A molecular phylogeny of minivets (Passeriformes: Campephagidae: *Pericrocotus*): implications for biogeography and convergent plumage evolution

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Abstract

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Minivets are conspicuous and mostly intensely colourful birds inhabiting wooded environments in tropical and subtropical South and Southeast Asia and temperate East Asia. We present a robust phylogeny of the group based on nuclear and mitochondrial DNA data including all 12 recognized species and also many subspecies representing disjunct populations in the Oriental mainland and in Indonesia. The study indicates that minivets radiated within mainland Asia and dispersed to the Indonesian archipelago. We also demonstrate that in accordance with studies on other bird groups, plumage characters are highly plastic and that the diversity of plumage patterns and colouration represents an example of convergent evolution.

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Introduction

Minivets comprise 12 medium-sized bird species inhabiting forests and forest edge habitats (Dickinson 2003; Taylor 2005). The group is distributed in mainland Asia in the west to the Pacific coast and Japan in the east, and south through the Indonesian archipelago reaching its easternmost distribution in the Philippines, Borneo and the island of Flores, which is just east of Wallace's line (Taylor 2005). Most minivets are non-migratory, colourful and conspicuous birds often foraging in an opportunistic manner in the forest canopy sometimes in small flocks (Taylor 2005). However, a small assemblage of less colourful species inhabits subtropical and temperate regions, and migrates into tropical wintering areas.

Recent molecular studies (Fuchs *et al.* 2007; Jønsson *et al.* 2008) have shown that minivets form a monophyletic clade within the family Campephagidae, sister to cuckooshrikes (*Coracina, Campephaga, Lobotos* and *Campochaera*) and trillers (*Lalage*). The family Campephagidae is nested within the core Corvoidea, the deeper branches of which are distributed in the Australo-Papuan realms (Jønsson & Fjeldså 2006; Jønsson *et al.* 2007, 2008). Minivets are mainly distributed in mainland Asia, although some species occur in the Indonesian and Philippine archipelagos, and it is of biogeographical interest to identify their area of origin and assess whether there was a gradual dispersal from Australia across Wallacea into Asia, or if a single dispersal event to Asia was followed by radiation and dispersal back into Wallacea.

In this study, we use molecular (nuclear and mitochondrial) data to investigate the phylogenetic relationships among all recognized minivet species, as well as some distinct populations or subspecies, to assess biogeographical patterns. The study forms part of a broader effort to increase knowledge about core Corvoidean systematics and biogeography in the area in and around

the Indo-pacific region (Jønsson *et al.* 2008), which is covered by very few molecular phylogenetic studies (e.g. Filardi & Moyle 2005; Jønsson *et al.* 2008).

Furthermore, we also study plumage evolution among minivets. Previous studies (e.g. Omland & Lanyon 2000; Allen & Omland 2003) have demonstrated that bird plumage characters are prone to high levels of homoplasy. Minivets are interesting in this respect as their diversity of plumage patterns and colouration seemingly are variations in the combination of rather few elements, and thus, we assess whether this variation follows phylogeny or ecology.

Materials and methods

Taxon sampling, amplification and sequencing

We included all 12 recognized species of minivets (Taylor 2005). Some minivet species have disjunct geographical distributions, with populations in the Asian mainland and in one or more of the Sunda Islands. For these species, we included individuals from different island populations to assess whether they are correctly interpreted as representing the same lineage, and the levels of divergence between them.

Two nuclear gene regions, ornithine decarboxylase (ODC) introns 6–7 (540–599 bp), glyceraldehyde-3-phosphodehydrogenase (GAPDH) intron 11 (286–296 bp) and 525 bp from the mitochondrial ND2 region have been sequenced and used to estimate the phylogenetic relationships. For each gene and taxon, multiple overlapping sequence fragments were obtained by sequencing with different primers. Positions where the nucleotide could not be determined with certainty were coded with the appropriate IUPAC code. GenBank accession numbers are given in Table 1 (see Allen & Omland (2003), Fjeldså *et al.* (2003), Irestedt *et al.* (2002), Jønsson *et al.* (2008), for extractions, amplifications, primers and sequencing procedures for fresh tissue/blood samples). Corresponding laboratory procedures for study skins are detailed in Irestedt *et al.* (2006). For amplification of the ND2 region from the study skin extracts, we used the primer ND2-Lmet (Hackett 1996) and three new primers, ND2per330F (5′-ATT CCA CTT YTG ATT CCC AGA AGT-3′), ND2-per340R (5′-CCT TGT AGT ACT TCT GGG AAT CA-3′) and ND2-per530R (5′-GAG GAG AAT GCT ATG ATT TTT CG-3′), were additionally designed for this study.

