



Neumann's Warbler *Hemitesia neumanni* (Sylvioidea): the sole African member of a Palaeotropical Miocene avifauna

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We present molecular evidence that Neumann's Warbler *Hemitesia neumanni* is deeply nested within the Cettiidae. The species' distribution in the Albertine Rift of East Africa is intriguing, as the family Cettiidae is principally an Asian radiation. This disjunct distribution could be a result of colonization of Africa by long-distance dispersal, or the Cettiidae may at some point in the past have had a much larger geographical distribution that also covered parts of Africa.

Keywords: Africa, Albertine Rift, Asia, biogeography, Cettiidae, dispersal, phylogeny, vicariance, Warbler.

Neumann's Warbler *Hemitesia neumanni* is a small passerine of uncertain affinities that has a restricted distribution in mountain forests in the Albertine Rift, East Africa. The short tail, relatively large head with a prominent whitish supercilium, black stripe through the eye, black lateral crown-stripe and a dark greenish grey central crown-stripe make it a very distinctive species. It is mostly found on or close to the ground (Bairlein *et al.* 2006). Rothschild (1908) originally described Neumann's Warbler as *Sylvietta neumanni*. However, except for its short tail, it shows no particular resemblance to the genus *Sylvietta* (crombecs) and Rothschild's decision to place it within this genus was probably influenced by a shared African distribution. Several external morphological differences between Neumann's Warbler and the genus *Sylvietta*, and the observation that Neumann's Warbler has many morphological features in common with the Asian warbler genus *Tesia*, led Chapin (1948) to place Neumann's Warbler in the monotypic

genus *Hemitesia*, in which it has been retained in subsequent classifications (e.g. Watson *et al.* 1986, Sibley & Monroe 1990, Bairlein *et al.* 2006).

The combination of being a restricted-range species in Africa and having a potentially close relationship with Asian warblers makes an investigation of the affinities of Neumann's Warbler interesting, as it may improve the understanding of the timing, frequency and direction of historical avifaunal exchanges between Africa and Asia. In this study, we examine the phylogenetic relationships of Neumann's Warbler and estimate divergence times for a diverse taxon sampling of Asian and African warblers by analysing nuclear and mitochondrial DNA sequences.

METHODS

Taxon sampling, PCR amplification and sequencing

We examined the phylogenetic relationships of *Hemitesia* by analysing DNA sequences from the mitochondrial cytochrome *b* gene and from three

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nuclear loci, myoglobin intron 2, ornithine decarboxylase introns 6–7 (ODC) and glyceraldehyde-3-phosphodehydrogenase intron 11 (GAPDH). The taxon sampling includes a broad selection of African and Asian warblers, including all major clades in the Cettiidae identified by Alström *et al.* (2006) and the genera *Sylvietta* and *Tesia*, to which *Hemitesia* has been associated. We have also included representatives from a selected number of other major oscine lineages, some suboscines and the Rifleman *Acanthisitta chloris*. The trees were rooted with a parrot, as parrots have been suggested to be the closest relatives to passerine birds (Hackett *et al.* 2008). Voucher and GenBank accession numbers are provided in Table 1.

For extractions, PCR amplification and sequencing procedures from study skin samples, we followed the procedures described in Irestedt *et al.* (2006). Two specimens of *Hemitesia*, one in the Swedish Museum of Natural History, Stockholm, Sweden, and one in The Natural History Museum, Tring, UK, were examined.

Phylogenetic analyses and estimation of divergence times

We used Bayesian inference to estimate phylogenetic relationships. The models of nucleotide substitution were selected for each gene individually using the Akaike information criterion implemented in the program MRMODELTEST 2.2 (Nylander 2004) in conjunction with PAUP* (Swofford 2002). Due to a rather low number of insertions in the non-coding nuclear loci, the sequences could be aligned easily by eye. All gaps were treated as missing data.

Posterior probabilities of nodes and parameters in the substitution models were approximated with MCMC and Metropolis-coupling using the program MRBAYES 3.1.1 (Ronquist & Huelsenbeck 2003). Analyses were performed for both the individual genes (10 million generations), nuclear (10 million generations) and a concatenated dataset (50 million generations), with trees sampled every 1000 generations. The program AWTY (Nylander *et al.* 2008b) was used to estimate when the chains had reached their apparent target distributions, and trees sampled during the burn-in phase were discarded. To evaluate further statistical support for the topology, maximum likelihood bootstrapping (1000 replicates) was performed on the concatenated sequences in TREEFINDER (Jobb *et al.*

2004, Jobb 2008) using default settings and the best-fit model proposed by TREEFINDER.

