Miocene diversification of an open-habitat predatorial passerine radiation, the shrikes (Aves: Passeriformes: Laniidae)

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Abstract

Diversification of avifaunas associated with savannah and steppes appear to correlate with open habitats becoming available, starting in the Miocene. Few comparative analyses exist for families for which all species are predominantly adapted to these habitats. One such group is Laniidae (Passeriformes), which are small to medium sized predatory passerines known for their distinctive behaviour of impaling prey. We used multispecies coalescent-based and concatenation methods to provide the first complete species-level phylogeny for this group, as well as an estimate of the timing of diversification. Our analyses indicate that Laniidae as currently delimited is not monophyletic, as the genus *Eurocephalus* is not closely related to the remaining species. The two species currently assigned to the monotypic genera *Urolestes* and *Corvinella* are part of the same clade as the *Lanius* species, and we propose that they are included in the genus *Lanius,* making Laniidae monogeneric. The initial diversification of the clade is inferred to have occurred very rapidly, starting about 7.2-9.1 million years ago, timing depending on calibration method, but in either case coinciding with the expansion of C4 grasses. An African origin is inferred in the biogeographic analysis. In the redefined Laniidae, cooperative breeding is inferred to be restricted to a single clade, characterized by gregarious behaviour and rallying. Migratory behaviour evolved multiple times within the family.

Keywords: *Lanius,* molecular phylogeny, biogeography, migratory behaviour, gregarious behaviour, radiation

Introduction

Open habitats (savannah, steppes) started to become predominant in many regions in the Miocene due to climatic changes favouring the spread of C4 grasses (Osborne and Beerling 2006, Strömberg 2011). Open habitats started to develop in the eastern Mediterranean region about 20-18 million years ago (mya) and became predominant in east Africa during the Middle Miocene (about 15–13 mya), whereas they only appeared in Pakistan much later (about. 11–9 mya). In the eastern Mediterranean and Pakistan, the amount of C4 cover has been suggested to have exceeded 20% of the vegetation cover around 8 mya (Edwards *et al.* 2010). This period was characterized by the establishment of the modern-type flora and fauna, with several lineages of browsers and grazers starting to diversify (Cetartiodactyla: Hassanin *et al.* 2012). Our knowledge regarding the biogeography and diversification patterns of the fauna associated with savannah and steppes, especially at the inter-continental level, all point towards a similar date for the diversification (9–6 mya), corresponding to the radiation of C4 grasses (e.g. *Anthus*: Voelker 1999, *Motacilla*: Alström *et al.* 2015, Harris *et al.* 2018, *Falco*: Fuchs *et al.* 2015, *Circus*: Oatley *et al.* 2016). Based on these phylogenetic data, adaptation to open habitat seems to be very recent in avian evolution and is in accordance with the fact that many bird lineages have forest-adapted ancestors. In the Alaudidae (larks), initial diversification appeared to have started slightly earlier than the C4 grasses radiations, at about 20 mya Alström *et al.* 2013). Yet, very few comparative data exist for families for which all species are adapted to steppes, savannas or grasslands. Species level phylogenies for such a lineage could bring further insights into the timing, ancestral area and diversification of open-habitat lineages.

The Laniidae (Passeriformes) is a very distinctive group of small to medium size predatory passerines (14–27 cm) that hunt large insects and small vertebrates (lizards, rodents, insectivores and occasionally other birds) and are known for their distinctive behaviour of impaling prey on thorns and twigs as food reserves. Current taxonomy recognizes 30–34 species divided into three or four genera. Lefranc and Norfolk (1997) and Harris and Franklin (2000) list 30 species in three genera, Yosef (2008) lists 31 species in four genera, del Hoyo and Collar (2016) list 33 species in four genera, whereas Dickinson and Christidis (2014) and Gill and Donsker (2018) list 34 species in four genera. The genus *Eurocephalus* (crowned shrikes) includes two species that are allopatrically distributed in eastern (*E. ruppelli*) and southern Africa (*E. anguitimens*), respectively, and have been suggested to form a superspecies (Hall and Moreau 1970). Two monotypic genera (*Urolestes melanoleucus* and *Corvinella*

corvina) are very different in plumage pattern, but have similar social behaviour, leading Harris and Franklin (2000) to place both in *Corvinella*. The two species are parapatrically distributed, with *C. corvina* being found in the woodland savannah and thorn bush of the Sudanian biome, whereas *U. melanoleucus* is restricted to the woodland savannah of the Zambezian biome.

The 26–30 species included in the genus *Lanius* are very similar in structure, plumage patterns and life style. The monophyly of *Lanius* has rarely been challenged by taxonomists, although Wolters (1975–82) considered the two *Corvinella* species to be part of *Lanius*. The genus *Lanius* is distributed across the Holarctic, Ethiopian and Oriental regions, with up to half of the extant species occurring in sub-Saharan Africa at some time of the year (10 sedentary species plus five Palearctic winter visitors), and the majority of the remaining species occur in the Western Palearctic (six breeding species, of which only two remain in winter), the Eastern Palearctic (seven breeding species, of which only two remain in winter), and the Oriental region (five breeding species, plus three Eastern palearctic winter visitors). Only two species have colonized the Nearctic, whereas Australasia (east to New Guinea) has only one species. The *Lanius* species exhibit marked differences in migratory behaviour; all species breeding in the Western and Eastern Palearctic and North America are mainly or entirely migratory, whereas the sub-Saharan species are sedentary or only disperse short-distances. Differences are also observed in the extent of migratory behaviour as some species (e.g. *L. collurio, L. senator, L. minor*) are long-distance migrants (breeding in the Western Palearctic, wintering in sub-Saharan Africa) whereas other species (e.g. *L. excubitor, L. cristatus*) are short-distance migrants.

The number of recognized species has been relatively stable through time (e.g. Lefranc and Norfolk 1997, Harris and Franklin 2000, Yosef 2008, Dickinson and Christidis 2014), with a recent increase (del Hoyo and Collar 2016, Gill and Donsker 2018) based on two phylogenetic/phylogeographic studies performed on two species complexes, *L. excubitor* (Olsson et al. 2010) and *L. collaris* (Fuchs *et al.* 2011). These studies provided new insights regarding the speciation patterns within these clades and highlighted several cases where the species limits were poorly understood. Olsson et al. (2010) found relationships inconsistent with current taxonomy but concluded that more research was needed because only mitochondrial DNA had been analyzed.

