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Phylogenetic relationships of rollers (Coraciidae) based on complete mitochondrial genomes and fifteen nuclear genes

Ulf S. Johansson[a,*], Martin Irestedt[b], Yanhua Qu[b,c], Per G.P. Ericson[b]

[a] Department of Zoology, Swedish Museum of Natural History, Box 50007, SE 104 05 Stockholm, Sweden
[b] Department of Bioinformatics and Genetics, Swedish Museum of Natural History, Box 50007, Stockholm 10405, Sweden
[c] Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

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ABSTRACT

The rollers (Coraciidae) constitute a relative small avian family with ca. 12 species distributed in Africa, western and southern Eurasia, and eastern Australia. In this study we examine the phylogenetic relationships of all species currently recognized in the family, including two taxa whose taxonomic status is currently contested. By using shotgun sequencing on degraded DNA from museum study skins we have been able to recover complete mitochondrial genomes as well as 15 nuclear genes for in total 16 taxa. The gene sequences were analyzed both concatenated in a maximum likelihood framework as well in a species tree approach using MP-EST. The different analytical approaches yield similar, highly supported trees and support the current division of the rollers into two genera, *Coracias* and *Eurystomus*. The only conflict relates to the placement of the Blue-bellied Roller (*C. cyanogaster*), where the mitochondrial, and the concatenated nuclear and mitochondrial data set, place this taxon as sister to the other *Coracias* species, whereas nuclear data and the species tree analysis place it as the sister taxon of *C. naevia* and *C. spatulatus*. All analyses place the Eurasian roller (*C. garrulus*) with the two African species, Abyssinian Roller (*C. abyssinica*) and Liliac-breasted Roller (*C. caudatus*), and place this clade as the sister group to the Asian *Coracias* rollers. In addition, our results support a sister group relationship between the morphologically rather dissimilar Purple Roller (*C. naevia*) and Racquet-tailed Roller (*C. spatulatus*) and also support the division of *Eurystomus* in an African and an Asian clade. However, within the Asian clade the Azure Roller (*E. azureus*) from Halmahera appears to be nested within the Dollarbird (*E. orientalis*), indicating that that this taxon is a morphological divergent, but a rather recent offshoot, of the widespread Dollarbird. Similarly, the Purple-winged Roller (*C. temminckii*) from Sulawesi group together with *C. benghalensis affinis* from Southeast Asia and these two in turn comprises the sister group to *C. benghalensis benghalensis* from India and western Asia.

1. Introduction

Rollers (Coraciidae) are medium-sized, stoutly built birds, superficially reminiscent of crows but more closely related to e.g., kingfishers (Alcedinidae) and bee-eaters (Meropidae) (e.g. Prum et al., 2015). Like many of their relatives the rollers are often colorful and conspicuous. The group includes approximately twelve species, which are distributed in Africa, Europe, southern Asia and Australasia. Most species are confined to open habitats with scattered arboreal vegetation in tropical and subtropical regions, but three species occur in tropical rainforest and two migratory species extend their breeding range into more temperate regions (Fry, 2001). Monophyly of the Coraciidae is strongly supported (Clarke et al., 2009) but species boundaries are in a few cases uncertain. For instance the Indian roller (*Coracias benghalensis*), whose distribution ranges over much of South Asia from Gulf of Aden to southern China and Southeast Asia, is sometimes (e.g. Del Hoyo and Collar, 2014) divided into two species, *C. benghalensis* in the west eastward to India and *C. affinis* from India and eastward, but with an apparent zone of hybridization from central Nepal through western Assam (Rasmussen and Anderton, 2005). Rollers are morphologically homogenous but two distinct groups can be discerned, *Coracias* and *Eurystomus*, which differ mainly in skull proportions and foraging behavior (Cracraft, 1971). In *Coracias* the bill is robust and rather straight with a small hook, whereas in *Eurystomus* the bill is shorter and broader at the base. Furthermore, *Coracias* rollers are primarily sit-and-wait predators that use perches as lookout post and pounce down upon insects and small vertebrates on the ground, whereas the *Eurystomus* rollers are more active hunters and often chase insects in the air (Fry, 2001).

Both *Coracias* and *Eurystomus* are represented both in Africa and

* Corresponding author.
E-mail address: ulf.johansson@nrm.se (U.S. Johansson).

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Asia. Five species of *Coracias* occur year around in Africa and one species, the European Roller (*C. garrulus*), breeds in Europe and western Asia but migrates to sub-Saharan Africa during the northern hemisphere winter. In addition to the European Roller and the above mentioned Indian roller, the genus *Coracias* is also represented in Asia by the Purple-winged Roller (*C. temminickii*) in Sulawesi. Within the genus *Eurystomus* four species are currently recognized, two each in Africa and in Asia. Of the African representatives, the Blue-throated Roller (*E. gularis*) is found in equatorial rainforests while the Cinnamon Roller (*E. glaucurus*) is a seasonal migrant that over the year occurs over much of the sub-Saharan Africa as well as in Madagascar. The Asian *Eurystomus* are the widely distributed Dollarbird (*E. orientalis*) and the Azure Roller (*A. azureus*) on Halmahera in the Maluku Islands (Moluccas).

