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Systematic placement of an enigmatic Southeast Asian taxon *Eupetes macrocerus* and implications for the biogeography of a main songbird radiation, the Passerida

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Biographic connections between Australia and other continents are still poorly understood although the plate tectonics of the Indo-Pacific region is now well described. *Eupetes macrocerus* is an enigmatic taxon distributed in a small area on the Malay Peninsula and on Sumatra and Borneo. It has generally been associated with *Ptilorrhoa* in New Guinea on the other side of Wallace's Line, but a relationship with the West African *Picathartes* has also been suggested. Using three nuclear markers, we demonstrate that *Eupetes* is the sister taxon of the South African genus *Chaetops*, and their sister taxon in turn being *Picathartes*, with a divergence in the Eocene. Thus, this clade is distributed in remote corners of Africa and Asia, which makes the biogeographic history of these birds very intriguing. The most parsimonious explanation would be that they represent a relictual basal group in the Passerida clade established after a long-distance dispersal from the Australo-Papuan region to Africa. Many earlier taxonomic arrangements may have been based on assumptions about relationships with similar-looking forms in the same, or adjacent, biogeographic regions, and revisions with molecular data may uncover such cases of neglect of ancient relictual patterns reflecting past connections between the continents.

Keywords: *Eupetes*; Oscine; biogeography; systematics; phylogeny

1. INTRODUCTION

The peculiar *Eupetes macrocerus* (Malaysian rail-babbler) is an uncommon bird of the lowland rainforests of the Malay Peninsula, Sumatra and Borneo. It belongs to the forest understorey, foraging on the forest floor among leaf litter and under fallen timber, using a walking gait with the neck extended forward and head jerking like a chicken. By appearance, it mostly resembles the *Ptilorrhoa* spp. (jewel-babblers) of New Guinea and early taxonomic treatments indeed placed them together in the genus *Eupetes* (Sharpe 1883; Temminck 1831). However, Peters (1940) noted some striking differences between *E. macrocerus* and the *Ptilorrhoa* spp. He pointed out several differences in the external morphology, but did not present evidence of a kind that would help placing these taxa in a phylogenetic context. Peters (1940) was the first to suggest that the genus *Eupetes* was monotypic and he proposed the genus name *Ptilorrhoa* (*genus novum*) for the Papuan birds. However, in his ambitious 'Birds of the World' (Peters 1964), he stuck with the name *Ptilorrhoa* to include the New Guinean species as well as the Malayan rail-babbler.

Serle (1952) noted a series of remarkable similarities between *Eupetes* and the West African *Picathartes* (rock-fowl): similar proportions, position of nostrils (different from *Ptilorrhoa*), shape of forehead and tail but did not insist on a relationship. Sibley (1973) considered the resemblance between *Picathartes* and *Eupetes* to be the result of convergence, but Olson (1979) argued that there could well be a relationship between them. He mentioned a series of similarities: morphology, proportions, plumage pattern and behaviour, but failed to identify clear synapomorphies between them. Sibley & Ahlquist (1990) simply ignored the divergence of opinions as they stated that 'The Cinclosomatinae includes the quail-thrushes (*Cinclosoma*), the three species of Papuan jewel-babblers (*Ptilorrhoa*), the Malaysian rail-babbler (*Eupetes*) and the whipbirds and wedgebills (*Psophodes*)'. Using molecular sequence data, Barker *et al.* (2004) and Beresford *et al.* (2005) associated *Ptilorrhoa* with Pachycephalidae (whistlers), which are placed above the Australian 'false babblers' (represented by the genera *Pomatostomus* and *Orthonyx*) in the Corvida phylogeny, but molecular data for *Eupetes* were lacking even in these studies.

