (the African and black-headed paradise-flycatchers) presents a challenge to systematists, but some common traits are evident. For example, all paradise-flycatchers display sexual dimorphism (Mulder *et al.*, 2002). Most of the members of *Terpsiphone* exhibit a crest, long central tail quills and rufous plumage. Five species lack long central tail quills, and they all occur in the primary forests of Africa (most of the *T. rufiventer* subspecies, *T. bedfordi*, *T. batesi*) or on islands (*T. cyanescens*, *T. bourbonnensis*). Apart from two Indian Ocean species (*T. mutata*, *T. bourbonnensis*), all island species display unicoloured plumages. This phenomenon is also known from other avian island taxa (Mayr & Diamond, 2001) and includes melanism (Theron *et al.*, 2001; Uy *et al.*, 2009; Driskell *et al.*, 2010). One explanation for this might be that rapid evolution after colonization and mutations linked with sexual selection or drift could account for the amount of endemism and occurrence of unicoloured plumage colours observed. However, a robust phylogenetic framework is required to understand such plumage evolution on islands and to improve our knowledge of systematic relationships.

Here we present the first comprehensive molecular phylogenetic reconstruction for the Old World Monarchidae. We



**Figure 1** World map representation of the present distributions of members of the genus *Terpsiphone*. Each 1° square represents 110 km × 110 km at the equator. The maximum number of species in a square (warmest colour) is four. *Terpsiphone* samples included in this study are indicated by stars on the map.

use the molecular phylogeny to explore the diversification processes within paradise-flycatchers. Furthermore, we use molecular dating and ancestral area analyses to determine spatio-temporal biogeographical patterns. Finally, we compare patterns of plumage evolution between *Terpsiphone* taxa on islands and continents. Our high-resolution phylogeny for the genus *Terpsiphone* allows us specifically to address the following questions. (1) What are the origins and colonization routes of Old World Monarchidae? (2) What role have colonization events played in speciation? (3) How have plumage characters evolved in island species compared with their continental counterparts?

## MATERIALS AND METHODS

### Taxon sampling

To study the phylogenetic relationships among the genus *Terpsiphone*, samples were obtained from 53 specimens (see Appendix S1 in Supporting Information) representing 92% (12/13) of the extant species and 70% (37/53) of the subspecies listed by Clements (2007). Included in the study are almost all of the Old World Monarchidae species (17/19), with the exception of the critically endangered Seychelles paradise-flycatcher (*Terpsiphone corvina*) and the Cerulean paradise-flycatcher (*Eutrichomyias rowleyi*) of Sangihe, Indonesia (Riley & Wardill, 2001). Afrotropical *Elminia* and *Erythrocerus* are no longer considered members of this group (Pasquet *et al.*, 2002; Nguembock *et al.*, 2008; Alström *et al.*, 2010) and were therefore not included. To root the trees and to assess the monophyly of the Old World Monarchidae, samples were also

obtained for a number of outgroup taxa, including representatives from the sister clade, the Australasian Monarchidae (*Myiagra*, *Monarcha* and *Grallina*), as well as from five representatives of more distantly related families of core Corvoidea (Appendix S1).

### DNA amplification, sequences and alignment

Ethanol-preserved tissue and blood samples as well as foot pad samples from study skins were obtained from several museums (Appendix S1). From fresh samples, total DNA extraction was carried out using a QIAamp DNA mini kit (Qiagen, Crawley, UK). Fragments from the following nuclear and mitochondrial genes were amplified and sequenced: cytochrome *b* (*cyt b*), glyceraldehyde-3-phosphodehydrogenase (*GAPDH*) intron 11, NADH dehydrogenase subunit 2 (*ND2*) and NADH dehydrogenase subunit 3 (*ND3*). Genes were amplified by polymerase chain reaction (PCR) and sequenced using the following primers: *cyt b*: L14990 (Kocher *et al.*, 1989) and H15916 (Edwards *et al.*, 1991); *ND2*: Lmet (Hackett, 1996) and H6312 (Cicero & Johnson, 2001); *ND3*: L10755 and H11151 (Chesser, 1999); and *GAPDH*: G3P13b and G3P14b (Fjeldså *et al.*, 2003). We used hot-start PCR with annealing temperatures for the first cycles a few degrees below the melting temperature of the primer with the lowest melting temperature. A representative thermocycling programme for a given primer combination started with an initial denaturation at 95 °C for 5 min, followed by a 40-cycle phase of 95 °C for 40 s, 54–63 °C for 40 s and 72 °C for 1 min. PCR products were purified from 1% agarose gel using Amicon Ultrafree-DNA columns (Millipore, Billerica, MA), and both strands were sequenced using a

Big Dye Terminator cycle sequencing kit (Applied Biosystems, Warrington, UK). Sequenced strands were run on an ABI 3100 automated sequencer (Applied Biosystems).

For extractions, amplifications, and sequencing procedures from study skin samples we followed the procedures described in Irestedt *et al.* (2006). However, 20  $\mu$ L of DTT (dithiothreitol) was added in the lysis phase and we amplified shorter (250 bp) fragments (Appendix S2).

Sequences were aligned with the MUST software ED editor (Philippe, 1993). From these sequences we built one supermatrix containing all samples, and another containing only the taxa for which we had all four genes.

### Phylogenetic analyses on the single and concatenated datasets

Phylogenetic trees were generated for each gene matrix and for the entire concatenated dataset using maximum likelihood and Bayesian methods. MODELTEST 3.07 (Posada & Crandall, 1998) was used to determine the best-fitting model of DNA sequence evolution according to the Akaike information criterion (AIC). Phylogenetic reconstructions generated from the partitioned datasets were performed using maximum likelihood as implemented in RAxML 7.0.4 (Stamatakis, 2006), which can implement partitioned analyses by appropriating to each partition either a GTR (general time-reversible) model with rate heterogeneity accommodated with a gamma ( $\Gamma$ ) distribution (GTR+ $\Gamma$ ), or a GTR+CAT model (general time-reversible model with rate heterogeneity accommodated with a number of discrete rate categories). For the partitioned datasets (four gene partitions and three codon partitions for coding genes), we used the GTR+MIX option of RAxML, which assumes the faster GTR+CAT model for topological tree research but assumes the GTR+ $\Gamma$  model when computing the likelihood value of each topology. The RAxML analyses used default parameters and comprised 1000 tree search replicates. Node stability on partitioned supermatrices was estimated with 1000 nonparametric bootstrap replicates (Felsenstein, 1985). Bootstrap percentages (BPs) were calculated using RAxML under a GTR+MIX model.

Phylogenetic trees were also inferred using MRBAYES 3.1.2 (Ronquist & Huelsenbeck, 2003). Models for the Bayesian analyses were identified using MODELTEST 3.07 (Posada and Crandall, 1998). All parameters except topology were unlinked across partitions, and two independent runs (one cold and three heated chains) were computed simultaneously, with trees sampled every 100th generation. MRBAYES analyses were run for  $5 \times 10^7$  and  $10 \times 10^7$  generations. In all cases, stationarity had been reached by the end of the analysis. Majority rule consensus trees were constructed, with a burn-in of either  $2.5 \times 10^6$  or  $5 \times 10^6$ .

### Molecular dating

We used BEAST 1.6.1 (Drummond *et al.*, 2002; Drummond & Rambaut, 2007) to estimate the divergence dates within Old

World Monarchidae, by applying the best-fitting model, as estimated by MODELTEST 3.07 (Posada & Crandall, 1998), to each of the partitions. We assumed a Yule speciation process for the tree prior, using an uncorrelated lognormal distribution for the molecular clock model (Ho *et al.*, 2007) and default prior distributions for all other parameters, and ran Markov chain Monte Carlo (MCMC) chains for 200 million generations with a 25% burn-in period and parameters logged every 1000th generation. We repeated the analysis four times to ensure independent convergences of models and used the program TRACER 1.5 (Rambaut & Drummond, 2007) to assess convergence diagnostics.