We used a relaxed clock model implemented in BEAST 1.5.3 (Drummond *et al.* 2006) to estimate divergence times between phylogenetic lineages based on the concatenated dataset. As a calibration point we used the split between *Acanthisitta* and all other passerines, as this has been linked to the geological separation between New Zealand and Antarctica (Barker *et al.* 2002, Ericson *et al.* 2002). The dating of this split has often been assumed to be between 85 and 82 million years ago (Mya), but this timing has recently been suggested to be less certain, 85–65 Mya (McLoughlin 2001, Ladiges & Cantrill 2007). To account for this uncertainty we used a normally distributed tree prior with a median at 76 Mya and a standard deviation of 8 Mya (quintiles 2.5% = 60.3 Mya; 5% = 62.8 Mya; 95% = 89.2 Mya; 97.5% = 91.7 Mya). As for the other priors, we used default settings with the exception of the tree prior that was set to reflect a Yule process and an uncorrelated log-normal distribution was used for the molecular clock model. We used the locus-specific models of nucleotide substitution and ran MCMC chains for 25 million generations. The program TRACER 1.4.1 (Rambaut & Drummond 2007) was used to evaluate the run to help ensure that adequate effective sample sizes and mixing had occurred for parameter and dating estimation.

RESULTS

Variation in the molecular dataset and model selection

Taking into account the absence of a few short fragments for some taxa, the alignments analysed are 420 bp for GAPDH, 720 bp for ODC, 742 bp for myoglobin and 900 bp for cytochrome *b*. Some indels in more variable regions were found to be autapomorphic, but most other indels were congruent with the phylogenetic tree obtained from the analysis of the combined dataset.

The prior selection of substitution models supported the GTR+I+ Γ model for cytochrome *b* and ODC, and the GTR+ Γ for GAPDH and myoglobin; for the maximum likelihood bootstrap, the GTR+I+ Γ model was used. After discarding the burn-in phase, the final inference was based on a total of 9000–9500 samples from the posterior for the individual loci and 49 000 samples from the