Phylogenetic inference and model selection

Due to a low number of insertions in the introns, sequences could easily be aligned manually. All gaps were treated as missing data in the analyses. Bayesian inference was used to estimate the phylogenetic relationships. Posterior probabilities of trees and parameters in the substitution models were approximated with Markov Chain Monte Carlo and Metropolis coupling using the program MRBAYES 3.1.1 (Ronquist & Huelsenbeck 2003). Analyses were performed for a nuclear gene partition (GAPDH and ODC), for a mitochondrial gene partition (ND2) and for a combined data set. In the analyses of the nuclear gene partition and the combined data set, the models selected for the individual gene partition were used. The chains for the individual gene partitions and for the combined data set were all run for 5 million generations, with trees sampled every 100th generation. The trees sampled during the burn-in phase (before the chain had reached its apparent target distribution) were discarded after checking for convergence, and the final inference was made from the concatenated outputs. The models for nucleotide substitutions used in the analyses were selected for each gene individually by applying the Akaike Information Criterion (Akaike 1973) and the program MRMODELTEST 2.2 (Nylander *et al.* 2004) in conjunction with PAUP* (Swofford 1998).

Dispersal–vicariance analysis

Dispersal–vicariance analysis (DIVA) version 1.1 (Ronquist 1996) was used to elucidate the relative influence of different processes in shaping the biogeographical history of minivets. DIVA is a simple program for reconstructing ancestral distributions based on a phylogeny and is a method in which ancestral distributions are inferred based on a three-dimensional cost matrix derived from a simple biogeographical model (Ronquist 1996, 1997). DIVA does not assume anything about the shape or existence of general biogeographical patterns. Therefore, it is particularly useful in reconstructing the distribution history of a group of organisms in the absence of a general hypothesis of area relationships. The method remains applicable even if area relationships are reticulate rather than hierarchic (Ronquist 1996, 1997).

We used the Bayesian 50% majority rule tree from the combined data set (Fig. 1) for the DIVA, which requires a fully bifurcate phylogeny. Our phylogenetic hypothesis is well-resolved towards the root, whereas some more distal branches have support values below 0.95 PP. Although these distal phylogenetic uncertainties are suboptimal for performing a DIVA, these are unlikely to affect the proposed ancestral areas at the base of the tree, which are of interest in this study.

In total, seven geographical regions were recognized for our study (Fig. 1): TeA: Temperate Asia; TrA: Tropical mainland Asia; S: Sumatra; J: Java; B: Borneo; Pl: Palawan; LS: Lesser Sundas. Maxarea values were set to 7. This is equivalent to assuming that the ancestors of the group in question have the same ability to disperse as their extant

Table 1 Taxonomic sampling.