We used Tajima's relative test (Tajima, 1993) implemented in the 'pegas' package (Paradis, 2010) in R (R Development Core Team, 2011) to test whether our dataset was clock-like. Because a molecular clock hypothesis could not be rejected within *Terpsiphone*, we applied both a strict and a relaxed uncorrelated lognormal molecular clock to our data, partitioning by genes and codons.

Because no fossil data are available for this group, we used a rate of evolution of 2% sequence divergence per million years ( $\text{Myr}^{-1}$ ) to obtain absolute dates for the *cyt b* sequence data (Weir & Schluter, 2008) and a rate of 2.8% sequence divergence  $\text{Myr}^{-1}$  for *ND2* sequence data (Norman *et al.*, 2007). Geological calibration points have been applied to several avian groups of oceanic islands, such as scops-owls (Fuchs *et al.*, 2008), sunbirds (Warren *et al.*, 2003) and white-eyes (Moyle *et al.*, 2009). However, we acknowledge the need to be sure that all taxa in the vicinity of the island in question have been sampled. Other possible scenarios, which could mislead date estimates based on island calibrations, include species/lineages that originated on islands that became submerged after colonizations of other newly emerged islands in the vicinity (Heads, 2011). Although this problem can never be entirely removed, the ideal criteria are fulfilled for the Indian Ocean islands of Mauritius and Réunion. To corroborate our '2% rule', we used the split between *Terpsiphone bourbonnensis desolata* from Mauritius (age c. 8 Ma) (McDougall & Chamalaun, 1969) and *Terpsiphone b. bourbonnensis* from Réunion (age c. 2 Ma) (Chevallier & Vatin-Perignon, 1982) in the Indian Ocean as a geological calibration point. We assumed that Mauritius was colonized before the emergence of Réunion, and that Mauritius was the source of colonization of Réunion following emergence of the latter c. 2 Ma. To obtain a calibration point based on the split between these two species, we applied an asymmetric distribution prior starting at 2 Ma (emergence of Mauritius) and asymptotically skewed towards the end of the Pleistocene. We also applied a uniform prior with an upper bound at 2 Ma (emergence of Mauritius) and a lower bound at 1 Ma. In both analyses we set a basal constraint depending on a secondary calibration point based on the Bayesian relaxed molecular clock for the divergence of core Corvoidea (Jönsson *et al.*, 2011). We used the estimated timespan of the core Corvoidea node as a uniform constraint for the root of our topology (33.4–42.8 Ma).



## Biogeographical analyses

We used LAGRANGE to elucidate ancestral patterns (Ree *et al.*, 2005; Ree & Smith, 2008; Smith, 2009) with a particular emphasis on the nodes leading to members of the *Terpsiphone*. In a maximum-likelihood biogeographical analysis as implemented in LAGRANGE (Ree *et al.*, 2005), ancestral areas are optimized onto internal nodes. LAGRANGE enables maximum likelihood estimation of the ancestral states (range inheritance scenarios) at speciation events by modelling transitions between discrete states (biogeographical ranges) along phylogenetic branches as a function of time. We assigned 10 geographical areas for the LAGRANGE analysis after considering the evidence available for historical relationships between geological plates and terrains in the Indo-Pacific region (Audley-Charles, 1991; Hall, 1998), but otherwise adhering to the following major regions: Africa (AFR), Gulf of Guinea Islands (GGI), Indian Ocean Islands (IOI), New Guinea and the Sahul Shelf (AUS), Northeast Asia (NAS), the Philippines (PHI), South Asia (SAS), continental Southeast Asia (SEA) and Sundaland (SUN), Sulawesi (SUL) and the Lesser Sunda islands (LSU).

On the dated tree, we estimated the area of origin of the *Terpsiphone* genus and the direction and sequence of colonization within Africa, Asia and the Indian Ocean islands. One great advantage of LAGRANGE is the ability to model connectivity scenarios. To test whether colonization followed a stepping-stone pattern (constrained) or a long-distance dispersal pattern (unconstrained), we used both an unconstrained model (M1) and two constrained biogeographical scenarios allowing for limited dispersal between areas (M2 and M3). M1 does not constrain colonization between areas. Movement between unconnected areas is prohibited in M2 and is unlikely in M3 by setting the dispersal parameter  $d$  (probability of dispersal between unadjacent areas) equal to 0 (M2) or 0.01 (M3). We set  $d = 1$  within Asia (Northeast Asia, the Philippines, South Asia, Southeast Asia, Sundaland, Sulawesi and the Lesser Sundas) and within Africa (Africa, Gulf of Guinea Islands), and between Africa and South Asia (South Asia plays in this case a stepping-stone role in the colonization between Africa and eastern Asia). In this model, Indian Ocean islands could be colonized either from Africa or from South Asia with a dispersal probability  $d = 1$ . As an example, direct dispersal from the Philippines to Africa or to the Indian Ocean islands was not allowed or was very unlikely ( $d = 0$  in M2 or  $d = 0.01$  in M3). In this way, we were able to compare the likelihood of the two biogeographical models (constrained and unconstrained) to test the stepping-stone hypothesis within Old World Monarchidae.

Using Bayes-LAGRANGE (Smith, 2009), it is possible to optimize not just across one tree but across multiple trees, whereby topological uncertainty is taken into account. For each analysis, we sampled 1000 trees (by thinning the chain stochastically) from the BEAST MCMC output and ran LAGRANGE on all of them. The frequency of the most likely ancestral areas for clades was recorded and plotted as marginal

distributions on the majority-rule consensus tree derived from the MCMC output. Using R scripts (available from P.-H.F. on request), we recorded for each node in the dated topology the area with the highest relative probability. The major advantage of the Bayes-LAGRANGE method is that the marginal distributions for the alternative ancestral areas at each node in the tree are the product of both the phylogenetic uncertainty in the biogeographical reconstruction of the node of interest and the uncertainty in the rest of the tree.

The analyses were carried out by constraining the maximum number of areas encompassed by the ancestral distributions to the maximum size of extant ranges using the maxareas (=2) option in LAGRANGE. However, we also ran additional analyses exploring the sensitivity of the maxareas parameter (setting maxareas = 3 and 4).

## Comparing plumage evolution on islands and continents

To evaluate speciation hypotheses within *Terpsiphone* we coded nine plumage characters and a single habitat character. Plumage characters were defined from previous taxonomic studies (Stresemann, 1924; Salomonsen, 1933a,b; Erard *et al.*, 1997; Coates *et al.*, 2006), and these data were augmented by data obtained from study skins at the Natural History Museum of Denmark, University of Copenhagen (ZMUC, Denmark), the Museum für Naturkunde (ZMB, Berlin, Germany), the University Museum of Zoology (UMZC, Cambridge, UK) and the Swedish Museum of Natural History (NRM, Stockholm, Sweden). The following characters were coded for all subspecies (males only): (1) insular or continental origin, (2) crest (presence, absence), (3) tail quills (normal or elongated), (4) crown colour (black, rufous or blue), (5) throat colour (black, rufous, blue or grey), (6) wing covert colour (black, rufous, blue, grey, white, purple or mixed colours), (7) tail colour (black, rufous, blue, grey, white or mixed colours), (8) breast colour (black, rufous, blue, grey or white), (9) vent colour (black, rufous, blue, grey, white or mixed colours), and (10) belly colour (black, rufous, blue, grey, white or mixed colours).

To compare plumage patterns between insular and continental taxa, we inferred ancestral state reconstruction at each node within our phylogeny using a maximum likelihood approach implemented in MESQUITE 2.74 (Maddison & Maddison, 2010) with the Mk1 rate model (Lewis, 2001). Polymorphic characters were coded as missing data because MESQUITE is unable to handle polymorphic data.