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

	Museum no.	Locality	Cytb	GAPDH	Myo	ODC
<i>Abroscopus superciliosus superciliosus</i>	NMNH B02119	Myanmar	DQ008515	HQ121540	DQ008567	EU680702
<i>Acanthisitta chloris</i>	NRM 569989 (GAPDH, myo, ODC)	New Zealand	AY325307	EU726202	EU726212	EU726220
<i>Acrocephalus dumetorum</i>	NRM 569279	Punjab, India	AJ004773	FJ357911	AY887682	EF625338
<i>Aegithalos caudatus caudatus</i>	NRM 976089	Sweden	AY228044	FJ357912	AY228281	EU680703
<i>Alauda arvensis arvensis</i>	NRM 966614	Sweden	AY228047	FJ357913	AY228284	EF625336
<i>Batis mixta/poensis</i>	ZMUC 02953 (cytb); MNHN CG 1998-783 (GAPDH, myo, ODC)	Africa	DQ011862	DQ406665	AY529907	EU272120
<i>Callaeas cinerea</i>	J. G. Ewen, uncat	New Zealand	HQ121529	EU272097	EU272108	EU272124
<i>Cettia cetti cetti</i>	DZUG U1936	France	HQ121525	HQ121543	HQ121534	HQ121555
<i>Cettia diphone borealis</i>	UWBM 75317	Russia	HQ121522	HQ121536	HQ121531	HQ121550
<i>Cettia flavolivacea intricata</i>	NRM 20066035	Sichuan, China	DQ673880	HQ121537	DQ673893	HQ121551
<i>Coracina lineata</i>	ANWC 39960 (cytb), ZMUC 95267 (GAPDH, myo, ODC)		FJ821115	EU380462	EU380493	EU380420
<i>Corvus corone</i>	NRM 986167 (cytb, myo); MNHN CG 1995-41 (GAPDH); MNHN 13-16 (ODC)		AY228087	DQ406663	AY228327	EU272116
<i>Donacobius atricapilla atricapilla</i>	NRM 966966	Paraguay	DQ008481	FJ357915	DQ008533	EU680723
<i>Erythrocerus mcallii</i>	NRM 570225 (GAPDH); FMNH 396684 (myo, ODC)	Africa	AF096465	HQ121544	EU680585	EU680727
<i>Hemitesia neumanni</i>	NRM 570210	Congo	HQ121520	HQ121535	HQ121530	HQ121549
<i>Hirundo rustica rustica</i>	NRM 973268	Sweden	DQ008516	EF441218	AY064258	EF441240
<i>Hylia prasina</i>	ZMUC 119039	Africa	HQ121527	HQ121545	EU680583	EU680732
<i>Leiothrix argenteauris</i>	MNHN 8-18	Captive bird	EU 447095	FJ 357942	FJ 357942	FJ 358107
<i>Locustella fluviatilis</i>	NRM 20046784 (cytb, GAPDH, myo); NRM 20026297 (ODC)	Sweden	DQ008475	HQ121546	DQ008527	HQ121556
<i>Menura novaehollandiae</i>	MV F722	Australia	AY064276	EF441220	AY064729	EF441242
<i>Merops viridis/nubicus</i>	ZMCU P935 (GAPDH, myo, ODC)	Indonesia, Sulawesi	MNU89185	AY600498	AY165815	DQ881752
<i>Orthotomus cucullatus hedyemeles</i>	DZUG U1642	Sweden	HQ121523	HQ121539	HQ121532	HQ121552
<i>Parus major major</i>	NRM 956363 (cyt b, GAPDH, myo); NRM 20036752 (ODC)	Sweden	AY228072	EU272098	AY228310	EU680749
<i>Pellorneum ruficeps</i>	MNHN 4-6F	Thailand	AF 094632	FJ 357887	FJ 357957	FJ 358056
<i>Philepitta castanea</i>	ZMCU S458	Madagascar	AY065726	AY336591	AY065790	DQ785938
<i>Phylloscopus collybita abietinus</i>	NRM 966410 (cytb); NRM 20036964 (GAPDH, ODC)	Sweden	HQ121526	FJ357920	DQ125966	FJ358084
<i>Pitta baudii</i>	ANSP 1224	Borneo	AY064280	DQ785903	AY064256	DQ785942
<i>Phoebastria albigaster albigaster</i>	NRM 20086723	Sichuan, China	HQ121521	FJ 357889	FJ 357959	FJ 358058
<i>Prinia familiaris</i>	NRM 20046794	Indonesia, Java	DQ008490	HQ121547	DQ008541	HQ121557
<i>Pycnonotus barbatus</i>	MNHN 2-21	Cameroon	HM633367	FJ357922	FJ357985	FJ358086
<i>Pyrrhura/Amazona</i>	LSUMNS B25884 (cytb); NRM 966989 (myo, ODC)		AY751643	AY194432	AY233367	DQ881775
<i>Sylvia atricapilla atricapilla</i>	NRM 976380 (GAPDH, myo, ODC)	Sweden; Germany (cytb)	Z73494	EF441232	AY887727	EF441254

Table 1. (Continued)

	Museum no.	Locality	Cytb	GAPDH	Myo	ODC
<i>Sylvietta whytii</i>	ZMUC 123492 (cytb, myo, ODC); NRM 552128 (GAPDH)	Africa	DQ008501	HQ121548	DQ008552	EU680772
<i>Tesia olivaea olivaea</i>	NRM 20046813	Yunnan, China	DQ008512	HQ121542	DQ008564	HQ121554
<i>Thamnophilus caerulescens</i>	NRM 967007	Paraguay	AY078176	AY336587	AY065783	DQ435504
<i>Thamnomis chloropetoides</i>	FMNH 436448	Madagascar	HQ121528	FJ357923	DQ125971	FJ358087
<i>Tickellia hodgsoni</i>	NRM 20046814	West Bengal, India	DQ008513	HQ121538	DQ008565	EU680774
<i>Timalia pileata dictator</i>	NRM 569652	Vietnam	AF 484882	FJ 357903	FJ 357972	FJ 358072
<i>Tityra cayana</i>	NRM 956584	Paraguay	AF453814	AY336580	AY338742	DQ435505
<i>Urosphena squameiceps</i>	NRM 20046877	Vietnam	HQ121524	HQ121541	HQ121533	HQ121553
<i>Zosterops japonicus simplex</i>	MNHN 16-6F	Yunnan, China	EU 391159	FJ 357910	FJ 357979	FJ 358079