Taxa	Voucher/tissue number	Locality	GAPDH	ODC	ND2
Pericrocotus brevirostris affinis	NRM569551	Myanmar	GQ249128	GQ249147	GQ255861
Pericrocotus cantonensis	NRM569607	Vietnam		GQ249144	GQ255858
Pericrocotus cantonensis	NRM599646	China	GQ249129	GQ249155	GQ255869
Pericrocotus cinnamomeus saturatus	NRM569549	Java	GQ249130	GQ249149	GQ255863
Pericrocotus cinnamomeus saturatus	NRM569613	Java	GQ249131	GQ249139	GQ255853
Pericrocotus cinnamomeus subsp	USNM B6146	Myanmar	EF052753	EU272117	EF052691
Pericrocotus cinnamomeus subsp	NRM700487	India	GQ249117	GQ249137	GQ255851
Pericrocotus divaricatus divaricatus	NRM569470	Vietnam	EU380485	EU380449	EU380514
Pericrocotus divaricatus divaricatus	UWBM 74728	Russia	EF052818	EU380450	EF052843
Pericrocotus divaricatus divaricatus	NRM569615	Japan	GQ249120	GQ249143	GQ255857
Pericrocotus divaricatus divaricatus	NRM556655	Korea	GQ249132	GQ249140	GQ255854
Pericrocotus divaricatus tegimae	NRM569555	Japan	GQ249123	GQ249148	GQ255862
Pericrocotus erythropygius albifrons	USNM B5659	Myanmar	EF052754	EU380451	EF052765
Pericrocotus erythropygius erythropygius	MNHN 1880-241	India	GQ249114	GQ249134	GQ255848
Pericrocotus ethologus annamensis	NRM569610	Vietnam	GQ249119	GQ249142	GQ255856
Pericrocotus ethologus ethologus	NRM569609	China	GQ249118	GQ249141	GQ255855
Pericrocotus ethologus subsp	AMNHJGG991	Nepal	EF052819	EU380452	EF052844
Pericrocotus flammeus insulanus	NRM569608	Borneo	GQ249116	GQ249136	GQ255850
Pericrocotus flammeus siebersi	NRM569612	Java		GQ249138	GQ255852
Pericrocotus flammeus subsp	MNHN CG 1989-75	Thailand	EF052821	EU380453	EF052845
Pericrocotus igneus igneus	NRM569550	Malaysia		GQ249152	GQ255866
Pericrocotus igneus igneus	ZMUC95263	Palawan	EU380486	EU380454	EU380515
Pericrocotus lansbergei	RMNH.AVES.85324	Flores	GQ249121	GQ249145	GQ255859
Pericrocotus lansbergei	RMNH.AVES.81409	Flores	GQ249122	GQ249146	GQ255860
Pericrocotus miniatus	NRM569553	Sumatra	GQ249125	GQ249151	GQ255865
Pericrocotus miniatus	NRM569552	Java	GQ249124	GQ249150	GQ255864
Pericrocotus roseus	MNHN 1880-237	India	GQ249113	GQ249133	GQ255847
Pericrocotus roseus	CAS	China	GQ249115	GQ249135	GQ255849
Pericrocotus solaris cineiregula	NRM700496	Borneo	GQ249127	GQ249154	GQ255868
Pericrocotus solaris montanus	NRM569554	Sumatra	GQ249126	GQ249153	GQ255867
Pericrocotus solaris subsp	BMNH1948.80.2191	Myanmar	EU380487	EU380455	EU380516
Outgroup					
Oriolus oriolus	MCSNC1415	Italy	EF052755	EU273363	EF052766
Coracina melaschista	MNHN 6-69	Laos	EF052807	EU380423	AY529913

All samples are vouchered.

AMNH, American Museum of Natural History, New York, USA; BMNH, British Museum of Natural History, Tring, UK; IZCAS, Institute of Zoology, Chinese Academy of Sciences, Beijing, China; MCSNC, Museo Civico di Storia Naturale di Carmagnola, Carmagnola, Italy; MNHN, Muséum National d'histoire Naturelle, Paris, France; NRM, Swedish Museum of Natural History, Stockholm, Sweden; RMNH, National Museum of Natural History, Leiden, The Netherlands; USNM, National Museum of Natural History, Washington, DC, USA; UWBM, Burke Museum, University of Washington, Seattle, USA; ZMUC, Zoological Museum, University of Copenhagen, Denmark.

descendants and, therefore, ancestral ranges were similar in size to extant ranges (Sanmartín 2003; Nylander *et al.* 2008).

The analysis was carried out several times, exploring the effect of changing the cost settings (co-divergence = 0–5, duplication = 0–5, sorting = 0–5, switching = 0–5). Changing the various parameters had no effect on the estimates of ancestral areas.

Results

We sequenced GAPDH, ODC and the first half of ND2. However, for some taxa small gene regions are lacking, and for three taxa, the entire GAPDH region is lacking. With the missing base pairs taken into account, the sequences obtained varied in length between 286 and 296 bp for the GAPDH, and 540 and 599 for the ODC region. No indels were found in the 525-bp long coding ND2 region. The few indels observed in the introns were either autapomorphic or congruent with the topology obtained from the Bayesian analyses of the combined data set, except for a single bp insertion in a repeated region in the GAPDH region.