## RESULTS

### Phylogenetic results and taxonomy

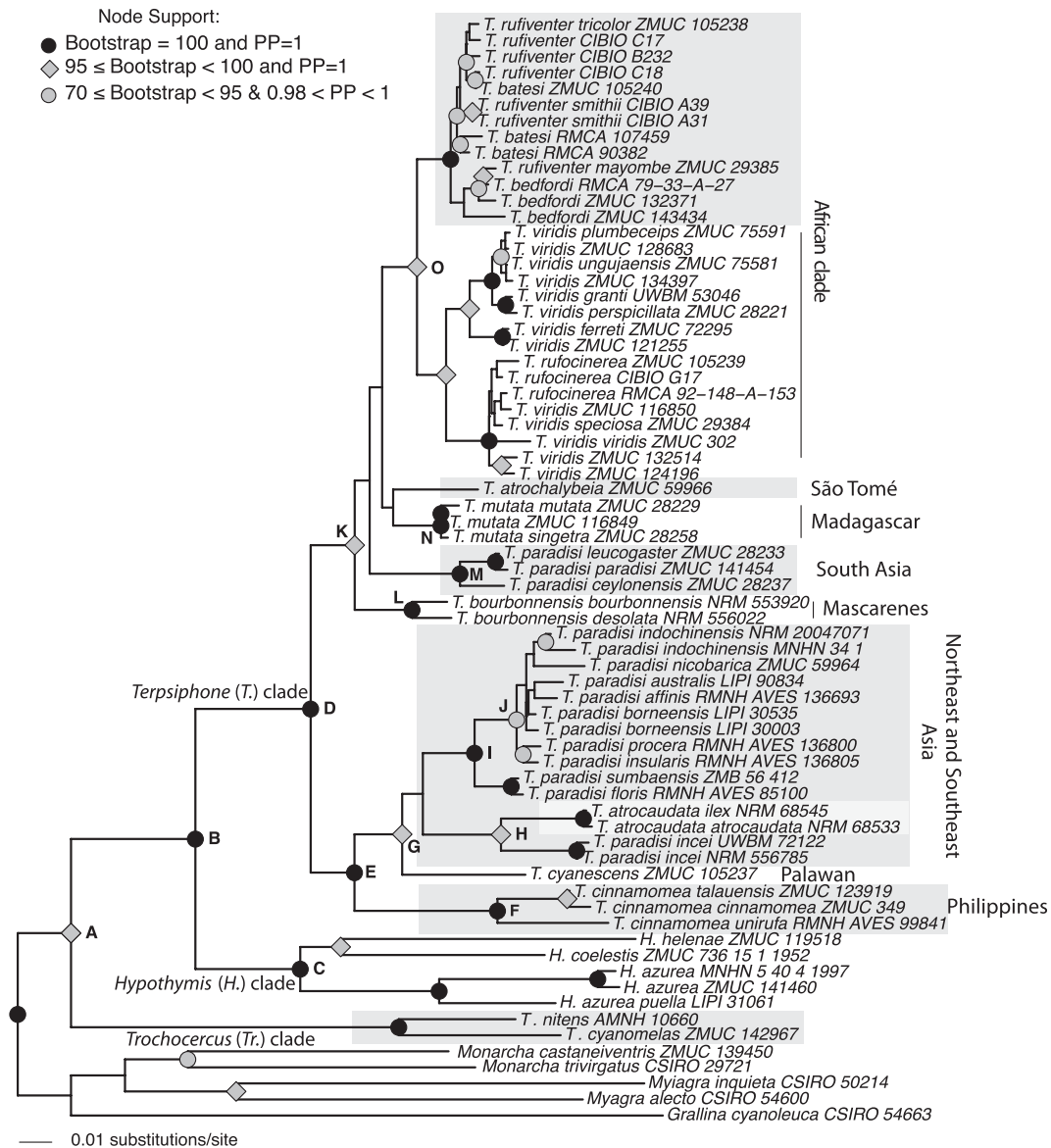
All new sequences were deposited in GenBank (Appendix S1). Owing to the degraded DNA retrieved from museum study skins, only half of the *cyt b* gene (605/1140) was obtained for

some specimens. For some specimens we were not able to obtain the complete *ND2* fragments (LIPI\_31061, ZMUC\_1511952, RMNH\_136693, LIPI\_90834).

Different probabilistic analyses from the combined dataset (unpartitioned and partitioned) produced similar phylogenetic results (Fig. 2, clades A to O). Individual gene topologies with node support values are displayed in Appendix S3. Our analyses recovered three well-supported clades within the Old World Monarchidae, confirming monophyly of the genera *Trochocercus*, *Hypothymis* and *Terpsiphone* [Clade A, 95 ≤ bootstrap (BP) <100, posterior probability (PP) = 1]. *Hypothymis* and *Terpsiphone* are sister clades (Clade B, BP = 100, PP = 1). Members of *Hypothymis* (Clade C) from the Philip-

pines (*H. coelestis* and *H. helenae*) form one clade and are closely related to *H. puella* from Sulawesi and to the widespread Asian/Philippine complex *H. azurea*.

Within the *Terpsiphone* (Clade D), two major geographical clades are recognized. Clade E comprises *T. cinnamomea* (Clade F, Philippines), *T. cyanescens* (Palawan) and a paraphyletic assemblage of *T. paradisi* (Clade I, Southeast Asia, Sundaland and Northeast Asia) and *T. atrocaudata* (Clade H, Japan, Philippines, Southeast and Northeast Asia). Clade K, distributed further to the west, contains the South Asian *T. paradisi* (Clade M), the Mascarene *T. bourbonnensis* (Clade L), the São Tomé *T. atrochalybeia*, the Madagascan *T. mutata* (Clade N) and all the African *Terpsiphone* taxa (Clade O). The



**Figure 2** Maximum likelihood topology of Old World Monarchidae produced from the combined analysis. Labelled clades are discussed in the text. Circles and diamonds at nodes represent maximum likelihood (ML) bootstrap support values and Bayesian posterior probabilities (PP). Black circle: ML bootstrap = 100 and posterior probability = 1; grey diamond: bootstrap ≥ 95 and PP = 1; grey circle: bootstrap ≥ 70 and PP ≥ 0.98. Voucher numbers are indicated for each specimen used for this study.

Mascarene *T. bourbonnensis* forms a clade, but its relationship with the South Asian *T. paradisi*, the other Indian Ocean assemblages (*T. mutata*) and the African *Terpsiphone* clade remains unresolved. *Terpsiphone paradisi* (Asian paradise-flycatcher) is polyphyletic with: (1) a South Asian clade closely related to the African and Indian Ocean *Terpsiphone* species (BP  $\geq$  95, PP = 1); (2) the subspecies *T. p. incei* from Northeast Asia, which is sister to *T. atrocaudata atrocaudata* (BP = 100, PP = 1); and (3) the subspecies of Southeast Asia and the Lesser Sundas. Within the African *Terpsiphone* clade (BP  $\geq$  95, PP = 1), we found a dichotomy between a 'T. rufiventer' clade (BP = 100, PP = 1) and a 'T. viridis' clade (BP  $\geq$  95, PP = 1). *Terpsiphone rufiventer* is paraphyletic owing to the inclusion of *T. bedfordi* and *T. batesi*. No phylogenetic signal supported the monophyly of these two taxa, which seem to be very recently derived forms nested within the *T. rufiventer* complex. *Terpsiphone viridis* is also paraphyletic owing to the presence of *T. rufocinerea*. *Terpsiphone rufocinerea* monophyly is also not supported.