The relationships among members of the genus *Lanius* have been investigated by Panov (2011) and Harris and Franklin (2000, p. 24), using overall similarity in morphology, vocalizations and behaviour. Harris and Franklin (2000) recognized eight groups (Fig. 1a) with uncertain relationships for several species (e.g. *L. minor, L. nubicus*) and a few groupings with a strong geographic component (e.g. the African group, and the mainly Palearctic '*phoenicuroides-tigrinus* group'). Harris and Franklin (2000) proposed to recognize two primary groups based on the type of alarm and advertising calls (Fig.

1b). These two groups also have a strong phenotypic component as species belonging to the 'keer alarm group' are mostly grey and black in plumage, whereas species belonging to the 'chatter alarm group' are mostly shades of brown. An intermediate group, suggested to belong in the 'chatter alarm group' is composed of species with brown, grey and black plumages (Harris and Franklin 2000). Fuchs et al. (2011) provided evidence of relationships incongruent with the vocalization-based groups proposed by Harris and Franklin (2000), as a member of the 'chatter alarm group' (*L. souzae*) was part of the same clade as three lineages of the 'keer alarm' group, that were in turn not monophyletic (*L. collaris*/*L. humeralis, L. mackinnoni, L. newtoni*).

Here, we present the first time-calibrated phylogeny of Laniidae, using mitochondrial and nuclear markers f**or all but one of the recognized species. We also evaluate previous hypotheses for structuring proposed subgroups, and discuss the biogeography and evolution of the group.**

Material and Methods

Sampling

Throughout this manuscript, we follow the taxonomy of Dickinson and Christidis (2014). We sampled 33 out of the 34 recognized species (Supplementary Table 1; only *E. anguitimensis* was not sampled) and selected a broad representation of corvoid families to test the monophyly of Laniidae, as this has never been tested based on molecular data. *Menura novaehollandiae* (Menuridae) was used as outgroup for rooting the phylogeny (e.g. Barker *et al.* 2004).

Laboratory protocols

DNA was extracted from fresh material (muscle, blood or feathers) using QIA Quick DNEasy Kit (Qiagen, Inc), according to the manufacturer's instructions, but with 30 µl DTT added to the initial incubation step for the extraction from feathers. We sequenced the mitochondrial cytochrome *b* (cytb) gene and two nuclear regions: myoglobin intron 2 (MB), ornithine decarboxylase (mainly) introns 6–7 (ODC) following the protocols described in Fregin *et al.* (2012). All sequences have been submitted to GenBank (Supplementary Table 1). The mitochondrial sequences were validated by the following evidence: (1) They showed no double signal in the electrophenograms. (2) The alignment showed no stop codons, insertions or deletions. (3) A vast majority of nucleotide substitutions were found in the 3rd codon position and resulted in few amino acid substitutions.

Phylogenetic analyses

Single locus analyses were performed using Bayesian inference (BI), as implemented in MRBAYES 3.2 (Ronquist *et al.* 2012), and Maximum Likelihood (ML), as implemented in RaxML 7.0.2 (Stamatakis 2006, Stamatakis *et al.* 2008). We used the *nst=mixed* and *rates=invgamma* options for the Bayesian inference analyses. Four Metropolis-coupled MCMC chains (one cold and three heated) were run for 10 million iterations with trees sampled every 100 iterations. For the ML analyses, the best-fit models were selected using TOPALI (Milne *et al.* 2009) under the Bayesian Information Criterion. Nodal support for the ML analyses was assessed through non-parametric bootstrapping (BS; 100 replicates).

Concatenated analyses and divergence times analyses

Maximum likelihood analyses on the concatenated data (partitioned by gene) were performed using RaxML 7.0.2 (Stamatakis 2006, Stamatakis *et al.* 2008). We estimated divergence times on the concatenated data set (three partitions) using BEAST 1.8.2. (Drummond *et al.* 2012), using the same substitution models as in the species tree analyses, with two different strategies.

We first used the substitution rates estimated by Lerner *et al.* (2011) for Cytochrome b (normal distribution 0.014 substitutions per site per million year, standard error: 0.0011) and ODC (0.0015 substitutions per site per million year, standard error; 0.0002). We assumed a strict clock model for the nuclear loci (the MB rate being estimated as part of the analyses) and an uncorrelated lognormal clock model for cytb.

As an alternative to the substitution rate calibration, we also used three independent Corvides fossils. The first fossil was *Kurrartapu johnnguyeni* (Nguyen *et al.* 2013) that was used to calibrate the split between *Peltops* and *Gymnorhina;* we used a lognormal distribution with an offset of 15.97 mya, corresponding to the Early Miocene (Nguyen *et al.* 2013) and a mean/standard deviation of 0.5/0.743, so that 97.5% of the distribution was within the Miocene. The second fossil, *Miocitta galbreathi* (Brodkorb 1972, Becker 1987), from the Middle Miocene, was used to calibrate the node *Aphelocoma/ Pica-Garrulus-Corvus-Nucifraga*), as *Miocitta* is considered to be closer to New World Jays than to other Corvidae; we used a lognormal distribution with an offset of 11.608 mya, corresponding to the beginning of the Middle Miocene, and a mean/standard deviation of 0.69/0.89, so that 97.5% of the distribution was within the Miocene. The third calibration point involved the early Miocene fossil *Longimornis robustirostrata* (Boles 1999) and was used to calibrate the split between *Oriolus* and *Sphecotheres;* we used a lognormal distribution with an offset of 15.97 mya, corresponding to the Early Miocene and a mean/standard deviation of 0.5/0.743), so that 97.5% of the distribution was within the

Miocene. Substitution rates for all three loci were estimated as part of the analyses. We assumed a uniform prior for the substitution rates.

For each calibration strategy (fossils or substitution rates), two runs were conducted for 25 million iterations, assuming a Birth-Death tree process with trees and parameters sampled every 1000 iterations. The first 5 million iterations were discarded as burn-in.

Species tree analyses

Species trees (ST) were reconstructed using the coalescent-based model implemented in *BEAST (Heled and Drummond 2010, Drummond *et al.* 2012). Three species (*Lanius borealis, Lanius phoenicuroides, Lanius giganteus*) could not be included in the species tree analyses as they require sequence data for all loci. Each locus had its own substitution rate matrix and clock model (all assigned to a strict clock model as convergence was more efficient). We used a Birth-Death process for the tree prior and the cyt b and ODC substitution rates, and associated errors, estimated by Lerner et al. (2011). Three runs were conducted for 100 million iterations, with trees and parameters sampled every 2000 iterations. The first 10 million iterations were discarded as the burn-in period.