The *a priori* selection of nucleotide substitution models suggested that the GTR+Γ model had the best fit for ODC, while HKY+Γ was suggested for GAPDH, and HKY+I+Γ for the ND2 region. After discarding the burn-in phase, the inference for the individual genes and the combined data set was based on a total of 40 000 samples
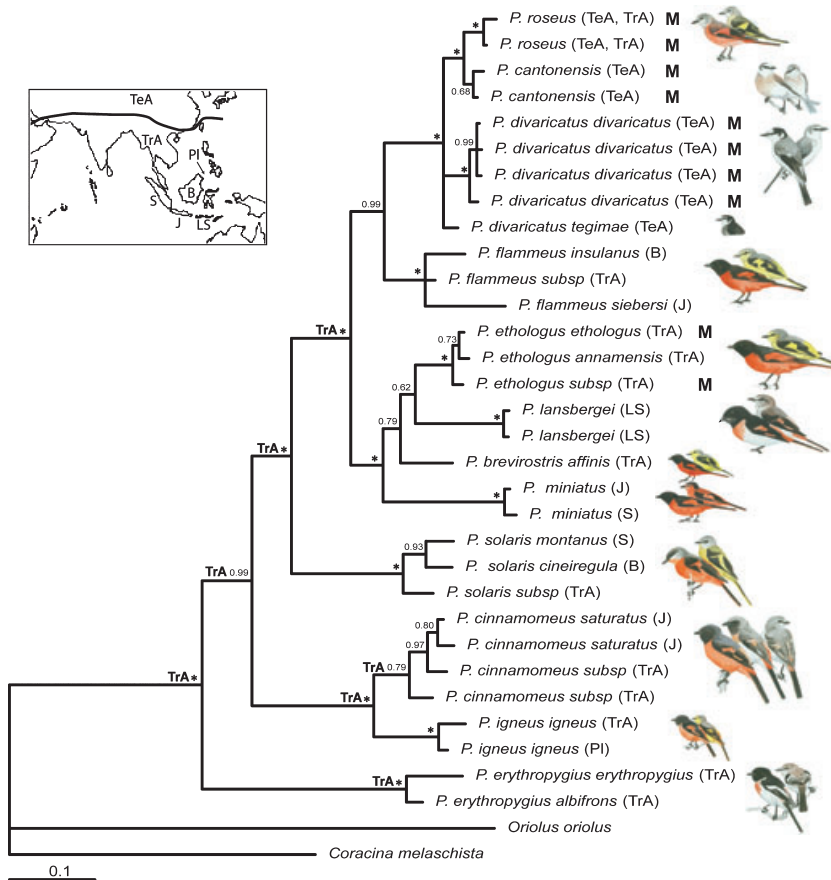
Fig. 1 The 50% majority rule consensus tree obtained from the Bayesian analysis of the combined nuclear data set (ODC, GAPDH and ND2). Posterior probabilities >0.50 are shown. An asterisk indicates posterior probabilities of 1.0. After the taxon name is indicated distribution according to the seven geographical regions used for DIVA: TeA, Temperate Asia; TrA, Tropical mainland Asia; S, Sumatra; J, Java; B, Borneo; Pl, Palawan; LS, Lesser Sundas. Migrating species are indicated with **M**. Nodes, which according to the DIVA are unequivocally identified as mainland tropical Asian of origin, have been assigned TrA. Ancestral areas for other nodes are ambiguous and are left out. To the right are shown water colours of minivet species.

each. The posterior distribution of topologies is presented as a 50% majority-rule consensus tree from the combined analysis in Fig. 1.

Analyses of the concatenated data set produced a robust hypothesis of minivet relationships and several well-supported clades were identified (Fig. 1). The phylogenetic analyses of the mitochondrial data set mostly provide support for the individual clades (Fig. 2A), whereas the combined nuclear data set (Fig. 2B) provides support for the relationships among these clades. This is expected because mitochondrial DNA (mtDNA) evolves at a faster rate compared with nuclear DNA (nuDNA) and thus mtDNA is expected to better resolve recent divergences, whereas nuDNA is expected to better resolve more basal relationships. All currently recognized species form monophyletic assemblages and thus, despite the quite distinct appearance of some subspecies, we can confirm that every species (as currently defined) represents a natural unit.