### Molecular dating and biogeographical analyses

A time-scale for the evolution of the Old World Monarchidae derived from the Bayesian dating analysis is shown in Fig. 3. Divergence estimates and confidence intervals for various models and supported nodes are shown in Table 1. Divergence-time estimates using global and relaxed clocks with the *cyt b* 2% and the *ND2* 2.8% Myr<sup>-1</sup> divergence rates and gene/codon partitions converged to similar results. Using the calibration point provided by the islands of Mauritius and Réunion, we estimated slightly older ages compared with the rate-based model, but with overlapping 95% confidence intervals (see Table 1).

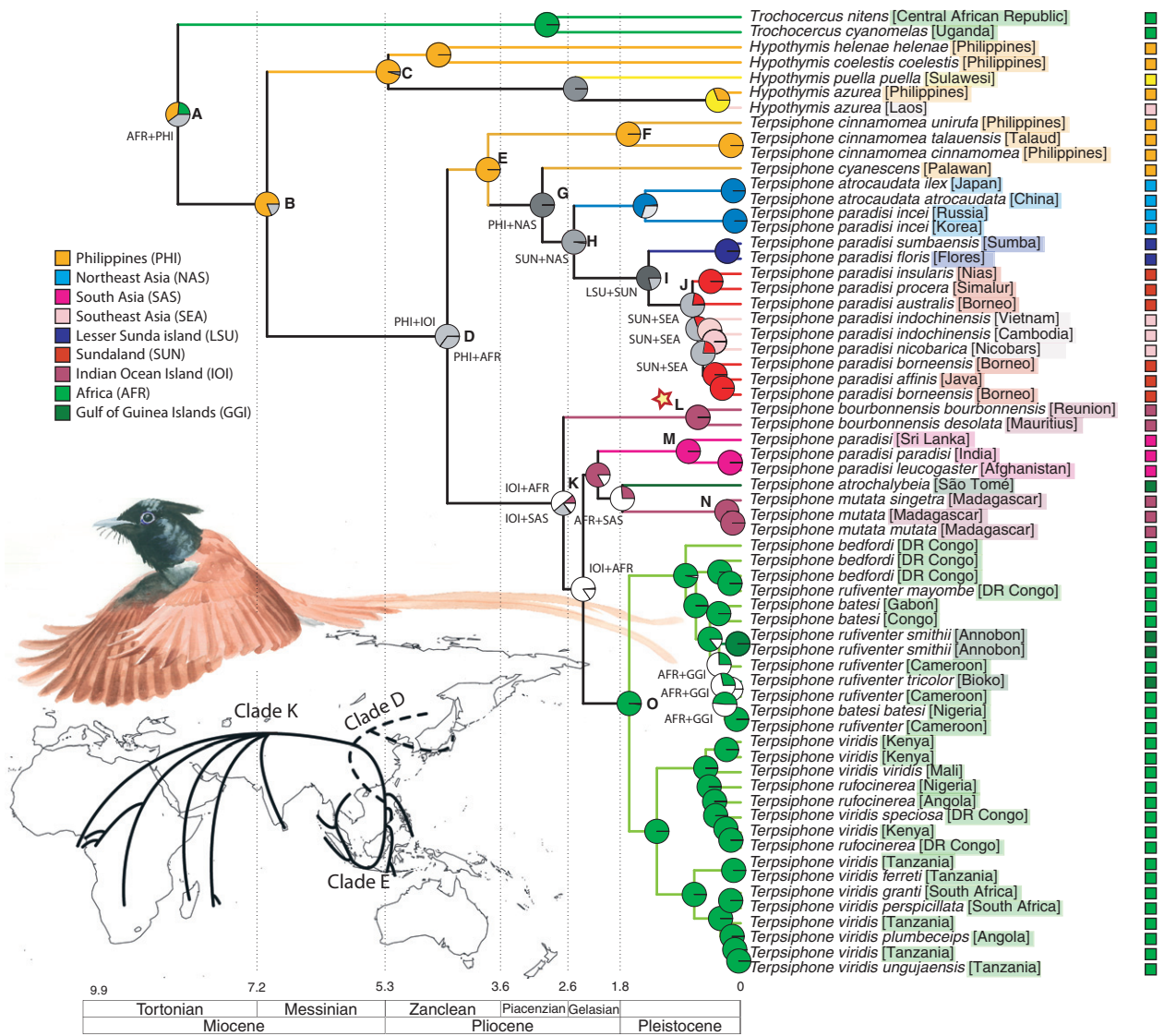
Results of the LAGRANGE (M1, M2, M3) and Bayes-LAGRANGE (BM1) analyses are shown in Table 2 and Fig. 3, respectively. All three models provided very congruent results for recent nodes (nodes E to O). Most of the discrepancies occurred at nodes A to D, owing to the introduction of dispersal constraints between Africa, Asia and Indian Ocean islands. Depending on the model, the origin of *Hypothymis/Terpsiphone* appears to have been in the Philippines (M1, BM1), South Asia/Africa (M2) or the Philippines/Africa (M3), whereas *Trochocercus* appears to be of African origin. This scenario requires the origin of the Old World Monarchidae clade to include two potential ancestral areas, of which the most probable are the Philippines or Africa/the Philippines according to M1, or only Africa according to M1 and M2. M1, M2 and BM1 estimate the ancestor of *Terpsiphone* to have originated in the Indian Ocean islands/the Philippines or in the Philippines/Africa in the late Miocene. However, M2, which involves stepping-stone dispersal between Africa and South Asia, indicated South Asia/Africa as the most likely ancestral hypothesis. This latter hypothesis involves extinction, which is higher in M2 (Table 2). A probable Philippines origin is identified for *Hypothymis* (M1, M3, BM1). At a relatively early stage, members of one *Terpsiphone* clade

(Clade K, Table 2) dispersed to Africa, the Indian Ocean islands and South Asia, where *Terpsiphone* subsequently diversified into at least six species. For Clade E, the Philippines seem to have played an important role initially (M1, M2 and M3 which include South Asia as the most likely ancestral estimation), and the placement of *T. cyanescens* indicates that Palawan may have played a role in the subsequent colonization of Northeast and Southeast Asia. From the Philippines, members of Clade E dispersed to Sundaland, the Lesser Sundas, Southeast Asia (*T. paradisi*, Clade I) and Northeast Asia (*T. paradisi incei* and *T. atrocaudata*, Clade H). The Southeast Asian *Terpsiphone* clade also dispersed to the Lesser Sundas (*T. paradisi sumbaensis* and *T. p. floris*). Ancestral reconstructions at node J indicate a Sundaland origin, and Southeast Asia seems to have been colonized simultaneously, as indicated by a lack of phylogenetic structure and BM1. Taxa from islands surrounding Sumatra appear to have been colonized early, and the Andaman island subspecies appears to be closely related to the mainland Southeast Asian *T. paradisi indochinensis*. The BM1 ancestral reconstruction for node K, including all *Terpsiphone* species from Africa, Southeast Asia and the Indian Ocean islands, is ambiguous, suggesting a simultaneous colonization of these areas. Moreover, the Indian Ocean islands seem to have been colonized twice by *T. mutata* and *T. bourbonnensis*, as indicated by the topological results and the high divergences between these taxa (Table 1). Finally, *T. atrochalybeia* and *T. rufiventer* appear to have independently colonized the New Guinea Gulf islands two or three times (São Tomé, Bioko and Annobon).

### Plumage state reconstruction

To examine how plumage transitions relate to diversification, we reconstructed ancestral states for nine discrete plumage characters and for insular/continental origin to address questions pertaining to the evolution of plumages on islands (blue branches) and continents (brown branches) (Figs 4 & 5). As shown above, the origin and early divergence within *Terpsiphone* is ambiguous with respect to insular or continental origin. Clade E is of insular origin and subsequently led to the colonization of Asia. The origin of Clade K is also ambiguous, owing to the simultaneous colonization of the Mascarenes, South Asia, Madagascar and Africa.