Analyses were run on the CIPRES 3.1 gateway server (www.cipres.org; Miller *et al.* 2010). We used TRACER v1.7 (Rambaut et al. 2014) to help ensure that the effective sample size for all Bayesian analyses of the underlying posterior distribution was adequate (>200) for meaningful estimation of parameters.

Biogeography

We analyzed the historical biogeography using the likelihood-based Dispersal-Extinction-Cladogenesis (DEC) model of LAGRANGE (Ree et al. 2005, Ree and Smith, 2008; see Ree and Sanmartin 2018 concerning the use of the DEC+j model (Matzke 2014) implemented in RASP v.4 (Yu *et al.* 2015). We specified five areas for the analyses: Afrotropics, Western Palearctic, Eastern Palearctic, Nearctic and Oriental (including Australasia since only one species, *L. schach* reaches Papua New Guinea). We considered both the breeding and wintering distributions combined as being the species' range. For all analyses, we used the maximum clade credibility trees from the BEAST concatenated analyses (fossil and substitution rates) and assumed a symmetric one-rate model and allowed for up to four ancestral areas. Analyses were conducted on 'core Laniidae' (*Lanius, Corvinella*

and *Urolestes*) based on the topologies from both the fossils and rates clades (clades A-F), with outgroups and the phylogenetically distant *Eurocephalus* pruned. We included *L. c. marwitzii* in the analyses based on Fuchs et al. (2011) even though it is not considered a species *sui generis* by Dickinson and Christidis (2014).

Reconstruction of migratory behaviour and social behaviour evolution.

Many species migrate to some extent, but some have evolved migration behaviour that involves inter-continental movements. Migration routes of similar lengths are also possible within a continent, but we coded a species as long distance migratory when they winter in a different biome than the breeding biome, using distribution maps from Harris and Franklin (2000). Coding sociality (solitary/gregarious species) was based on Harris and Franklin (2000). All reconstructions of ancestral character states were performed using the R packages APE (Paradis *et al.* 2004) and PHYTOOLS (Revell 2012). Analyses were performed on the MCC trees (fossils and substitution rates) with only the members of the 'core Laniidae' included. For the stochastic mapping analyses, we performed 100 simulations using the Early Radiation model and plotted the results on one randomly chosen simulation from the 100 simulations.

Diversification rates

Estimation of the diversification rates through time for the Laniidae *s.s.* was obtained with APE (Paradis et al. 2004), LASER (Rabosky 2006a, b), BAMM (Rabosky 2014) and BAMMTOOLS (Rabosky et al. 2014) in R3.01 (http://www.r-project.org/; R Core Team, 2013). The BAMM (Rabosky 2014) and BAMMTOOLS (Rabosky et al. 2014) analyses were run under the '*speciationextinction*' model, assuming a sampling probability of 1 and defaults priors. The MCMC simulations were run for $500*10^6$ iterations, using four chains, sampled every 1000 iterations. We estimated the empirical gamma statistic (Pybus and Harvey 2000) on the maximum clade credibility (MCC) trees (fossil and substitution rates topologies) from the BEAST v1.8 analyses using the *gamStat* command. We ran the analyses with and without *L. c. marwitzii* as its species status is uncertain (see Fuchs et al. 2011)

Results

Phylogenetic analyses

Single-locus analyses

Laniidae was not found to be monophyletic in any of the single-locus analyses (Supplementary

Figures S1, S2, S3) because the genus *Eurocephalus* was part of a large basal polytomy in the Corvoidea involving the Monarchidae, Corvidae, Paradisaeidae, Dicruridae, Rhipiduridae, *Chaetorhynchus, Corcorax, Lamprolia, Melampitta,* and *Platylophus*. None of the single locus analysis had a topology, even without support, where the genus *Eurocephalus* was sister to the remaining Laniidae (*Lanius*/*Corvinella/Urolestes* -hereafter referred to as 'core Laniidae'). Species from the three latter genera formed a clade in all gene trees (Posterior Probability [PP]/Bootstrap Support: cytb: 1.0/100, MB: 0.96/86, ODC: 1/100). The sister genera *Corvinella* and *Urolestes* (PP/BS Cytb: 1/88, MB: 1/98 , ODC: 1/96) were nested within *Lanius* in all single locus analyses (PP: 1.0 in all gene trees), and were inferred to be related to a set of Eurasian species (*L. tigrinus-L. bucephalus* clade) in cytb (PP/BS: 0.86/<50), to *L. cabanisi*/*L. excubitoroides* in MB (PP/BS: 0.78/26) or to *L. cabanisi* and *L. minor*/*L. senator* in ODC (PP: 0.59/32). Very little resolution was found regarding relationships among *Lanius* superspecies or species complexes in the single locus analyses. There was nevertheless a strong trend for five clades involving more than two species in the analyses. The first clade (A) included eight species of large size: *L. dorsalis, L. somalicus, L. excubitor, L. ludovicianus, L. meridionalis, L. borealis, L. giganteus* and *L. sphenocercus* which are distributed in the Afrotropics, Western/Eastern Palearctic and North America; this clade was recovered in all loci (Cyt b: PP/BS: 1.0/91; MB: PP/BS 0.68/79; ODC: PP/BS: 1.0/79). The second clade (B) consisted of the six species from the *L. collaris* superspecies (*L. collaris, L. humeralis, L. c. marwitzi, L. mackinnoni, L. newtoni, L. souzae*) as well as *L. gubernator*; this afrotropical clade was found in all analyses although support was not always strong (cytb: PP/BS: 0.63/52; MB: PP/BS: 0.59/NA, ODC: PP/BS: 1/69). The third clade (C), only recovered in the cytb single locus analysis (PP/BS: 1.0/91), included eleven species that are breeding in the Palearctic (*L. collurio, L. isabellinus, L. phoenicuroides, L. cristatus, L. bucephalus*) and South-East Asia (*L. vittatus, L. collurioides, L. tigrinus, L. tephronotus, L. schach, L. validirostris*) with one species (*L. schach*) reaching Indonesia and Papua New Guinea. The MB and ODC single locus analyses recovered subclades of clades C. Clade D includes two species distributed in Eastern Africa, *L. excubitoroides* and *L. cabanisi*; this grouping was recovered in two of the three loci (cytb PP/ BS: 1.0/85; MB PP/BS 1.0/99). Clade E consisted of *L. minor* and *L. senator,* which breed in the Mediterranean and steppe regions of the southern Palearctic and winter in Africa. Clade E was recovered in the ODC single locus analysis (PP/BS 1.0/92). The position of *L. nubicus* was unresolved in the basal polytomy involving *Corvinella/Urolestes* and the five primary clades of *Lanius* in the cytb and MB single locus analyses, whereas it was sister to *L. tigrinus* in the ODC single locus analysis (PP/ BS: 1/91).