The phylogenetic relationships among the roller have so far been poorly investigated. Some interspecies relationships within the *Coracias* have been proposed mainly based on plumage similarities and for instance the European Roller have been proposed to form a species group with the African species, Lilac-breasted roller (*C. caudata*), Abyssinian roller (*C. abyssinica*), and Racket-tailed roller (*C. spatulata*) (e.g. Snow, 1978).

In this study we examine the phylogenetic relationships within Coraciidae. We include all twelve species of rollers currently recognized (Dickinson and Christidis, 2014) as well as the southeastern subspecies of *Coracias benghalensis*, *C. b. affinis*, which sometimes is regarded as a distinct species, and whose relationship to the Purple-winged roller is unresolved. Furthermore, we also included three individuals of the Dollarbird, one from mainland Southeast Asia and one from Australia and New Guinea, respectively, in order to examine the relationship of this species relative to the Azure Rollerbird on Halmahera, whose morphological distinctiveness has often rendered it species status, but whose distribution may indicate a close relationship with the dollarbirds in the Wallacea region. By using Next-Generation shotgun sequencing on degraded DNA from museum study skin we have been able to recover complete mitochondrial genomes as well as 15 nuclear genes from all 16 taxa and we analyze these sequences both as concatenated as well as in a species tree approach.

2. Material and methods

2.1. Library preparation and sequencing

Genomic DNA was extracted from toe-pad samples of museum study skins kept at the Swedish Museum of Natural History, the Museum national d́Historie naturelle in Paris, and the Natural History Museum of Denmark (Table 1), following the precautions described in Irestedt et al. (2006). The genome library preparation for Illumina high-throughput sequencing followed the protocol published by Meyer and Kircher (2010). The libraries were pooled with other species and sequenced on an Illumina Hiseq 2500 platform at the Science for Life Laboratory (National Genomics Institute). Using a whole genome shotgun strategy we generated a total of 277 Gb of paired-end reads of 126 basepairs (bp) length.

2.2. Sequence quality checking and filtering

To avoid reads with artificial bias in the process of library construction and sequencing (i.e. low quality reads, which mainly resulted from base-calling duplicates and adapter contamination), we used a custom designed, clean-up workflow that is available at https://github.com/mozesblom. The workflow uses Super Deduper (http://dstreett.github.io/Super-Deduper) to remove read duplicates introduced by the PCR amplification. TRIMMOMATIC (v.0.32; Bolger et al., 2014) was used to remove sequencing adapters and to filter away low-quality reads. The reads to be retained should exceed 30 bp in length. Paired-end reads were merged using PEAR (Zhang et al., 2014) if they overlap with at least 20 bp (with the probability threshold set to 0.001). As the

Table 1
Museum specimens used in the study. Statistics for depths and breadths of mapping coverage were estimated using the *genomecov* tool in *bedtools* (v. 2.26.0).

Scientific name	Voucher no.	Locality	Date	Mt genome (17,744 bp)		25 nuclear genes (11,982 bp)	
				Cov. depth	Cov. breadth	Cov. depth	Cov. breadth
Coracias abyssinicus	NRM 571569	Ghana, Northern Region, Bole	1935-01-09	338	0.80	35	1.00
Coracias benghalensis affinis	MNHN 1998-22	Thailand, Khao Soi Dao, 10 km w dePong Nam Ron	1986	388	0.86	23	1.00
Coracias benghalensis benghalensis	MHNH 1957_869	Iran, Bender- Abbas	1956	161	0.78	21	1.00
Coracias caudatus lorti	NRM 571486	Kenya, Nakuru, Njoro	1911-02-20	231	0.80	13	0.99
Coracias cyanogaster	ZMUC 70_406	Gambia river	1916-05-17	323	0.85	6	0.93
Coracias garrulus garrulus	NRM 690167	Hungary, Tolna, Fácánkert	1965-08-07	459	0.84	26	1.00
Coracias naevius naevius	NRM 710044	Ghana, Lower River, Jappeni	1968-03-08	461	0.81	28	1.00
Coracias spatulatus spatulatus	MNHN 1965-1038	DRC, Kantaga, Kolwezi	1955	50	0.74	9	0.99
Coracias temminckii	MNHN 1198-91	Indonesia, Sulawesi		363	0.82	18	1.00
Eurystomus azureus	NRM 571466	Indonesia, Moluccas [Maluku Islands]	1894	1949	0.86	45	0.99
Eurystomus glaucurus suahelicus	NRM 571546	Kenya, Meru Province, Luazomela [between Meru and Isiolo ca 0.18°N 37.57°E]	1911-02-02	417	0.85	24	0.99
Eurystomus gularis gularis	NRM 571461	Ghana, Ashanti region, Ejura	1935-01-28	1647	0.85	46	0.99
Eurystomus orientalis orientalis	NRM 571527	Thailand, Chiang Mai province, Chiang Dao	1938-04-16	6593	0.86	12	0.92
Eurystomus orientalis pacificus	NRM 571499	Australia, Western Australia, Kimberley, Noonkanbah	1910-12-04	358	0.86	18	0.98
Eurystomus orientalis waigiouensis	NRM 571521	Indonesia, West Papua, Aitinjoe [1.43°S 132.38°E]	1949-02-15	932	0.85	12	0.97
Atelornis pittoides	NRM 571822	Madagascar, 60 km east of Fianarantsoa	1928-11-20	231	0.86	25	0.71