By comparing the root of *Terpsiphone* to the various island and continental lineages of our phylogeny (Figs 4 & 5), we identified 12 island lineages (*atrocaudata*, *atrochalybeia*, *bourbonnensis*, *cinnamomea*, *cyanescens*, *mutata*, four of *paradisi* and two of *rufiventer*) and 10 continental lineages (*bedfordi*, five of *paradisi*, two of *rufiventer*, *rufocinerea* and *viridis*). These were used for the island/continent ancestral area reconstruction (Fig. 5, right). We consider *T. bedfordi* and *T. rufocinerea* to be one lineage because they represent recent divergence and because the status of these taxa cannot be assessed in detail with our current dataset. We find that island lineages display more apomorphic characters (crest absence 58% of



**Figure 3** Ancestral area reconstructions of Old World Monarchidae. The tree is a chronogram (strict molecular clock) based on a BEAST Markov chain Monte Carlo (MCMC) analysis of the combined dataset. Maximum likelihood ancestral area reconstructions were conducted on 1000 randomly sampled trees (allowing for alternative topologies to be included) from the posterior distribution of the BEAST analysis. The result from the Model 1 (M1) is presented here. The distribution for each taxon is presented to the right of the taxon name. Coloured pies indicate the origin of a given node. White- and grey-shaded pies indicate mixed origin, as indicated next to the pie in abbreviated form. The map indicates the inferred dispersal and colonization routes of members of the *Tersiphone*. The star indicates the island calibration points used for the absolute dating. Water colour by Jon Fjeldså.

apomorphy, normal tail 33%, crown colour 16%, throat colour 33%, wing coverts colour 42%, tail colour 50%, breast colour 67%, vent colour 41%, belly colour 42%) compared to continental clades (cf. crest absence 10%, normal tail 20%, crown colour 0%, throat colour 10%, wing coverts colour 20%, tail colour 20%, breast colour 20%, vent colour 50%, belly colour 40%). These results show that *Tersiphone* male plumages that evolved on islands are more derived and of uniform colour compared with those that evolved on continents. In fact, members of *T. cinnamomea* display only rufous colours, whereas males of *T. atrochalybeia*, *T. corvina* (not included in this analysis) and *T. atrocaudata* are mainly black,

and males of *T. cyanescens* are mainly blue. Island taxa also display more homogeneous plumages, as exemplified by the Lesser Sunda leucistic *T. paradisi* and the Madagascan *T. mutata* males, which have a rufous or white throat. The ancestral plumage colour of members of *Tersiphone* is inferred to be close to the plumages of the *T. paradisi* or *T. viridis* complexes for six plumage characters (see Figs 4 & 5) with crest,  $P = 0.80$ ; elongated tail quills,  $P = 0.99$ ; black crown and throat,  $P = 1.00$ ; rufous wing coverts and tail  $P = 0.99$ . Elongated tail quills seem to have disappeared independently in two island taxa (*T. bourbonnensis*, *T. cyanescens*) and in most of the members of *T. rufiventer*. Finally, the presence



**Table 1** Divergence times of Old World Monarchidae in millions of years ago (Ma) with 95% highest posterior densities obtained using molecular strict and relaxed clock rates and island constraints. Letters correspond to clades that are discussed in the text (Figs 2 & 3).

Clade	Divergence times (Ma)		Island calibration	
	mt rate (cyt <i>b</i> : 2%/ND2: 2.7%)		Exponential	Uniform
	Strict	Relaxed		
A	8.4 (7.7–9.3)	10.1 (8.6–11.8)	13.5 (10.7–16.8)	13.1 (10.4–16.2)
B	7.1 (6.4–7.8)	8.2 (6.9–9.7)	10.7 (8.4–13.3)	10.4 (8.2–12.9)
C	5.3 (4.6–6.0)	5.9 (4.7–7.2)	8.0 (6.1–10.1)	7.7 (5.9–9.8)
D	4.4 (3.9–4.9)	4.9 (4.1–5.8)	6.5 (5.1–8.2)	6.3 (5.0–7.9)
E	3.8 (3.3–4.3)	4.1 (3.4–5.0)	5.8 (4.5–7.4)	5.6 (4.3–7.1)
F	1.7 (1.3–2.1)	1.8 (1.2–2.5)	2.6 (1.7–3.6)	2.5 (1.7–3.4)
G	3.0 (2.5–3.4)	3.2 (2.6–4.0)	4.3 (3.2–5.4)	4.1 (3.1–5.3)
H	1.4 (1.1–1.8)	1.5 (1.0–2.0)	2.1 (1.4–2.8)	2.1 (1.4–2.7)
I	1.4 (1.1–1.7)	1.4 (1.1–1.9)	2.1 (1.4–2.7)	1.9 (1.4–2.6)
J	0.7 (0.5–0.9)	0.8 (0.5–0.9)	1.0 (0.7–1.4)	1.0 (0.7–1.3)
K	4.4 (2.3–3.1)	2.8 (2.3–3.4)	4.0 (3.0–5.1)	3.8 (2.9–4.9)
L	0.6 (0.4–1.0)	0.6 (0.3–0.9)	1.3 (1.0–1.8)	1.2 (1.0–1.5)
M	0.8 (0.5–1.1)	0.8 (0.5–1.2)	1.1 (0.7–1.7)	1.1 (0.6–1.6)
N	0.5 (0.3–0.7)	0.2 (0.1–0.4)	0.4 (0.2–0.7)	0.6 (0.2–0.6)
O	1.7 (1.4–1.9)	1.7 (1.4–2.1)	2.4 (1.8–3.1)	2.3 (1.3–3.0)

cyt *b*, cytochrome *b* gene; ND2, NADH dehydrogenase subunit 2 gene.

of a crest seems to have been lost in three island taxa (*T. cinnamomea*, *T. bourbonnensis*, *T. cyanescens*) and in some members of *T. rufiventer*, *T. viridis* and *T. rufocinerea*.

## DISCUSSION

### Biogeographical origin of the Old World Monarchidae

The origin of the Monarchidae is uncertain owing to the simultaneous colonization of, and diversification within, Australasia (e.g. *Grallina*, *Myiagra*, *Monarcha* groups; Filardi & Moyle, 2005), Africa (cf. *Trochocercus*) and Asia (cf. *Hypothymis*, *Terpsiphone*). The Philippines appear to be a key area for the early radiation of *Terpsiphone* and *Hypothymis*, with some deep divergent lineages (*T. cinnamomea*, *H. coelestis*, *H. helena*). However, our constrained model approaches (M2, M3) indicated a role for South Asia in terms of the dispersal of Asian taxa into Africa and to Indian Ocean islands. For the Southeast Asian *Terpsiphone* (Clade E) our biogeographical analysis indicates colonization of Asia from the Philippines to Palawan, Northeast Asia, the Lesser Sundas and Sundaland/Southeast Asia, contradicting the dispersal patterns of other passerine bird groups in the region (Gamauf & Haring, 2004; Moyle *et al.*, 2007, 2009; Outlaw & Voelker, 2008; Nyári *et al.*, 2009; Esselstyn *et al.*, 2010; Lohman *et al.*, 2010; Oliveros & Moyle, 2010). The southern oceanic Philippine archipelago originated during the late Eocene and was never connected to mainland Asia (Hall, 1998, 2002), and it is plausible that its complex geological and climatic history influenced dispersal events (Heaney, 1986; Heaney & Rickart, 1990). Our results indicate a late Miocene dispersal in the Philippine archipelago leading to the *Terpsiphone/Hypothymis* clade, in accordance

with other important faunal exchanges between Asia and the Philippines at that time (Steppan *et al.*, 2003; Jansa *et al.*, 2006; Esselstyn *et al.*, 2010) and in agreement with previously cited avian studies. The Sahul/Sulawesi and South Philippine areas include several dynamic volcanic archipelagos that may continuously have provided stepping-stone islands (Hall, 2002). The extant species pattern within the Monarchidae supports the idea that the Old World clade originated in such an environment, giving rise to early dispersal to Africa (*Trochocercus*), Sangihe (*Eutrichomyias*) and the South Philippines (*Hypothymis*, *Terpsiphone cinnamomea*), and thereafter an additional wave of dispersal across the ocean via Palawan to Asia.