Concatenation and species tree topologies

The topologies were very similar between the two calibration strategies (fossils and substitution rates) and variations in posterior probabilities were minor (maximum 0.02). We here describe the fossil topology, but we mention when a different relationship was recovered in the substitution rate calibrated topology.

Results from the multi-locus analyses performed under the concatenated and species tree (*BEAST) algorithms (Fig. 2; substitution rates species tree topology Figure S4) suggest that *Eurocephalus* (Laniidae) was either sister to *Platylophus* ($PP_{CO[Concatenated]}$: 0.34, $PP_{ST[Species\ Tree]}$: 0.20) or to the Corvidae (BS_{CO}: 41), or in an unresolved position in the Corvoidea that also included the Paradisaeidae, Rhipiduridae/*Chaetorhynchus/Lamprolia*, Monarchidae, *Melampitta*, Dicruridae, *Corcorax*, and the 'core Laniidae' (BS_{CO}: 100, PP_{CO}: 1, PP_{ST}: 0.99); most of the relationships among these primary lineages were unresolved or poorly supported. The monophyly of the 'core Laniidae' was strongly supported (BS_{CO}: 100, PP_{CO}: 1, PP_{ST}: 1) and monophyly of clades A, B, C, D, E and the *Corvinella*/*Urolestes* clade were supported in both the concatenated and species tree analyses (minimum BS_{CO}: 87 for clade D, all PP_{CO}: 1,0; minimum PP_{ST}: 0.93 for clade D). Within the 'core Laniidae', six primary lineages were found, corresponding to *L. nubicus,* clades A, B, C and E, as well as a clade consisting of clade D and *Corvinella*/*Urolestes* (BS_{CO}: 42: PP_{CO}: 0.94, PP_{ST}: 0.67), but relationships among these six lineages were not resolved. Within clade A, the two Afrotropical species of this clade (*L. dorsalis, L. somalicus*) were the first lineages to sequentially diverge. Within clade B, *L. souzae* was sister to *L. collaris*/*L. c. marwitzi* (BS_{CO}: 99, PP_{CO}: 1, PP_{ST}: 0.96). Within clade C, *L. tigrinus* was the first species to split off (BS_{CO}: 52, PP_{CO} : 0.66, PP_{ST}: 0.88). Of the ten remaining species from clade C, *L. collurioides* clustered with *L. vittatus* (BS_{CO}: 47, PP_{CO} : 0.51, PP_{ST}: 0.99) and *L. collurio* grouped with *L. phoenicuroides* (BS_{CO}: 99, PP_{CO} : 1, PP_{ST}: NA) and *L. isabellinus* (BS_{CO}: 100, PP_{CO} : 1, PP_{ST}: 1). The five remaining species from clade C, found from the Eastern Palearctic throughout South-East Asian to Papua New Guinea, clustered together (BS_{CO}: 100, PP_{CO}: 1, PP_{ST}: 0.99).

Divergence times

The divergence times obtained from the concatenated dataset using the two calibration strategies (fossils versus substitutions rates) were very similar (Table 1). The core Laniidae diverged from its sister-group between 20.6 and 25.7 mya. The genus *Eurocephalus* diverged from its closest

relative about 18–22 mya (fossils: 18.0 mya 95% HPD: 15.1–20.6; substitutions rates: 22.4 mya 95% HPD: 17.9–26.8). The initial diversification of the core Laniidae into the six primary lineages occurred very rapidly, starting about 7.2–9.1 mya, about 13–15 million years after the divergence from their closest, not yet determined, relatives. The afrotropical clades B, and D/*Corvinella-Urolestes* started to diversify about 4.4-5.6 mya and 5.9-7.5 mya, respectively. In clade A, the Afrotropical *L. dorsalis* split from the other members of this clade at a similar time (4.6–5.9 mya). Several speciation events between Afrotropical sister species occurred at similar times during the 3–5 mya period (e.g. substitutions rates: *U. melanoleucus*/*C. Corvina* 3.7 mya, *L. cabanisi*/*L. excubitoroides* 4.6 mya, *L. mackinnoni*/*L. gubernator* 4.7 mya). We noticed that the relative and absolute timing of divergence were more recent in the species tree approach (substitution rates e.g. *L. cabanisi*/*L. excubitoroides:* 3.4 mya, *U. melanoleucus*/*C. corvina*: 2.0 mya), suggesting that discrepancies are present between the concatenation and species tree (Figures S4) methods regarding divergence times in specific and recent parts of the tree.

The Western Palearctic species have different origins in times, *L. minor* and *L. senator* diverged from each other about 3.9-5.0 mya, *L. collurio* and *L. meridionalis* split from their closest relatives about 0.6-0.7 mya (fossils: 0.6 mya 95% HPD: 0.3–0.9; substitutions rates: 0.7 mya 95% HPD: 0.3–1.2) and 0.4-0.5 mya (fossils: 0.4 mya 95% HPD: 0.2–0.7; substitutions rates: 0.5 mya 95% HPD: 0.2–0.9), respectively.

The *L. excubitor* species complex started to diversify slightly before the Pliocene/Pleistocene boundary, about 2.5–3.2 mya (fossils: 2.5 mya 95% HPD: 1.9–3.3; substitutions rates: 3.2 mya 95% HPD: 2.3–4.2). The New Word *L. ludovicianus* diverged from its closest relatives about 1.6-2.0 mya (fossils: 1.6 mya 95% HPD: 1.1–2.0; substitutions rates: 2.0 mya 95% HPD: 1.4–2.6).

The Oriental species started to diversify about 4.9–6 mya (fossils: 4.9 mya 95% HPD: 3.9–6.0; substitutions rates: 6.1 mya 95% HPD: 4.8–7.5) with the divergence of the Eastern Palearctic *L. tigrinus*. The next divergence involved the three species from the Western (*L. collurio*) and Central Palearctic (*L. phoenicuroides*), and *L. isabellinus* about 0.6-0.7 mya (fossils: 0.6 mya 95% HPD: 0.3–0.9; substitutions rates: 0.7 mya 95% HPD: 0.3–1.2) and 1.9-2.3 mya (fossils: 1.9 mya 95% HPD: 1.2–2.6; substitutions rates: 2.3 mya 95% HPD: 1.6–3.2), respectively; the first divergence is close to the Pliocene/Pleistocene boundary. The remaining Eastern Palearctic and Oriental species diversified during the 1.1-2.3 mya (fossils) or 1.4–2.9 mya (substitutions rates) time periods. The most recent divergence involves *L. bucephalus*, a short-distance migratory species from the Eastern Palearctic and *L. validirostris*, which is endemic to the Philippines (fossils: 1.1 mya 95% HPD: 0.7-1.6; substitutions rates: 1.4 mya 95% HPD: 0.9–2.0).