Cytb, cytochrome b; GAPDH, glyceraldehyde-3-phosphodehydrogenase intron 11; Myo, myoglobin intron 2; ODC, ornithine decarboxylase introns 6–7. DZUG, Department of Zoology, University of Gothenburg, Göteborg, Sweden; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MV, Museum Victoria, Melbourne, Australia; MNMH, National Museum of Natural History, Washington, DC, USA; NRM, Swedish Museum of Natural History, Stockholm, Sweden; ZMUC, Zoological Museum of the University of Copenhagen, Denmark; UWBM, University of Washington Burke Museum, Seattle, WA, USA; FMNH, Field Museum of Natural History, Chicago, IL, USA; ANSP, Academy of Natural Sciences of Philadelphia, Philadelphia, PA, USA; LSUMNS, Louisiana State University Museum of Natural Sciences, Baton Rouge, LA, USA.

concatenated dataset. For the phylogenetic inference of the concatenated dataset of all genes, the mode of the posterior distribution of topologies is presented as a 50% majority-rule consensus tree (Fig. 1).

Phylogenetic relationships and divergence time estimates

The four single-locus gene trees are variously but generally well resolved; the myoglobin tree shows the most structure and the GAPDH tree the least structure. Although there are multiple incongruences among the gene trees, very few of these are strongly supported in two or more trees (Supporting Information Figs S1–S5). The tree based on the concatenated multilocus dataset (Fig. 1) is fairly well resolved and mostly well supported. *Hemitesia* is nested within Cettiidae (*sensu* Alström *et al.* 2006) and sister to the Asian Stubtail *Urosphena squameiceps*, with strong support. This placement within the Cettiidae is recovered in all single-locus analyses, and the sister relationship with *U. squameiceps* is inferred in three of the gene trees. The maximum likelihood bootstrapping of the concatenated multilocus dataset also strongly supported this position for *Hemitesia* (bootstrap support values are shown in Fig. 1). The Chestnut-capped Flycatcher *Erythrocerus mccallii* is recovered as sister to the Cettiidae with high posterior probability (1.0).

The chronogram (Fig. 2) agrees well in topology with the phylogram (Fig. 1), at least with respect to the strongly supported nodes. The deepest split within Cettiidae is inferred to have taken place *c.* 23 Mya, while the *Hemitesia*–*Urosphena squameiceps* split is estimated at *c.* 17 Mya. The separation between *Erythrocerus mccallii* and Cettiidae was considerably earlier, *c.* 30 Mya.

DISCUSSION

The position of *Hemitesia* as deeply nested within Cettiidae is strongly supported by both the individual loci and the concatenated dataset. There is also good support for a close relationship between *Hemitesia* and *U. squameiceps*, as all major clades in the Cettiidae identified by Alström *et al.* (2006) are represented in the present study. However, as *c.* 20 Cettiidae species are missing from the present study, a denser taxon sampling is needed to conclusively establish the exact position of *Hemitesia*