One interpretation of our results is that the Philippine taxa represent relicts of an early radiation that was historically widespread across Australasia. An alternative explanation involves early dispersal from an Australasian ancestor to the Philippines, followed by colonization of Sundaland/Southeast Asia during the Pliocene. In the latter scenario, Clade E (eastern Asian *Terpsiphone* clade) constitutes another case of 'upstream' colonization from islands (the Philippine archipelago including Palawan) to a continent (Sundaland/Southeast Asia). If this scenario is true, the *Terpsiphone* genus provides an example in which Palawan acted as a stepping stone for colonization from the Philippines to the Lesser Sundas and Southeast Asian areas. Examples of such a link between Palawan and Southeast Asia are unusual amongst birds (Jones & Kennedy, 2008) and other vertebrates (Esselstyn *et al.*, 2010). In their biogeographical analyses, Esselstyn *et al.* (2010) note that among a set of 39 terrestrial vertebrate lineages from the Philippines, the Sunda Shelf and Palawan, only 17 displayed a relationship between the Philippines and

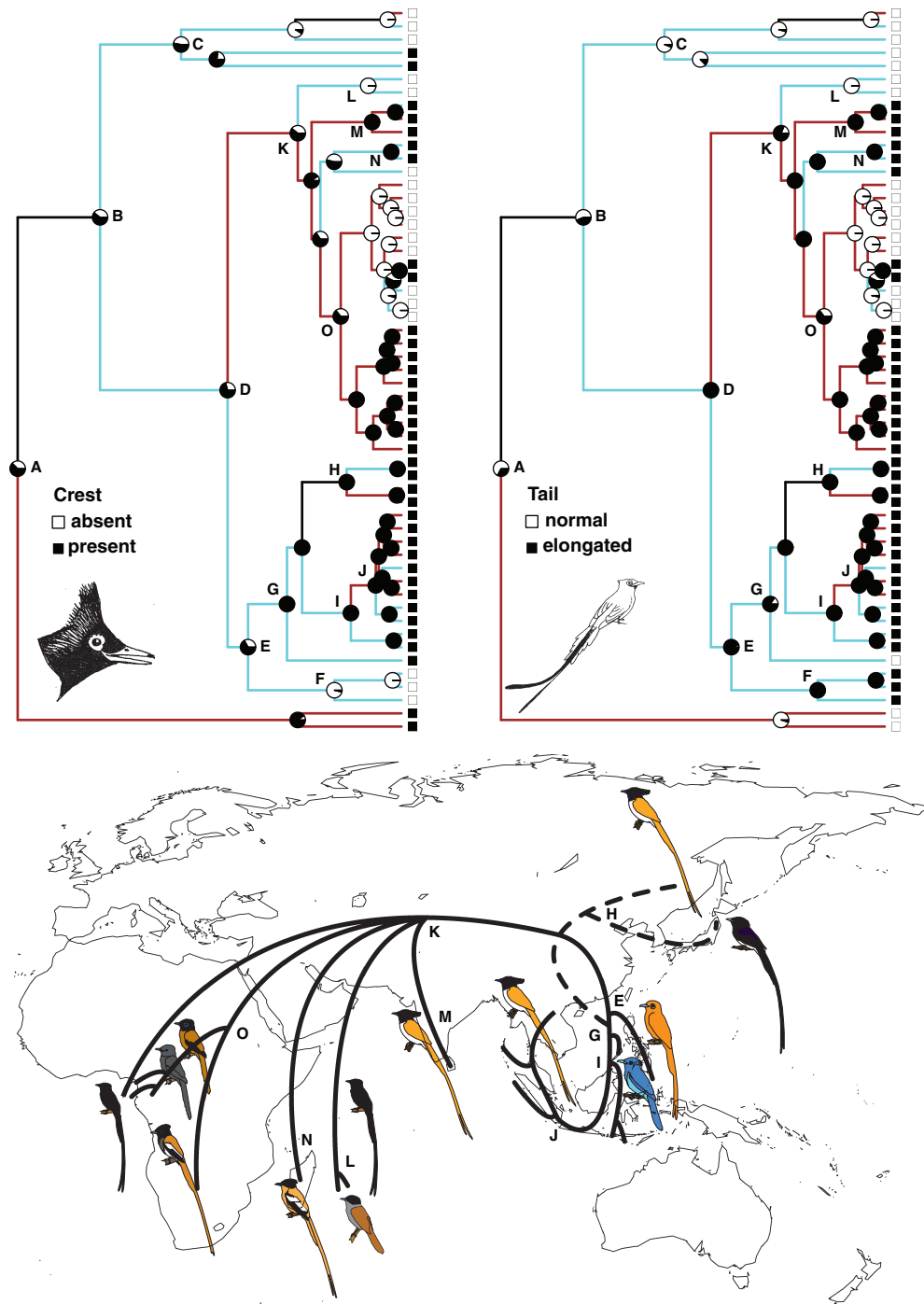
**Table 2** LAGRANGE ancestral area estimation for Old World Monarchidae based on the strict molecular clock chronogram and three dispersal models (M1, M2, M3). Model 1 (M1), equal dispersal rate between all biogeographical areas; Models 2 and 3 (M2 and M3), constrained dispersal ( $d$  parameter) between Africa, Asia and Indian Ocean islands (see Materials and Methods for details). LnL, log likelihood of the LAGRANGE reconstruction;  $d$ , estimated dispersal rate;  $e$ , estimated extinction rate. Areas: SAS, South Asia; GGI, Gulf of Guinea Islands; IOI, Indian Ocean islands; SUN, Sundaland; LSU, Lesser Sunda islands; NAS, Northeast Asia; SEA, Southeast Asia; PHI, Philippines; SUL, Sulawesi; AFR, Africa.