Biogeography

The most likely reconstruction for the ancestral area at the most basal Laniidae node was the Ethiopian bioregion (fossils P: 0.62; substitution rates P: 1.0; Fig. 3); the Ethiopian/Western Palearctic had a probability of 0.38 for being the ancestral area in the fossils based calibration topology. More recent nodes were not dependent on the input topologies. The resident Philippine endemic *L. validirostris* was nested within a clade composed of migrating species from Eastern Palearctic to Australasia. The speciose clade D shows a very complex pattern after splitting off from the African *L. dorsalis*. The biogeographic analyses indicated that North America may have been part of the ancestral range already at the base of the *L. excubitor-L. giganteus* clade, and probability of this increased to 0.88 (fossils) at the *L. somalicus-L. giganteus* clade. However, exact patterns are obscure.

Evolution of migratory and social behaviour

Reconstruction of the ancestral behaviour regarding migration suggested that the 'core Laniidae' ancestor was most likely a non-migratory species (Figure 4A; sedentary, p=0,93, migratory p=0,07), with six shifts at edges towards a migratory behaviour (stochastic mapping; 8.31 changes along the tree on average across the 100 simulations). Reconstruction of the social behaviour indicated only one shift from solitary to gregarious behaviour (at the base of the *U. melanoleucus*/*C. corvina*/*L. cabanisi*/*L. excubitoroides* clade) (Figure 4B). The reconstructions of the ancestral states were not dependent on the topology used (fossils or substitution rates)

Diversification rates

The γ statistics on the maximum clade credibility trees were significantly negative (fossils without *L. c. marwitzi* γ= -2.7156242042, p: 0.0033; fossils with *L. c. marwitzi*: γ= -2.473156 p: 0.00669; rates without *L. c. marwitzi* γ= -2.723424, p: 0.0032; rates with *L. c. marwitzi*: γ= -2.480653 p: 0.00557), indicating decrease in diversification rates through time. We did not find any discrete changes in diversification rates for the 'core Laniidae' using BAMM (Figure 5A); in all analyses, the highest probability of rate shifts was 0, p: 0.79–0.88). Instead, there was evidence of decrease in diversification rate that appeared to be gradual, with the extant speciation rate being about half of the initial speciation rate (Figure 5B).

Discussion

Higher level relationships of shrikes

Traditional taxonomy considered shrikes to be closely related to other shrike-like passerines (African bush-shrikes, Malaconotidae; Peters 1960, Wolters 1975-82), until the Sibley and Ahlquist (1990) DNA/DNA hybridization study challenged this view by suggesting that Malaconotidae and Laniidae were not closely related although both taxa were nested within a larger clade (Corvides) that contained many predatory and shrike-like passerines. Yet, short internodes and methodological problems prevented further conclusions. Phylogenetic studies based on DNA sequence data confirmed that Malaconotidae and Laniidae are not closely related (Fuchs *et al.* 2004, 2006, Barker *et al.* 2004, Jønsson *et al.* 2016). Instead, most recent studies have found that the Laniidae are nested in a subclade of the Corvides that also includes the Corcoracidae, Corvidae, Dicruridae, Monarchidae, Paradisaeidae, Rhipiduridae, but the branching pattern and detailed relationships among these family-level clades were not fully resolved (Barker *et al.* 2004, Jønsson *et al.* 2016, Moyle *et al.* 2016), although strong support was found for a sister relationship between Laniidae and Corvidae (Jønsson *et al.* 2016, Moyle *et al.* 2016). Our analyses confirm the affinities of the Laniidae with the above-mentioned families but could not identify a specific sister lineage to the Laniidae.

Monophyly of Laniidae

None of our analyses recovered the Laniidae as currently defined (e.g. Dickinson and Christidis 2014) as monophyletic, as *Eurocephalus* formed a sister clade to the Oriental monotypic Crested Jay *Platylophus galericulatus* (Corvidae) in the concatenated analyses, although support values were always low (PP: 0.42–0.57). In the species tree analyses, the *Eurocephalus–Platylophus* clade was placed as sister to the 'core Laniidae' clade but again without support (PP: 0.14). The two genera *Eurocephalus* and *Platylophus* are also joined by very long branches in the tree and are inferred to have diverged at a time when, based on our analyses, most extant Corvides families appeared. The age of the inferred split between *Eurocephalus* and *Platylophus* is of the same magnitude as between most other clades and lineages in the group that are currently treated as different families, suggesting that family level recognition for each of these two may be in order.

The genus *Eurocephalus* was traditionally considered close to the Afrotropical helmet-shrikes (*Prionops*) (Mayr 1943), based on similar tarsal scutellation (Rand 1959), whereas DNA-DNA hybridization data (Sibley and Ahlquist 1990), skull characters, and potentially hindlimb muscle arrangements data (Raikow et al. 1980), and behaviour (Harris and Franklin 2000) indicated

similarities with the 'core Laniidae'. Molecular data indicate that the genus *Prionops* is nested in a group that also includes the flycatcher-shrikes (*Bias, Megabyas*), philentomas (*Philentoma*), and vangas (Vangidae) (Fuchs *et al.* 2004, 2006, 2012, Moyle *et al.* 2006, Jønsson *et al.* 2012, Reddy *et al.* 2012). This latter assemblage is part of a different primary clade within the Corvides than the one containing *Eurocephalus* and 'core Laniidae' (Jønsson *et al.* 2016). Hence, all phylogenetic data indicate that the genera *Eurocephalus* and *Prionops* are not related. Harris and Franklin (2000) considered the genus *Eurocephalus* to be the most primitive living shrikes and, to some extent, "its jay-like behaviour, combined with other characters, suggests that it shares a common ancestor with the corvids (Corvidae)". Hence, the behavioural and morphological characters used to group *Eurocephalus* with either *Prionops,* the 'core Laniidae', or even the Corvidae, could consist of highly labile characters and/or plesiomorphic character states within the larger Corvides clade.

Laniidae sensu stricto

Our study provides the most complete molecular phylogeny of shrikes published to date. The relationships among species within species complexes are generally well supported but the relationships among the deeper nodes are mostly unresolved, a result that we attribute most likely to rapid radiation at the base and the use of a small number of nuclear loci. The sister-genera *Corvinella* and *Urolestes* are nested within *Lanius.* Consequently, we here suggest including the two species from these two genera in *Lanius,* in agreement with Wolters (1975–82).