It seems highly probable that earlier taxonomists simply looked for similar-looking forms within the same or adjacent geographical areas, thus *a priori* ruling out relationships between species living far apart. In order to scrutinize alternative possibilities, we used DNA sequence data to assess the systematic affinities of the Malaysian rail-babbler. The mere fact that *E. macrocerus* is distributed in Southeast Asia and that *Ptilorrhoa* is distributed only in New Guinea to the other side of Wallace's Line and *Picathartes* in West Africa makes the systematic status very interesting in relation to the current hypotheses about how songbirds (Oscines) dispersed out of the Australian region and colonized other parts of the world (Ericson *et al.* 2002; Barker *et al.* 2002, 2004; Jønsson & Fjeldså 2006*b*) and, for that sake, to similar cases in other taxonomic groups.

2. MATERIAL AND METHODS

We compared the DNA sequences of *Eupetes* with data from 21 taxa representing a broad sampling of the passeriform radiation (as summarized by Jønsson & Fjeldså 2006*a*). The aligned dataset consists of 1742 bp obtained from three nuclear gene regions, myoglobin intron 2, ornithine decarboxylase (ODC) introns 6–7 and glyceraldehyde-3-phosphodehydrogenase (G3PDH) intron 11. See the electronic supplementary material for laboratory procedures,

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Table 1. List of samples used in the study. (Acronyms are PFI, Percy FitzPatrick Institute, Cape Town; ZMUC, Zoological Museum of Copenhagen; AM, Australian Museum, Sydney; MV, Museum Victoria, Melbourne; NHMT, Natural History Museum, Tring; NRM, Swedish museum of Natural History.)

species	family	source	G3P	ODC	Myo
Chaetops frenatus	Picathartidae	PFI uncat.	EF441212	EF441234	AY228289
Colluricincla sanghirensis	Pachycephalidae	ZMUC123921	EF441213	EF441235	EF441256
Corcorax melanorhamphos	Corcoracidae	AM LAB 1059	EF441214	EF441236	AY064737
Cormobates placens	Climacteridae	MV E309	EF441215	EF441237	AY064731
Eopsaltria australis	Petroicidae	MV 1390	EF441216	EF441238	AY064732
Eupetes macrocerus	Cinclosomatidae	NHMT 1936.4.12.58	EF441217	EF441239	EF441257
Hirundo rustica	Hirundinidae	NRM 976238	EF441218	EF441240	AY064258
Malurus amabilis	Maluridae	MV C803	EF441219	EF441241	AY064729
Menura novaehollandiae	Menuridae	MV F722	EF441220	EF441242	AY064744
Oriolus flavocinctus	Oriolidae	MV1603	EF441221	EF441243	EF441258
Orthonyx temminckii	Orthonychidae	MV B831	EF441222	EF441244	AY064728
Pachycephala albiventris	Pachycephalidae	ZMUC117176	EF441223	EF441245	EF441259
Pachycephalopsis hattamensis	Petroicidae	NRM552153	EF441224	EF441246	EF441260
Picathartes gymnocephalus	Picathartidae	LSU B-19213	EF441225	EF441247	AY228314
Pomatostomus temporalis	Pomatostomidae	MV D257	EF441226	EF441248	AY064730
Prunella modularis	Prunellidae	NRM976138	EF441227	EF441249	AY228318
Ptilonorhynchus violaceus	Ptilonorhynchidae	MV B836	EF441228	EF441250	AY064742
Ptiloprora plumbea	Meliphagidae	MV C173	EF441229	EF441251	AY064736
Ptilorrhoa leucosticte	Cinclosomatidae	NRM 84405	EF441233	EF441255	EF441261
Saltator atricollis	Cardinalidae	NRM 966978	EF441230	EF441252	AY228320
Sturnus vulgaris	Sturnidae	NRM966615	EF441231	EF441253	AY228322
Sylvia atricapilla	Sylviidae	NRM 976380	EF441232	EF441254	AY228323

alignments, selection of models for nucleotide substitutions, parsimony analysis and Bayesian analyses of individual gene regions (table 1).