Dispersal models			
Model	M1 ( $d = 1.00$ )	M2 ( $d = 0.00$ )	M3 ( $d = 0.01$ )
parameters	LnL = 120.74; $d = 0.05$ ; $e = 0.05$	LnL = 113.99; $d = 0.05$ ; $e = 0.07$	LnL = 110.64; $d = 0.05$ ; $e = 0.04$
Node A	PHI+AFR 0.25 AFR 0.23 PHI 0.22 PHI+AUS 0.06 PHI+SUL 0.04	AFR 0.39 IOI 0.12 PHI+AFR 0.09 SUL+AFR 0.08 SAS+AFR 0.08 IOI+AFR 0.07	AFR 0.53 PHI+AFR 0.22 IOI 0.08
Node B	PHI 0.41 PHI+AFR 0.34 PHI+SUL 0.09 PHI+IOI 0.07	SAS+AFR 0.51 SAS+IOI 0.20 PHI+AFR 0.09 SUL+AFR 0.08	PHI+AFR 0.78 PHI+IOI 0.16
Node C	PHI 0.52 PHI+SUL 0.34	PHI+SAS 0.38 SAS 0.13 PHI 0.13 PHI+SUL 0.13 SUL+SAS 0.08	PHI 0.57 PHI+SUL 0.30
Node D	PHI+AFR 0.47 PHI+IOI 0.39	SAS+AFR 0.55 SAS+IOI 0.22 PHI+AFR 0.10	PHI+AFR 0.79 PHI+IOI 0.17
Node E	PHI 0.82	PHI+SAS 0.43 PHI 0.22 SAS 0.10	PHI 0.82
Node F	PHI 0.97	PHI 0.72 PHI+SAS 0.20	PHI 0.96
Node G	PHI+SEA 0.56 PHI+NAS 0.12 PHI+LSU 0.11 PHI+SUN 0.09 PHI 0.09	PHI+SEA 0.25 PHI+NAS 0.12 PHI+SUN 0.10 PHI 0.09 PHI+LSU 0.09 PHI+SAS 0.07 SEA+SAS 0.05	PHI+SEA 0.44 PHI+NAS 0.16 PHI+LSU 0.14 PHI+SUN 0.14 PHI 0.10
Node H	SEA 0.42 SEA+NAS 0.38 NAS 0.16	SEA+NAS 0.38 SEA 0.30 NAS 0.24	SEA+NAS 0.39 SEA 0.34 NAS 0.22
Node I	LSU+SEA 0.44 LSU+SUN 0.30 SEA 0.07 SUN+SEA 0.07	LSU+SUN 0.44 LSU+SEA 0.21 SUN 0.06 SUN+SEA 0.07	LSU+SUN 0.45 LSU+SEA 0.30
Node J	SUN+SEA 0.58 SUN 0.41	SUN 0.66 SUN+SEA 0.31	SUN 0.58 SUN+SEA 0.41
Node K	IOI+AFR 0.64 IOI 0.24	IOI+AFR 0.75 IOI 0.14	IOI+AFR 0.85
Node L	IOI 0.98	IOI 0.97	IOI 0.99
Node M	SAS 0.81 SAS+IOI 0.14	SAS 0.74 SAS+IOI 0.18	SAS 0.77 SAS+IOI 0.17
Node N	IOI 0.99	IOI 0.99	IOI 0.99
Node O	AFR 0.89	AFR 0.93	AFR 0.95

Palawan, and 11 showed a relationship between the Sunda Shelf and Palawan.

During the Plio-Pleistocene, *Terpsiphone* members rapidly colonized South Asia, Africa and the Indian Ocean islands from eastern Asia. However, it remains uncertain how many

dispersal events were involved. Poor support and short branch lengths (essentially a polytomy) among the basal lineages may be attributed to rapid radiation (Lara *et al.*, 1996; Leite & Patton, 2002; Steppan *et al.*, 2004; Rabosky & Lovette, 2008). Many phylogenetic studies have demonstrated



**Figure 4** Chronograms based on the maximum likelihood tree showing island (blue) and continental (brown) *Terpsiphone* lineages. Pie charts represent the probability of the ancestral plumage character. The map shows the inferred dispersal and colonization routes of members of the *Terpsiphone*, with the plumages of terminal taxa indicated.

that major avian radiations are linked to historical events such as colonizations of new landmasses (Barker *et al.*, 2002; Ericson *et al.*, 2002). Range expansions and contractions are considered important factors for speciation (Rundell & Price, 2009; Kisel & Barraclough, 2010; Pigot *et al.*, 2010), together with geographical isolation and corresponding reductions in

gene flow between populations (Coyne & Orr, 2004). Our results highlight the extensive role of range expansions by dispersal across oceans and support the idea that dynamic colonization of new habitat and new geographical areas is likely to be the main factor driving *Terpsiphone* diversification.





## Biogeography of Asian paradise-flycatchers

Our multigene analyses support the paraphyly of *T. paradisi* into three biogeographical assemblages: Clade H (Northeast Asian and Japan migratory paradise-flycatchers), Clade I (Southeast Asia, Sundaland, Lesser Sunda) and Clade M (India, Sri Lanka). The geographical distribution and intra-specific variation of Asian paradise-flycatchers (*Terpsiphone paradisi*; Salomonsen, 1933b) were probably shaped by major Plio-Pleistocene climatic (Heaney, 1991), eustatic (Haq *et al.*, 1987; Miller *et al.*, 2005) and vegetational (Heaney, 1991; Bird *et al.*, 2005) changes that also influenced the biogeographical patterns of other forest birds in the region (Lim *et al.*, 2011; Päckert *et al.*, 2012).

*Terpsiphone paradisi* (Clade H) has colonized Southeast Asia and Northeast Asia (Fig. 3); the latter colonization may be the result of seasonal migratory behaviour, which has led to speciation of the Japanese paradise-flycatcher *T. atrocaudata* and *T. p. incei*. Consistent with a study of 16 forest-edge passerine species by Lim *et al.* (2011), we did not find phylogenetic structure between populations of *T. paradisi* in Sundaland, the Malay peninsula and Southeast Asia. In this area, the Isthmus of Kra has been predicted to be a biogeographical barrier (Hughes *et al.*, 2003; Woodruff, 2003; de Bruyn *et al.*, 2005; Woodruff & Turner, 2009). Lack of phylogenetic structure within *T. paradisi* (Clade J in our study) indicates that there was more dispersal across the Isthmus of Kra than expected. More structure is evident, however, within the *T. paradisi* subspecies on the Lesser Sundas and on the Nias and Simalue islands, which could be an indication of greater isolation in these two archipelagos.

Clade M constitutes an independent lineage isolated from other Asian lineages. This phylogenetic differentiation could be explained by the biogeographical barrier of the North-western Myanmar.

## Asia as an area of origin for African and Indian Ocean *Terpsiphone*

In agreement with previous work on Indian Ocean taxa, for example *Coracina* (Jönsson *et al.*, 2010b), *Hypsipetes* (Warren *et al.*, 2005), *Nectarinia* (Warren *et al.*, 2003) and *Zosterops* (Warren *et al.*, 2006), our results overall demonstrate an Asian origin (Warren *et al.*, 2010). Taxa from Mauritius and Réunion represent an old divergent clade within the *Terpsiphone* and do not show a close relationship with the Madagascan clade. Warren *et al.* (2010) proposed the potential role of the Indian winter monsoon winds between the Indian subcontinent and Madagascar (Goswami & Rajagopal, 2003; New *et al.*, 2005; Cheke & Hume, 2008) and recent sea-level fluctuations, which could have provided stepping stones between the granitic Seychelles, Mascarenes and India (Haq *et al.*, 1987; Miller *et al.*, 2005).

Colonization of Africa/São Tomé probably also originated from an Asian ancestor, as inferred for *Oriolus* (Jönsson *et al.*, 2010c), *Dicrurus* (Pasquet *et al.*, 2007) and *Turdus* (Melo *et al.*,

2010). Alternatively, some *Terpsiphone* taxa might have gone extinct on the African mainland. In this respect, the similar plumages of *T. corvina* from the Seychelles should be added in future studies to improve the resolution of our topology and also to shed light on affinities between *T. corvina* and *T. atrochalybeia*. Colonization of Bioko and Annobon islands occurred independently from a *T. rufiventris* ancestor and has resulted in two very derived subspecies (*T. r. smithii* and *T. r. tricolor*).

## Plumage evolution on islands and continents within the genus *Terpsiphone*

The most striking pattern revealed by our analyses concerning plumage differentiation of *Terpsiphone* is that insular taxa often display more divergent male plumages than do continental forms (except for *T. rufiventris*). Continental taxa display less marked plumage variability, as displayed by the polyphyletic *T. paradisi* assemblage. The homogeneity of plumages for continental *Terpsiphone* taxa (cf. *T. paradisi*, *T. viridis*) constitutes an interesting question concerning the range expansion of this genus and the evolution of plumage variation on islands and continents. The crest, the tail quill and the plumage coloration are the most marked plumage signals in *Terpsiphone* males, and the degree of colourfulness and plumage variation is assumed to be the outcome of sexual selection (Andersson, 1994). First, sexual selection could increase the risk of extinction by promoting traits that increase mating success at the cost of survival (McLain *et al.*, 1999; Morrow & Pitcher, 2003). Moreover, small populations of polygamous taxa could be exposed to an increased extinction risk on islands owing to small effective population size (Berger, 1990; Manne *et al.*, 1999). Following this hypothesis, colourful and/or sexually dichromatic species may be evolutionarily less successful in maintaining viable populations on islands than drab and monomorphic birds. Second, ecological conditions acting on islands may lead to a decrease in sexual selection intensity. Barton (1996) and Griffith (2000) have shown that selection has less effect on islands than on continents, and that most populations diverge more quickly on islands because of genetic drift, the founder effect and dispersal limitation, although another study disagrees with this hypothesis (Price *et al.*, 2010). The unicoloured 'island' plumage pattern of island *Terpsiphone* taxa is also seen in other small bird populations, as some aberrant plumage variants (e.g. leucistic *Acrocephalus* warblers, Galapagos finches, island granivores) are more common compared to continental forms (Price, 2008). These drift effects on plumage colour could explain why plumage has evolved more rapidly on islands than on continents.