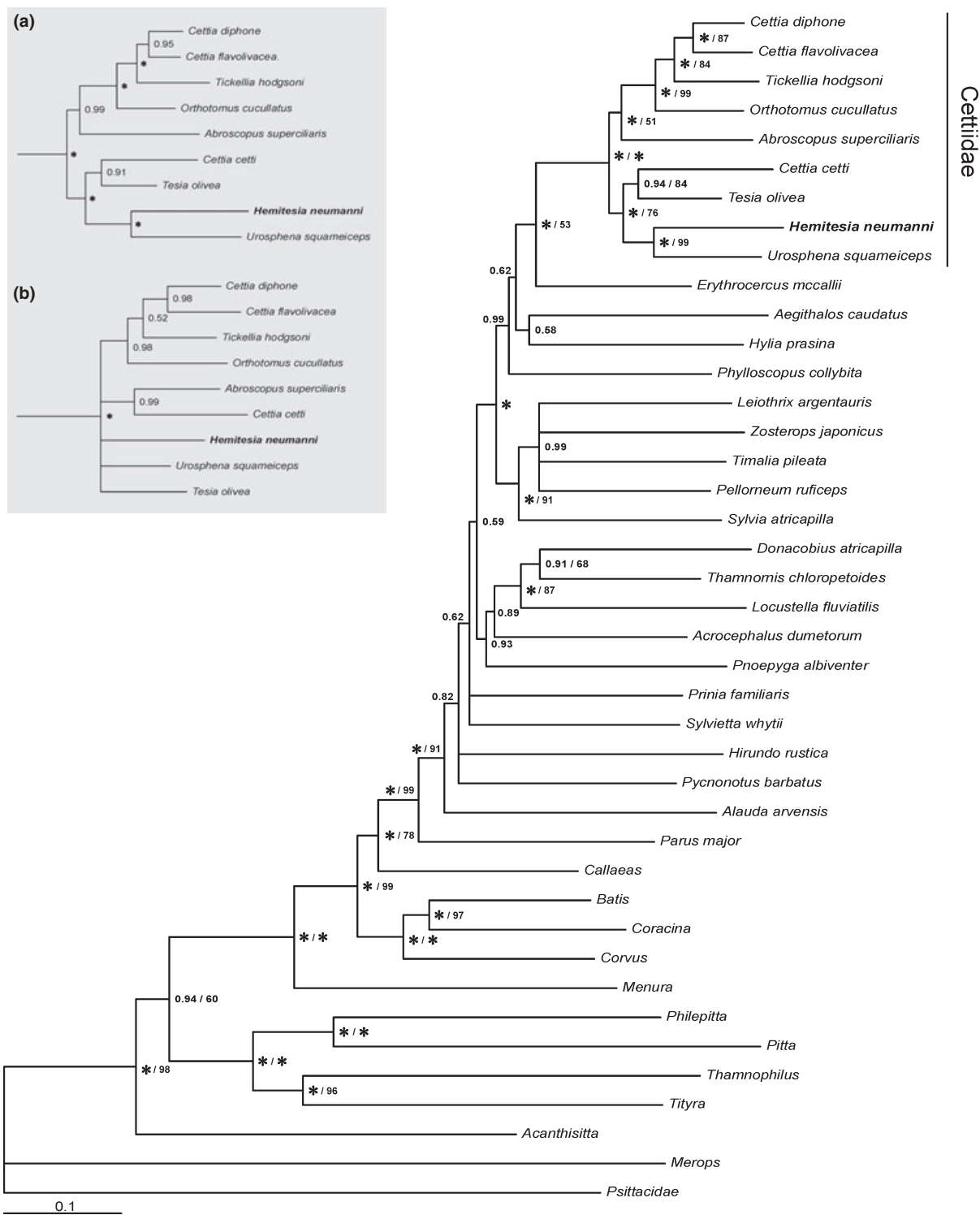


Figure 1. The majority-rule consensus tree obtained from the Bayesian analysis of concatenated sequences (cytochrome *b*, myoglobin, ODC and GAPDH). Posterior probabilities (left) and maximum likelihood bootstrap support values (right) are indicated at nodes. Posterior probabilities of 1.0 and bootstrap support values of 100% are indicated with an asterisk. Shaded box: relative positions of *Hemitesia neumanni* within the family Cettiidae (*sensu* Alström *et al.* 2006) in (a) the mitochondrial (cytochrome *b*), and (b) the nuclear tree (myoglobin, ODC and GAPDH). The complete mitochondrial and the individual nuclear gene trees are shown in Supporting Information Figures S1–S5.



Figure 2. Chronogram with divergence and confidence intervals (grey bars), estimated under a relaxed clock model implemented in BEAST 1.5.3 (Drummond *et al.* 2006). For calibration of the chronogram, the postulated separation of *Acanthisitta* from all other passerines in the phylogeny was used.

within Cettiidae. In terms of external morphology, *Hemitesia* shares more features with *Urosphena* and *Tesia* than with the African genus *Sylvietta*, such as long legs with large feet, broad, flattened bills and plumage patterns on the head (Chapin 1948, Bairlein *et al.* 2006). In addition, *Hemitesia* has 10 rectrices, in common with other Cettiidae species (Alström *et al.* 2006) but unlike most other passerines.