We also investigated whether *Eupetes* or *Pachycephalopsis* possesses the insertion of one codon in exon 3 of the nuclear *c-myc* gene, which has been proposed to be diagnostic of Passerida (Ericson & Johansson 2003). Laboratory procedures are described in the electronic supplementary material.

An average rate of substitutions in myoglobin intron 2 in passerines has been calculated as 0.145% Myr ago^{-1} (Fjeldså *et al.* in press) and this rate was used to estimate the timing of the splits between *Eupetes* and its closest relatives (electronic supplementary material).

3. RESULTS AND DISCUSSION

We were able to sequence all the three gene regions almost completely for all included taxa (*Prunella* lacks 70 bp in the $3'$ end in myoglobin, and in ODC all sequences obtained from study skins lack a 22 bp fragment in exon 7). With the missing base pairs taken into account, the sequences obtained varied in length between 708 and 729 bp for myoglobin intron 2, between 253 and 307 bp for G3PDH intron 11 and between 591 and 621 bp for the ODC region. The combined alignment consists of 1742 bp.

Analysis of three markers all provide strong support that *E. macrocerus* is nested within the *Chaetops*/*Picathartes* clade, its closest relatives being the rock-jumpers, which are endemic to the South African Cape region. A relationship between *Chaetops and Picathartes* was first suggested (with some hesitation) by Sibley & Ahlquist (1990) as a result of their DNA–DNA hybridizations, and it was later supported by several other studies using DNA sequence data (Barker *et al.* 2004; Beresford *et al.* 2005). It was unexpected as they are phenetically rather different: *Chaetops* resembling Australian grass wrens and inhabiting rocky places in open terrain, and Picathartes being larger and inhabiting rainforest understorey (Fry *et al.* 2000). Which of these specializations represent the ancestral condition is difficult to tell; on one hand southern Africa lost its forest cover far back in the Tertiary (Axelrod & Raven 1978), but it is also possible that range dynamics driven by climatic instability will gradually push species towards the more productive environments, leading to a general tendency for old lineages to persist in the major rainforest tracts (Storch *et al.* in press). According to the molecular clock model used (a discussion of the error margins for such clock estimates is trivial and we simply note that our estimates only represent a very rough idea of divergence times), the *Picathartes*/*Chaetops*/*Eupetes* clade diverged from the Australian Petroicidae (represented here by *Eopsaltria* and *Pachycephalopsis*) 48 Myr ago, in the Mid- Eocene. According to figure 1, the *Picathartes*/*Chaetops*/*Eupetes* clade is sister to the Australian Petroicidae and these in turn are sister to the Passerida (represented here by *Hirundo*, *Sylvia*, *Sturnus*, *Prunella* and *Saltator*). These nodes are poorly supported by our data, but the insertion of one codon in a conserved region of the *c-myc* gene in the Passerida and the *Picathartes*/*Chaetops*/*Eupetes* clade, as opposed to that in the Petroicidae and all Corvida groups, would seem to suggest that the Australian Petroicidae and Corvida groups are basal to the large Old World radiation of songbirds (Ericson & Johansson 2003).

Biogeographically, it is of great interest to find the Asian *E. macrocerus* nested together with two African taxa in a terminal position. Fuchs *et al.* (2006) and Jønsson & Fjeldså (2006*b*) proposed the idea that an Australian ancestor of the Passerida dispersed directly to Africa across stepping-stones in the southern Indian Ocean during the warm Eocene period (Kennett 1995), and that Passerida originated in Africa and from there radiated and dispersed to Eurasia and then to the