The 'grey minivets' assemblage is monophyletic and includes *Pericrocotus cantonensis*, *Pericrocotus divaricatus* and *Pericrocotus roseus*. Although we only included one specimen of *Pericrocotus divaricatus tegimae* from Japan, our study indicates that it represents an independent lineage

within the broader *divaricatus/cantonensis/roseus* complex and potentially should be considered a valid species, as it falls outside the highly supported *P. d. divaricatus* clade. However, assessment of levels of speciation will ultimately depend on a clearly articulated species concept and consideration of a variety of data including but not limited to DNA. Also well-supported is a sister relationship of the grey minivets to *Pericrocotus flammeus*, which is one of the strikingly coloured minivets, where males are black/red and females are yellow/black. Sister to the 'grey minivets'/*P. flammeus* clade is *Pericrocotus miniatus/Pericrocotus brevirostris/Pericrocotus ethologus/Pericrocotus lansbergei*. The first three are red/yellow minivets, whereas *P. lansbergei* is rather different in appearance with males having black throat, head and back; white belly with a red patch on the upper breast; red lower back and tail coverts; and a red wing patch. The females have grey head and back, a whitish throat and lack the red breast patch. Finally, it is well-supported that *Pericrocotus cinnamomeus* and *Pericrocotus igneus* are sister species. The males of these two species have nearly identical red and black plumages, although *P. cinnamomeus* has a greyer crown, nape and back. The females, however, differ markedly. *Pericrocotus cinnamomeus* females
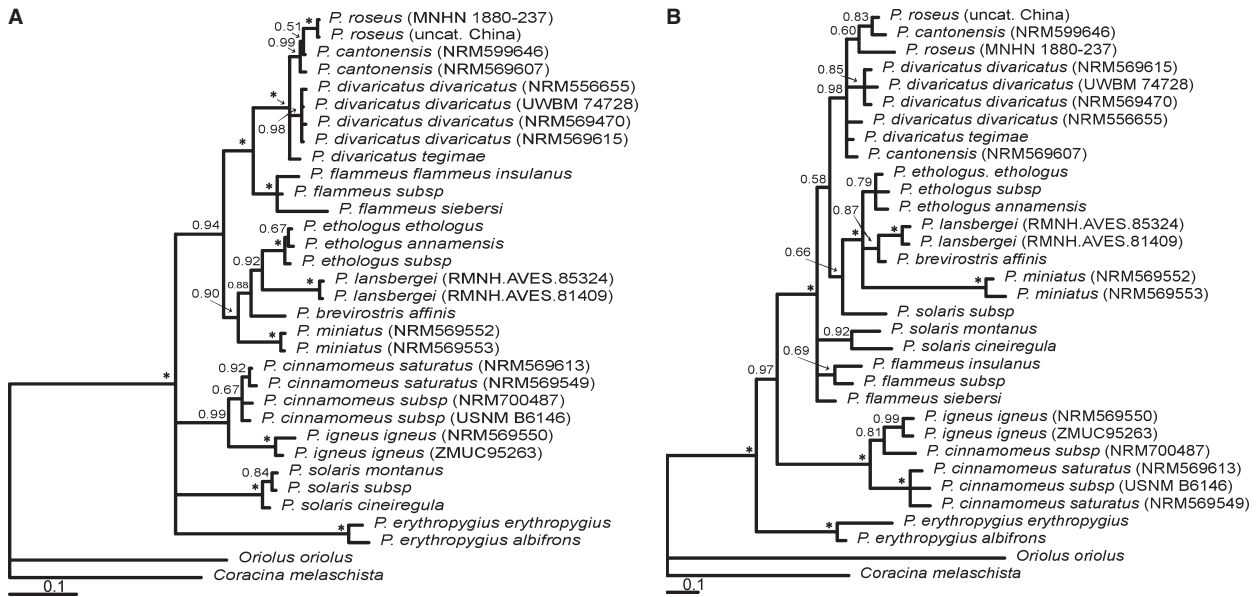
Fig. 2 A. The 50% majority rule consensus tree obtained from the Bayesian analysis of ND2. Posterior probabilities >0.50 are shown. An asterisk indicates posterior probabilities of 1.0. —B. The 50% majority rule consensus tree obtained from the Bayesian analysis of the combined nuclear data set (ODC and GAPDH). Posterior probabilities >0.50 are shown. An asterisk indicates posterior probabilities of 1.0.

of the nominate form and of the *pallidus* subspecies have a white throat and belly, and light grey crown, nape and back. The *P. cinnamomeus sacerdos* subspecies (not included in the study) females have a yellow belly (Taylor 2005).