Panov (2011) proposed a phylogenetic hypothesis for the genus *Lanius* based on zoogeographical, morphological and behavioural data, in which he divided it into seven groups. A major incongruency with our results is the placement of his 'group 1', *L. souzae* and *L. gubernator*, which he placed together with his 'groups 5–7', the latter corresponding to our clade A (Fig. 2). According to our results, *L. souzae* and *L. gubernator* are part of an African clade (clade B), suggesting that the expression of phaeomelanin in males may be of limited phylogenetic importance. Panov's 'group 2' includes the remaining eight African species, largely corresponding to our clade B, but also including parts of our clades A (*L. somalicus, L. dorsalis*) and D (*L. excubitoroides, L. cabanisi*) (Fig. 2). Panov's 'group 3' corresponds to the Holarctic representatives of our clade A, but excludes *L. dorsalis* and *L. somalicus* (Fig. 2). Panov's 'group 4' includes *L. nubicus, L. minor* and *L. senator* (the latter two make up our clade E, Fig. 2), not recognizing that *L. nubicus* appears to be a unique ancient lineage without obvious close relatives.

The relative positions of many species within the respective vocalization category of Harris and Franklin (2000) are incongruent with our hypothesis, e.g. the position of *L. tigrinus, L. bucephalus/L. cristatus, L. senator/L. minor, L. somalicus, L. mackinnoni* and *L. nubicus*, but only two species, *L. gubernator* and *L. souzae,* display vocalisations at odds with a well-supported phylogenetic position. The position of *L. senator* and *L. minor* differ between the present study and the one proposed by Harris and Franklin (2000). However, as the deep nodes in Laniidae are unresolved, we are unable to reject that there might be a phylogenetic signal in the vocalisations, such that the division between the two alarm types may, with the exception of *L. gubernator* and *L. souzae,* represent a divergence going back to the most recent common ancestor of the entire clade. Alternatively, the homology of the vocalisation characters could have been imprecisely defined. For example the 'long whistle' state defines four nested nodes in the Harris and Franklin (2000)'s hypothesis (*L. humeralis-L cabanisi* clade, *L. humeralis-L. nubicus* clade, *L. humeralis-L. collaris* clade and *L. humeralis*), with several losses (e.g. *L. collaris, L. nubicus*/*L. newtoni*) or modifications (whistled phrase; *L. cabanisi-L. mackinnoni* clade).

The taxonomy and biogeography of two of the five primary clades have been the focus of previous studies (e.g. clade A, *Lanius excubitor* complex, Olsson *et al.* 2010; clade B, *Lanius collaris* complex; Fuchs et al. 2011). These studies highlighted several discrepancies between the phylogenetic relationships and the superspecies hypotheses of Panov (1995) and Harris and Franklin (2000), respectively, and we will not discuss these relationships again as the original results were corroborated here. The only exception involves *L. gubernator*, which was not sampled by Fuchs *et al.* (2011), which is nested within the *L. collaris* superspecies and possibly sister species of *L. mackinnoni*. This species has been suggested to possibly be related to *L. souzae* (Harris and Franklin 2000, Yosef 2008) but a sister-group relationship between these two species was never recovered in our analyses. The plumage differences between *L. mackinnoni* and *L. gubernator* are substantial and represent the two different plumage types defined by Harris and Franklin (2000): grey and black for *L. mackinnoni* and mainly brown for *L. gubernator.* The two species are parapatrically distributed: *L. mackinnoni* occurs along forest edges and woodland of the Congolian forest block whereas *L. gubernator* occurs in grassland savannas with scattered bushed and open woodland of the Sudanian bioregion. Plumage traits can be overall poor indicators of phylogenetic relationships (e.g. Christidis *et al.* 2010, Shultz and Burns 2013, Alström *et al.* 2015). We here have another example in Africa where sister-species are distributed in parapatry and occupy different habitat types, reinforcing the view that the speciation dynamics for

species distributed in the Guinean and Congolian forest block and the northern savannas biome was possibly driven by repeated habitat specialization (Zhen *et al.* 2017, Fuchs *et al.* 2018).

Our clade C is identical to Panov's 'group 5' (*L. collurio* and *L. isabellinus*), Panov's 'group 6' (*L. cristatus, L. tigrinus* and *L. bucephalus*) and Panov's 'group 7' (*L. tephronotus, L. validirostris* 'subgroup 7A'; *L. vittatus, L. collurioides, L. schach* 'subgroup 7B') in content, but the detailed phylogenetic position of individual species of our clade C is at odds with almost every detail of 'groups 6' and '7' of Panov (2011), except the sister relationship of *L. vittatus* and *L. collurioides*. The eleven species from clade C breed in the Palearctic and Oriental bioregions. Zhang *et al.* (2007) analysed a set of species, largely corresponding to our clade C (Fig. 2), and concluded that *L. tephronotus* and *L. schach* are not conspecific (*contra* Mayr and Greenway 1960). Our results corroborate this conclusion. Initiated by Stresemann (1927), *L. collurio, L. isabellinus* and *L. cristatus* have frequently been regarded as parts of a superspecies, or otherwise closely related (see Panov 2011 for review). The results in this study both indicate that first, *L. collurio, L. phoenicuroides* and *L. isabellinus* represent separate lineages, and second, that neither is closely related to *L. cristatus.* Species from clade C appear to have retained strong capacities to hybridize, even among non-closely related species (e.g. *L. collurio/L. cristatus, L. phoenicuroides/L. schach),* the offspring of these hybridization events being even described as an independent taxa (e.g. *Lanius darwinii* for the *L. phoenicuroides/L. schach* hybridization) (McCarthy 2006).

A very strong relationship was recovered between *L. excubitoroides* and *L. cabanisi.* These two species have been thought to be closely related based on behavioural characters (Harris and Franklin 2000). A novel finding is that these two species are suggested to share a more recent common ancestor with the two species in the genera *Corvinella* and *Urolestes* than to any other *Lanius* species. This result is at odds with Panov (2011), who explicitly argued that *Corvinella* (including *Urolestes*) is not part of *Lanius,* and who also supported dividing the two species into separate genera.

In summary, despite that the relative positions of the primary lineages were not supported in our analyses, our phylogenetic hypothesis differs in many respects from the relationships proposed by Harris and Franklin (2000) based on vocalizations (songs and alarm calls), or those proposed by Panov (2011) based on zoogeographical, morphological and behavioural data. Apparently, all of the traits analysed by earlier authors are highly homoplastic, with many cases of parallel evolution as well as cases of strongly divergent morphological differentiation (notably *Corvinella* and *Urolestes*).