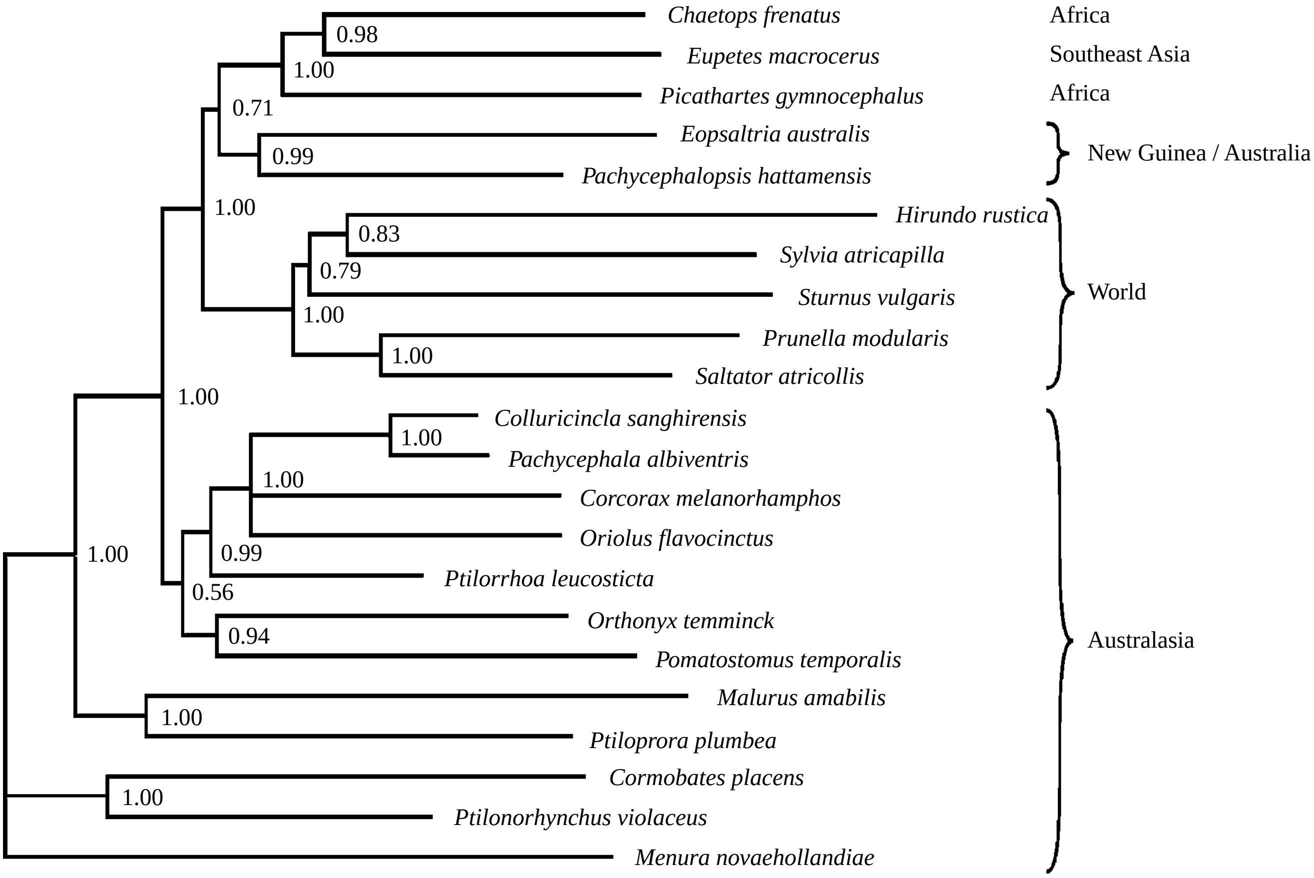

Figure 1. The 50% majority rule consensus tree obtained from the Bayesian analysis of the combined dataset (G3PDH intron 11, the myoglobin intron 2 and ODC introns 6–7) with geographical distributions. Posterior probability values are indicated to the right of the nodes.