Our ancestral character analyses indicate that the ancestral *Terpsiphone* form had a plumage similar to that of members of the contemporary Asian *T. paradisi* (Asian paradise-flycatcher). Together with our biogeographical inferences, this result reinforces the hypothesis of a range expansion of a *T. paradisi*-like ancestor into eastern Asia (Northeast and Southeast Asia) and the Western Old World (Africa, Indian Ocean

islands, South Asia). Furthermore, our ancestral reconstructions indicate that the plumage of the ancestors of *Terpsiphone* could have been close to the general continental plumage of *T. paradisi* and *T. viridis*. These results lend support to a scenario of dispersal followed by speciation on islands or in primary forest habitat within Africa. The success of *Terpsiphone* compared with other genera of Old World Monarchidae (*Hypothymis* and *Trochocercus*) could also be explained by the derived sexual dimorphisms (tail quills, crest, plumage colour heterogeneity), which could have driven the speciation process within this genus. However, in view of the large number of subspecies within *Hypothymis azurea* and *Trochocercus*, a more detailed study of these taxa within the Old World Monarchidae is required to understand their evolutionary history.

### Systematics and taxonomy

To date, the systematics of the Old World Monarchidae has been based on plumage assessments only, whereas our detailed study is the first to use molecular data to characterize the evolutionary history of this diverse group of birds. Our results show some discrepancies with the taxonomy of Clements (2007) and the IUCN lists. We based the delineation of our taxonomic units on the topological results and on the molecular dating divergences. In agreement with Pasquet *et al.* (2002), our results show that the Old World Monarchidae comprises three well-supported monophyletic clades: *Terpsiphone*, *Hypothymis* and *Trochocercus* (represented by *T. nitens* and *T. cyanomelas*). *Hypothymis helenae* and *Hypothymis coelestis* from the Philippines are sister taxa and form the sister clade of another well-supported clade that consists of *Hypothymis azurea* and the Wallacean *Hypothymis puella*. The split between the latter two species dates back to the mid-Pliocene, and lends support to a separate species status for *Hypothymis puella* (Oberholser, 1911; Coates *et al.*, 2006). Our results also support monophyly of the genus *Terpsiphone*, but at the same time suggest more complicated relationships than depicted by the current taxonomy (Clements, 2007).

The systematic and taxonomic status of the members within *Terpsiphone* has been a subject of much debate (Stresemann, 1924; Salomonsen, 1933a,b; Chapin, 1948), with multiple subspecies described for *T. paradisi* (26 subspecies; Salomonsen, 1933a), *T. rufiventer* (11 subspecies; Chapin, 1948; Erard *et al.*, 1997) and *T. viridis* (10 subspecies; Erard *et al.*, 1997). Based on our phylogenetic results, the Asian paradise-flycatcher complex (*T. paradisi*) can be split into three biogeographical groups: (1) a South Asian clade (including *T. p. paradisi*, *T. p. leucogaster* and *T. p. ceylonensis*), (2) a Northeast Asian clade *T. p. incei* (Coates *et al.*, 2006), and (3) a Southeast Asian clade (including *T. p. affinis*, *T. p. australis*, *T. p. borneensis*, *T. p. floris*, *T. p. insularis*, *T. p. nicobarica*, *T. p. procera* and *T. p. sumbaensis*). A reassessment of *T. paradisi* based on plumages, vocalization and behaviour is clearly warranted in view of this polyphyly.

Recent divergences within *T. viridis* and *T. rufiventer* add to the taxonomic complexity of the genus *Terpsiphone*. Earlier

taxonomists have shed light on important plumage variation and potential hybrid forms among the African taxa (Chapin, 1948, 1962; Erard *et al.*, 1997; Dowsett-Lemaire, 1998), and our molecular analyses support this view, with complex branching patterns of *T. batesi* and *T. bedfordi* nested within the *T. rufiventer* group and of *T. rufocinerea* nested within the *T. viridis* group. Our sampling, however, did not allow us to delineate a *T. viridis* and *T. rufiventer* clade. The mixture of haplotypes (cf. introgression) concerning *T. rufocinerea*, *T. batesi* and *T. bedfordi* suggests potential hybridization between these groups, probably reflecting recent (and ongoing) speciation within the Guinea–Congo rain forest. Members of *T. rufiventer* represent a continental exception as they show a great variety of plumage morphs (Chapin, 1948, 1962). This species group represents a recent shift in habitat from thickets, forest edges and secondary forest to mature forest habitat. Climatic events and the geological history of Africa must have played a major role in the recent diversification of these taxa in Africa.

The relatively deep divergence of *T. cinnamomea* (Philippine archipelago), *T. atrochalybeia*, *T. mutata*, *T. cyanescens* and *T. bourbonensis* when compared with other taxa suggests that these taxa constitute valid species. Our results highlight a general need for subspecies-level phylogenies (Phillimore & Owens, 2006) in order to clarify taxonomy and evolutionary processes. The difficulty of confidently classifying some of the taxa is exacerbated by the high degree of plumage variation between subspecies, hybridization, sexual dimorphism and the presence of white morphs within three of the species (*T. mutata*, *T. paradisi*, *T. viridis*) (Mulder *et al.*, 2002; Mizuta, 2003).

### ACKNOWLEDGEMENTS

We are grateful to the following people and institutions for granting access to toe-pad, blood and tissue samples: Eric Pasquet (MNHN), Floris Breman (RMCA), Jan Bolding Kristensen (ZMUC), Leo Joseph (ANWC), Martim Melo (CIBIO), Michael Brooke (UMZC), Michelle Louette (RG), Pascal Eckhoff (ZMB), Paul Sweet (AMNH), Per Ericson (NRM), Sharon Birks (UWBM), Steven van der Mije (RMNH), Sri Sulandari (LIPI), Sylke Frahnert (ZMB), Ulf Johansson (NRM), Takema Saitoh (YIO) and Walter Boles (AM). We thank Joao Lourenco and Benoit Nabholz for their comments and corrections on earlier drafts. R.B. and J.G. acknowledge support from the Darwin Initiative. P.-H.F., K.A.J. and J.F. acknowledge the Danish National Research Foundation for funding to the Center for Macroecology, Evolution and Climate.

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## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

**Appendix S1** Taxonomic sampling, voucher numbers and loci used in this study.

**Appendix S2** Primers used for the study skin samples.

**Appendix S3** The maximum likelihood trees of the Old World Monarchidae obtained from the RAxML analysis of *GAPDH*, *ND2*, *ND3* and *cyt b*.

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## BIOSKETCHES

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Author contributions: P.-H.F. conceived the ideas, designed the methods, analysed the data and wrote the paper; P.-H.F. and M.I. produced the DNA sequences; R.B. and J.G. contributed some DNA sequence data; M.I., J.F., R.B., J.G. and K.A.J. played a large part in the writing of the paper.

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Editor: Malte Ebach