The DIVA analysis reveals that seven of the most basal nodes of the *Pericrocotus* phylogeny are unambiguously tropical Asian (Fig. 1) and thus the origin of *Pericrocotus* seems convincingly to be mainland Asia. More recent secondary dispersal confounds the results of more distal nodes in the phylogeny and thus we only report ancestral origins for nodes where we are certain of the origin.

Discussion
Systematics and taxonomy
Our results constitute the first molecular phylogeny that includes all minivet species. We conclude that minivets constitute a natural group and with a few exceptions, previously proposed systematic relationships for the group hold true. *Pericrocotus cinnamomeus* and *P. igneus* are sister species. However, *P. lansbergei*, which has generally been associated with the two species, is surprisingly linked to a group consisting of *P. ethologus*, *P. brevirostris* and *P. miniatus* (Taylor 2005). Resolution within the latter clade was poor and the actual inter-species relationships could not be determined. We also established a rather tight-knit relationship between the grey minivets (*P. cantonensis*, *P. divaricatus*, *P. tegimae*) and, as traditionally thought, a tight link between the more colourful Himalayan *P. roseus* and the dull lowland associ-

ated *P. cantonensis* (Taylor 2005). We found strong support (PP = 1.00) for monophyly of all recognized species, except for *P. cantonensis* (PP = 0.68) and *P. cinnamomeus* (PP = 0.79). We also note that only one specimen of *P. brevirostris* was included and thus, as for *P. divaricatus tegimae*, support for monophyly was lacking.

Biogeography
We find that minivets have their centre of origin within continental Asia (Fig. 1). This is interesting in view of its sister group of cuckoo-shrikes, trillers and allies (core Campephagidae), which have their origin in the Australo-Papuan region (Jønsson *et al.* 2008, submitted). Phylogenetic evidence suggests that the radiation of core Corvoids had an Australo-Papuan origin (Barker *et al.* 2002, 2004; Ericson *et al.* 2002) and, therefore, it seems that minivets dispersed out of Australia to colonize the Asian mainland where they radiated, and some species dispersed back eastwards to the Greater Sunda Islands (Sumatra, Java, Borneo), Palawan, the Philippines and to Flores (one species). The distance of open sea separating the land-bridge islands west of the New Guinean Birdshead Peninsula and the Greater Sunda Arc was, at that time, only 400–500 km, and the Greater Sunda Arc (Sumba, Java, Sumatra) was closely linked with the Myanmar peninsula, thus providing a fairly direct avenue for colonization to the area which presently has the highest diversity of minivet species.

The secondary colonization of the Greater Sunda Islands, Palawan and the Philippines is best understood in light of historic terrane movements and Pliocene water fluctuations. The Greater Sunda Islands and Palawan have been connected to mainland Asia up until the Late Miocene (Moss & Wilson 1998) and probably also at times during the Pliocene, when sea levels fluctuated and at times were ca. 140 m lower than at present, causing Borneo, Palawan, Sumatra and Java to be connected with mainland Asia (Chappell 1987). Thus, rather than minivets island-hopping across the Indonesian Archipelago, the biogeographical analysis and interpretation of terrane movements suggest that minivets colonized Southeast Asia in a single dispersal event, from where they dispersed into the Indonesian and Philippine Archipelagos.

The molecular data further suggests that there is relatively little distinction of populations from different islands and regions within minivet species. The historical connection of the Greater Sunda Islands to mainland Asia has probably prevented long-time isolation of subpopulations and maintained mixed gene pools within species; thus, present day island subpopulations are simply a result of relatively recent changes in sea levels and minor terrane movements. However, to properly investigate this, more taxa from various populations are needed.