rest of the world. It is of no doubt that the systematic position of *Eupetes* makes the diversification and dispersal patterns even more complex. Since several taxa representing deep branches within the Passerida are African (Beresford *et al.* 2005), and the Asiatic *Eupetes* and South African *Chaetops* are in a terminal position within their clade having diverged from *Picathartes ca* 44 Myr ago, the most parsimonious interpretation is still a dispersal of an Australian ancestor directly to Africa. The distribution of *Picathartes*, *Chaetops* and *Eupetes* would then be relictual, following a range expansion whereby this clade spread out of Africa. *Eupetes* retreated into the rainforests of the most south-eastern part of mainland Asia and the closely associated islands of Sumatra and Borneo. At this time, the distance between Asia (with Greater Sundas) and terranes of Australian origin was too far apart for further range expansion. The other possible—though markedly less parsimonious—interpretation involves a dispersal event from Australia to Asia and then two independent dispersal events onwards to two different parts (and environments) of Africa.

A denser taxon sampling around the transition between Corvida and Passerida (e.g. Petroicidae) is a high priority for future work, as this might give a better idea about the ecological adaptations of the form that made the great leap out of Australia, whether that was via Asia or across the Indian Ocean. However, there is also a broad range of other odd relationships that, if correctly interpreted, would suggest ancient biogeographic connections between regions that are not connected today, such as the rainforests of Africa and the Australasian regions (for details see Olson 1973). Over the last decades, many such cases have been discussed in relation to plate tectonics, while earlier ideas about ancient land bridges were abandoned. However, the idea of trans-oceanic connections, including radiations within oceanic archipelagos, has recently received renewed attention (De Queiroz 2005; Filardi & Moyle 2005). For an understanding of the relative importance of vicariance driven by plate tectonics, or dispersal by past land bridges or island arcs, or sweepstake long-distance dispersal, it is important to revisit the suggested cases now with molecular data. Such data have revealed several previously neglected cases, where odd-looking species had been compared mainly with other taxa within the same part of the world, and thus were erroneously interpreted as aberrant members of such groups (e.g. Ericson *et al.* 2002; Fjeldså *et al.* 2003; Fuchs *et al.* 2006). A more systematic approach is now needed to compare a broad selection of potential cases of biotic links between ancient land masses.

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Axelrod, D. I. & Raven, P. H. 1978 Late Cretaceous and Tertiary vegetation history of Africa. In *Biogeography and ecology of southern Africa* (ed. M. J. A. Werger), pp. 77–130. The Hague, The Netherlands: Dr. W. Junk Publications.

Barker, F. K., Barrowclough, G. F. & Groth, J. G. 2002 A phylogenetic hypothesis for passerine: birds: taxonomic and biogeographic implications of an analysis of nuclear DNA sequence data. *Proc. R. Soc. B* **269**, 295–308. (doi:10.1098/rspb.2001.1883)

Barker, F. K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. 2004 Phylogeny and diversification of the largest avian radiation. *Proc. Natl Acad. Sci. USA* **101**, 11 040–11 045. (doi:10.1073/pnas.0401892101)

Beresford, P., Barker, F. K., Ryan, P. G. & Crowe, T. M. 2005 African endemics span the tree of songbirds (Passeri): molecular systematics of several evolutionary ‘enigmas’. *Proc. R. Soc. B* **272**, 849–858. (doi:10.1098/rspb.2004.2997)

Ericson, P. G. P. & Johansson, U. S. 2003 Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. *Mol. Phylogenet. Evol* **29**, 126–138. (doi:10.1016/S1055-7903(03)00067-8)

Ericson, P. G. P., Christidis, L., Cooper, A., Irestedt, M., Jackson, J., Johansson, U. S. & Norman, J. A. 2002 A Gondwanan origin of passerine birds supported by DNA sequences of the endemic New Zealand wrens. *Proc. R. Soc. B* **269**, 235–241. (doi:10.1098/rspb.2001.1877)

Filardi, C. E. & Moyle, R. G. 2005 Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature* **438**, 216–219. (doi:10.1038/nature04057)