Erythrocercus mccallii was also found to be sister to the Cettiidae by Johansson *et al.* (2008) based on three nuclear loci (ODC, myoglobin, β -fibrinogen intron 5), although the support was considerably lower than in the present study. This species has an exclusively African distribution. However, except for Cetti's Warbler *Cettia cetti*, which ranges into Europe and North Africa, and *Hemitesia*, the family Cettiidae is principally an Asian radiation.

The current geographical distribution of *Hemitesia* may have been shaped by multiple historical biogeographical events, but the major competing scenarios to account for its present distribution would be based on either dispersal or vicariance in combination with local extinction. First, it is possible that the ancestor of *Hemitesia* colonized Africa by long-distance dispersal from Asia. A number of extant Cettiidae species are migratory, and some species (e.g. Palau Bush Warbler *Cettia annae*, Shade Bush Warbler *Cettia parens*, Fiji Bush Warbler *Cettia ruficapilla*) have been able to colonize islands in the Pacific (Bairlein *et al.* 2006, LeCroy & Barker 2006). *Urosphena* consists of one migratory species breeding in northeast Asia and wintering in southeast Asia (*U. squameiceps*), and two endemic species in the mountains of Borneo (Bornean Stubtail *Urosphena whiteheadi*) and Timor (Timor Stubtail *Urosphena subulata*). Long-distance dispersal between Africa and Asia has also been hypothesized to explain the current distribution of other passerine clades with complex distributions shared between these two continents (e.g. Fuchs *et al.* 2007, Jönsson *et al.* 2008, Nylander *et al.* 2008a, Voelker *et al.* 2009, Jönsson *et al.* 2010a).

Another possibility based on vicariance and local extinction is that an ancestral species in the clade that gave rise to *Hemitesia* and *Urosphena* at some point in time had a much larger geographical distribution that also covered parts of Africa. The occurrence of land connections between Asia and northeast Africa (Vrielynck *et al.* 1997, Rögl 1998,

Harzhauser *et al.* 2002) and continuous forests from eastern Asia to central Africa (Mandaville 1977, Utescher *et al.* 2007) during the mid-Miocene could have made it feasible for organisms occupying forests or forest edge to have distributions that included both Africa and Asia. Whereas much of Asia has stayed largely forested, the forests of Africa, the Arabian Peninsula and southwestern Asia contracted and became fragmented during the mid- to late Miocene (Mandaville 1977, Retallack 1992, Vrba 1993, Flower & Kennett 1994 and references therein). The loss of humid forest environments in Africa may thus have led to extinctions or reduced relict distributions of surviving avian forest clades in Africa (Fjeldså & Bowie 2008), as opposed to Asia, where diverse forests continued to allow further diversification.

In recent avian phylogenetic literature there are numerous examples of avifaunal exchanges between Africa and Asia (e.g. Beresford *et al.* 2005, Moyle & Marks 2006, Nylander *et al.* 2008a, Fuchs *et al.* 2009), but as these include cases of various ages as well as clades adapted to different types of habitats (e.g. xeric and forested) it is not straightforward to find a pattern to support whether the dispersal or vicariance scenario is the most plausible explanation for the enigmatic distribution of *Hemitesia*. However, we suggest that the vicariance hypothesis may be supported by some recent phylogenetic studies, where occasional African forest species of a similar age have been found to be nested within large Asian forest clades, e.g. *Illadopsis* and *Ptyrticus* within Timaliidae (Gelang *et al.* 2009), African Pitta *Pitta angolensis* and Green-breasted Pitta *Pitta reichenowi* within the otherwise Asian–Australasian Pittidae (Irestedt *et al.* 2006, Moyle *et al.* 2006), two clades of African orioles nested within the Asian *Oriolus* (Jönsson *et al.* 2010b), and the occurrence of the Congo Peacock *Afropavo congensis* in central Africa (Crowe *et al.* 2006). We also suggest that past extinctions may have played an important role in forming the present distribution of avian clades. Additional phylogenetic studies with divergence time estimates of forest clades shared between Africa and Asia are warranted to test this hypothesis.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figures S1–S5. The majority-rule consensus trees obtained from the Bayesian analysis of the individual genes and the concatenated nuclear genes. S1: cytochrome *b*, S2: myoglobin intron 2 (myo), S3: ornithine decarboxylase introns 6–7 (ODC), S4: glyceraldehyde-3-phosphodehydrogenase intron 11 (GAPDH), and S5: the concatenated nuclear genes (myo, ODC and GAPDH).

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