Evolution and plasticity of plumage patterns

Minivets are known as sexually dimorphic birds where males are black with a distinctly coloured red breast, belly, rump and wing-patch, while the corresponding body parts in females are yellow (Fig. 1). This is true for *Pericrocotus solaris*, *P. ethologus*, *P. brevirostri*s and *P. flammeus*. For *P. miniatus*, both males and females are red, the most distinct difference between the sexes being that females have a red upper back (black in males). Besides their similar colouration, these five species are also markedly larger than other minivets, ranging between 17 and 21 cm in length. The colourful appearance is in great contrast to that of most other campephagids, which are mainly grey.

Pericrocotus igneus has a similar colourful plumage, but is markedly smaller (15–16.5 cm) and has different proportions. *Pericrocotus cinnamomeus* also has red and yellow colours but males have grey crown and mantles, and white lower underparts in most populations, and in most populations the females lack yellow. *Pericrocotus roseus* is the last species to exhibit the red and yellow sexual dimorphism. It is as large (18–20 cm) as the first four species, but differs in having a light throat and a greyish wash to forehead, ear-coverts, nape and back. Furthermore, the plumage colours of both males and females are rather different from the strong colours of the other red/yellow dimorphic species. This combined with size and shape makes the appearance of *P. roseus* somewhat similar to that of the *P. cantonensis/divaricatus/tegimae* complex, although these are all dull greyish birds. In addition to the species mentioned above, there is also a group of small (15–16.5 cm) *Pericrocotus* species (*P. lansbergei* and *P. erythropygius*) with a more variegated plumage, in which the males have some red (breast patch and rump) in their plumage and the females are generally more black, grey and white.

Based on plumage patterns and size alone, one would assume the large red/yellow birds to form a monophyletic group, the large dull coloured birds to form another monophyletic group, and then, with *P. cinnamomeus* as a possible link, the small birds with more variegated plumages as a third group. This is not the case. The red/yellow sexually dimorphic birds (even if maintaining a rather conservative view only including *P. solaris*, *P. ethologus*, *P. brevirostri*s and *P. flammeus*) represent four different lineages. Although this may seem surprising at a first glance, a similar observation of repeated convergence and reversal in plumage colouration has been made in the New World orioles (Omland & Lanyon 2000; Allen & Omland 2003). As for New World orioles, many minivet species are sympatric and occur in the same habitats. This in turn could lead to convergent evolution of plumage colouration to improve signal efficiency and crypsis (Morton 1975; Ryan *et al*. 1990; McCracken & Sheldon 1997) and to mimic other species for social behaviour reasons (Moynihan 1968) or for predator avoidance (Barnard 1979; Diamond 1992).

It is striking that the three minivet species breeding in the temperate zone, *P. cantonensis*, *P. divaricatus* and *P. tegimae*, are the only species sharing a dull plumage, with no red or yellow colours. Thus, it seems that the colourful plumages are restricted to tropical birds and that plumage colour for minivets is highly plastic (Fig. 1). The dull minivet species breeding in the temperate zone are also the only true migratory species. *Pericrocotus ethologus* also shows some altitudinal migratory pattern, but this seems to merely reflect that this species is a high-altitude (>900 m) breeding species, which during the winter drops down to lower altitudes. This pattern is also to a certain degree true for *P. roseus*, although this species breeds at somewhat lower altitudes (>300 m). However, it is noticeable from the phylogeny that the two colourful migratory birds are confined to the tropics, whereas the migratory birds of the temperate zone are colourless.

It seems possible that the energy expenditure of being migratory could put constraints on colour evolution. Tropical forest birds would have constant forest cover where colours would not attract attention from potential predators. Being migratory, however, necessitates visits to environments where it is important to be well-concealed to

avoid predation. Thus, brightly coloured birds are more likely to be predated, whereas dull birds will have an overall better chance of survival. That migratory species within conspicuous avian radiation have more cryptic coloured plumages have been observed in other tropical groups, e.g. Pittidae (Irestedt *et al.* 2006). We agree with previous studies (e.g. Omland & Lanyon 2000) that the convergence in overall plumage types among distantly related birds results from a combination of convergence, reversal and retained ancestral states in individual characters (Price 2008).

Acknowledgements

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