Biogeography, diversification and the evolution of migratory behaviour

Reconstructing the higher-level biogeography of the Laniidae is complicated by two primary parameters: 1) the long time (about 13–15 million years) between the divergence of Laniidae from its sister-group and the first diversification within 'the core Laniidae', implying that even if the exact extant sister group of the Laniidae was known, the geographic origin of the stem group may not be the same as that of the most recent common ancestor , e.g. if now extinct lineages, branching off from the lineage leading to the 'core Laniidae', occupied areas no longer inhabited; and 2) the large polytomy at the base of the Laniidae. Hence, our biogeographic reconstructions are mostly restricted to the 'core Laniidae'.

The oldest fossil evidence of the genus *Lanius* is *Lanius capeki,* dated to Mammal Neogene 13 (7.2–6.8 mya) from Polgárdi, Hungary (Kessler 2013). A more controversial fossil named *Lanius miocaenus* (Milne-Edwards, 1871) was found in Aquitanian (23.0–20.4 mya) deposits in Langy, central France. Even if this fossil cannot with certainty be determined to belong to Laniidae, it seems less likely to be related to any other extant family. A possibility that it has a common ancestor with Laniidae somewhere along the long branch following the split from other Corvoidea cannot be dismissed. If so, a 'proto *Lanius*' lineage may have existed in the south-western Palearctic very early on, possibly adding support to a Mediterranean-centered ancestral area of Laniidae *sensu stricto*.

Our analyses suggest that the 'core Laniidae' diversified into six primary lineages (clades A, B, C, D-*Corvinella-Urolestes*, E and *L. nubicus*) about 7.2–9.1 mya, at the same time as some other predatory bird lineages adapted to open habitats and feeding on insects and small mammals (falcons *Falco* spp., Fuchs *et al*. 2015; harriers *Circus* spp., Oatley *et al*. 2016). The biogeographic reconstruction of the deepest node is ambiguous, suggesting that the core Laniidae likely originated in either the Afrotropics or the Western Palearctic, or both. The mixed signal for the origin of the most recent common ancestor (MRCA) of Laniidae in the biogeographic analysis may reflect that the large desert area, currently uninhabited by shrikes, is imposing a very broad separation between the Mediterranean and Afrotropical regions. It is possible that this uncertainty in choice between these two very different regions is a false dichotomy caused by the geographic location of the ancestral habitat of the MRCA being incompatible with current bioregions. It has been suggested that around the time the clade began to diversify, before the onset of increasing aridification (Zhang *et al*., 2014), northern Africa was dominated by steppe-like habitats. Hypothetically, the ancestor of Laniidae may at that time have occupied a cohesive suitable habitat covering southern parts of the current Western Palearctic and northern parts of the current Afrotropical region. Different conditions within this hypothesized

ancestral area may have initiated the radiation in the clade, later enhanced by the barrier formed by the expanding desert separating both the ancestral species and its habitat into a northern entity in the current Western Palearctic, and a southern entity in the current Afrotropical region. Two (*L. nubicus, L. minor*/*L. senator*) out of the six primary lineages presently breed in the Mediterranean area, and winter south of the Sahara.

The speciation patterns in sub-Saharan Africa have received greater attention over the last decade with often very congruent patterns regarding divergence across the arid and semi-arid zones of Africa. A common pattern is that of two primary genetic lineages, of which one is restricted to the northern savannah (Ethiopia to Senegal) and the other to the eastern/southern savannah (Somalia/Tanzania to South Africa), possibly meeting in Kenya (e.g. *Dicrurus* sp: Fuchs *et al.* 2017, 2018; *Emberiza gosling*/*E. tahapisi;* Olsson *et al.* 2013), a pattern found here for *U. melanoleucus*/*C. corvina*. This pattern is also shared with several lineages of mammals (Hartebeest, Flagstad *et al.* 2001, Warthog, Muwanika *et al.* 2003; Spotted Hyena, Rohland *et al.* 2005; Bushbuck, Moodley and Bruford 2007; Grant's Gazelle, Lorenzen *et al.* 2008, Lorenzen *et al.* 2012, lion, Bertola *et al.* 2016) and also corresponds to a transition zone among major floristic regions (Droissard *et al.* 2018). One exception involves *L. collaris* where the subspecies restricted to the Zambezian bioregion sensu Linder *et al.* (2012) is closer to taxa from the northern savannah than to the southern subspecies (Fuchs *et al.* 2011). No other clade in the Afrotropics analysed to date displays the pattern.

The predominantly Asian clade (C) is a mixture of rather different species, morphologically united by the presence of phaeomelanine in the plumage of all species. Several species are long distance migrants and one species (*L. tigrinus*) is more forest adapted than the others. The clade is divided into four geographically significant subclades, the single lineage *L. tigrinus* in the far east, the *L. collurio*/*isabellinus* clade, which is distributed mainly west and north of the Qinghai-Tibetan plateau, the *L. collurioides*/*vittatus* clade, which is distributed mainly south of the Qinghai-Tibetan plateau, and a clade containing *L. schach* and its nearest relatives, which is mainly distributed east of the Qinghai-Tibetan plateau. *L. tigrinus* emanates from the deepest node, which was reconstructed as non-migratory, and appears to have originated by direct dispersal from Africa. It presently has one of the more easterly distributions in the clade and is both a forest dweller and a long distance migrant. The latter characteristic is inferred to have evolved independently, as the ancestors at almost all nodes in the clade are inferred to having been non-migratory. The exception is the ancestor of *L. collurio* and *L. isabellinus,* which was inferred to have been a long distance migrant, although there is a very mixed signal regarding its geographic origin. This subclade also differs from the rest of clade C by migrating