Fjeldså, J., Zuccon, D., Irestedt, M., Johansson, U. S. & Ericson, P. G. P. 2003 *Sapayoa aenigma*: a New World representative of ‘Old World suboscines’. *Proc. R. Soc. B* **270**, S238–S241. (doi:10.1098/rsbl.2003.0075)

Fjeldså, J., Irestedt, M., Jønsson, K. A., Ohlson, J. I. & Ericson, P. G. P. 2007 Phylogeny of the ovenbird genus *Upucerthia*: a case of independent adaptations for terrestrial life. *Zool. Scr.* **36**, 133–141. (doi:10.1111/j.1463-6409.2006.00270.x)

Fry, C. H., Keith, S. & Urban, E. K. 2000. *The birds of Africa*, vol. VI. London, UK: Academic Press.

Fuchs, J., Fjeldså, J., Bowie, R. C. K., Voelker, G. & Pasquet, E. 2006 The African warbler genus *Hyliota* as a long lost lineage in the oscine songbird tree: molecular support for an African origin of the Passerida. *Mol. Phylogenet. Evol* **39**, 186–197. (doi:10.1016/j.ympev.2005.07.020)

Jønsson, K. A. & Fjeldså, J. 2006*a* A phylogenetic supertree of oscine passerine birds (Aves: Passeri). *Zool. Scr.* **35**, 149–186. (doi:10.1111/j.1463-6409.2006.00221.x)

Jønsson, K. A. & Fjeldså, J. 2006*b* Determining biogeographic patterns of dispersal and diversification in oscine passerine birds in Australia, Southeast Asia and Africa. *J. Biogeogr.* **33**, 1155–1165. (doi:10.1111/j.1365-2699.2006.01507.x)

Kennett, J. P. 1995 A review of polar climatic evolution during the Neogene, based on the marine sediment record. In *Paleoclimate and evolution with emphasis on human origins* (eds E. S. Vrba, G. H. Denton, T. C. Partridge & X. Burckle), pp. 49–64. New Haven, CT: Yale University Press.

Olson, S. L. 1973 A classification of the rallidae. *Wilson Bull.* **85**, 381–416.

Olson, S. L. 1979 *Picathartes*—another West African forest relict with probable Asian affinities. *Bull. Br. Ornithol. Club* **99**, 112–113.

Peters, J. L. 1940 A genus for *Eupetes caerulescens* Temminck. *Auk* **57**, 94.

Peters, J. L. 1964 *Check-list of birds of the world*, vol. X. Worchester, MA: The Heffernan Press, Inc.

Queiroz, A. 2005 The resurrection of oceanic dispersal in historical biogeography. *Trends Ecol. Evol.* **20**, 68–73. (doi:10.1016/j.tree.2004.11.006)

Serle, W. 1952 The affinities of the genus *Picathartes* lesson. *Bull. Br. Ornithol. Club* **72**, 2–6.

Sharpe, R. B. 1883. *Catalogue of the birds in the British Museum*, vol. 7. London, UK: British Museum.

Sibley, C. G. 1973 The relationships of *Picathartes*. *Bull. Br. Ornithol. Club* **93**, 23–25.

Sibley, C. G. & Ahlquist, J. E. 1990 *Phylogeny and classification of birds. A study in molecular evolution*. New Haven, CT: Yale University Press.

Storch, D. *et al.* 2006 Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity. *Ecol. Lett.* **9**, 1308–1320. (doi:10.1111/j.1461-0248.2006.00984.x)

Temminck, C. J. 1831 Nouveau recueil de planches coloriées d’Oiseaux pour servir de suite et de complément aux planches enluminées de Buffon. *Pl 516*. In Dickinson, E. C. 2001 Systematic notes on Asian birds. 9. The "Nouveau recueil de planches coloriees" of Temminck & Laugier (1820–1839) *Zool. Verh.* **335**, 7–56. Levrault, Paris.