in a south-westerly direction, some as far as to South Africa. The *L. collurioides/vittatus* clade, on the other hand, is non-migratory and is inferred to have originated from an ancestor in the Oriental region, where the extant species still live. The *L. schach* clade is inferred to have originated from the same ancestor, with its sister lineages then gradually having radiated toward the north and east. The Philippine endemic *Lanius validirostris* is nested in this clade of otherwise migratory species and was inferred to be sister to *L. bucephalus*, which breeds in the Eastern Palearctic and winters in southeast China, suggesting that *L. validirostris* might be the result of a migratory population from the *L. bucephalus*/*L. validirostris* common ancestor that lost its migratory habit and settled in the Philippines. The ancestral state reconstruction analyses suggested that the common ancestor of *L. bucephalus*/*L. validirostris* was sedentary. This particular result might be doubtful because at the time the two species diverged, the Philippines were isolated from any continental landmasses (see Brown *et al.* 2013 for a review), and any colonization must have been by long distance colonization. Furthermore, the two species closest to *L. bucephalus*/*L. validirostris* are both migratory. Hence, it seems reasonable to consider that the common ancestor of *L. bucephalus*/*L. validirostris* may have been long distant migrant. Such a close relationship between migratory species breeding in the easternmost parts of the Palearctic and year-round endemics in the Philippines has also been documented in the *Otus scops* Owls (Miranda *et al.* 2011), *Horornis* bush warblers (Alström *et al.* 2011) and *Phylloscopus* leaf warblers (Alström *et al.* 2018), suggesting that a component of the avian endemism in the Philippines result from migratory species from the Eastern Palearctic becoming resident (Miranda *et al.* 2011). Moreover, there are multiple similar examples of evolution of sedentary forms from migratory ancestors followed by speciation (Voelker *et al.* 2013; Rolland *et al.* 2014; Winger *et al.* 2014, Alström *et al.* 2015), and there are several present-day examples of northern migratory birds establishing breeding populations along migration routes or in winter quarters (e.g. Hockey *et al.* 2005, Billerman *et al.* 2011).

Gregarious behaviour and cooperative breeding

Gregarious behaviour has been reported in *Corvinella, Urolestes,* and two species in *Lanius* (Lefranc and Norfolk 1997, Harris and Franklin 2000); among these four species, cooperative breeding has been confirmed in three (Lefranc and Norfolk 1997, Harris and Franklin 2000), with the breeding system of *L. cabanisi* being currently unknown. Cooperative breeding in birds is usually defined as breeding systems where nests are attended by more than two birds (Cockburn 2006). Often the extra helpers are recruited among grown offspring that delay dispersal and help their parents to raise subsequent broods (Brown 1987, Ligon and Stacey 1991, Ligon and Burt 2004), but there are also

more complex systems and a generalised predictive framework is still lacking (Cockburn 1998, Hatchwell and Komdeur 2000). Selander (1964) proposed that offspring, when opportunities for dispersal and independent breeding are limited, may remain as helpers on their natal territory. This hypothesis was refined by Emlen (1982) into the generalized ecological constraints hypothesis, and by Koenig *et al*. (1992) into the delayed dispersal threshold model. Both of these suggest that individuals will stay as helpers if the benefits of remaining and delaying their own reproduction are outweighed by the costs of dispersing and breeding independently, hence differing mainly in whether placing the emphasis on the costs of leaving or on the benefits of staying (Koenig *et al.* 1992, Mumme 1992, Emlen 1994, 1997).

Our results indicate that both gregarious behaviour and cooperative breeding may have evolved in the most recent common ancestor of clade D-*Urolestes-Corvinella* (Fig. 4). Our study places *L. cabanisi,* for which the breeding system is uncertain, as sister to *L. excubitoroides*. Whether cooperative breeding evolved in the most recent common ancestor of clade D-*Urolestes-Corvinella* and was lost or suppressed in *L. cabanisi*, or evolved twice independently are equally parsimonious, and cannot be answered by this study but we predict the *L. cabanisi* is likely, even occasionally a cooperative breeder. *L. cabanisi* and *L. excubitoroides* seem to provide an excellent system in which to compare differences in ecology and life histories that may further our understanding of factors favoring cooperative breeding. Komdeur *et al*. (2008) pointed out that if the benefits of cooperation are dependent on help being directed towards kin, for fitness gains to be maximized, some mechanism of kin recognition may be required. All species from the clade D-*Urolestes-Corvinella* lineage practice rallying behaviour, which may thus play an important role in the evolution of cooperative breeding in this group.

Ecological and life history differences have been studied between *L. excubitoroides* and the non-cooperative *L. humeralis*, revealing that territories were more stable and population turnover lower in *L. excubitoroides* than in *L. humeralis* (Zack and Ligon, 1985a). *Lanius excubitoroides* also occupied a richer woodland habitat than *L. humeralis*, all hypothesized to be factors favouring group living (Zack and Ligon, 1985b). Group size in *L. excubitoroides* seems to correlate to the richness of the habitat, but may also be dependent on competition, e.g. with *L. humeralis*.

Cooperation seems to be facultative in *L. excubitoroides*, and western and eastern populations may offer an opportunity for observational and experimental tests to study intraspecific differences influencing the degree of cooperative breeding. In the east, *L. excubitoroides* occupies areas of higher amount of vegetation cover; in the west it occurs further to the north, where amount of vegetation cover is generally lower. Furthermore, western populations tend to be dispersing during the wet season,

whereas eastern ones are sedentary. Thus, although this has to our knowledge not been studied, western populations may be hypothesized to be less prone to cooperative breeding, and there may exist areas with only a low degree of seasonal dispersal where factors influencing cooperative breeding may be more easily elucidated. Differences in less prominent life history traits between eastern and western populations, such as adult survival, degree of delayed maturity, reproductive rates, clutch size, and dispersal rates may thus shed light on the relative importance of factors impacting cooperative breeding, and whether the costs of leaving or the benefits of staying are most important in favoring offspring to stay as helpers (Koenig *et al.* 1992; Mumme 1992; Emlen 1994, 1997).

Conclusions

The genus *Eurocephalus* is not closely related to the 'core Laniidae' and should be removed from the family Laniidae. More focused studies are needed to determine whether *Eurocephalus* should be included in any currently recognized family or, as suggested by current evidence, be placed in a family of their own. The two species currently in the genera *Urolestes* and *Corvinella* are part of 'core Laniidae', and we propose that they are included in the genus *Lanius.* The family Laniidae thus becomes monogeneric, with *Lanius* the only included genus. The redefined Laniidae probably originated in Africa, from which at least two dispersal events lead to the colonisation of the Holarctic and Oriental regions. Cooperative breeding is restricted to a single clade in the redefined Laniidae, which should offer excellent opportunities to study the evolution of cooperative breeding in this group.

Acknowledgments

References

Alström P, Barnes KN, Olsson U, Barker FK, Bloomer P, Khan AA, Qureshi MA, Gillaumet A, Crochet PA, Ryan PG, 2013. Multilocus phylogeny of the avian family Alaudidae (larks) reveals complex morphological evolution, non-monophyletic genera and hidden species diversity. *Molecular Phylogenetics Evolution* 69: 1043-1056.

Alström P, Höhna S, Gelang M, Ericson PGP, Olsson U, 2011. Non-monophyly and intricate morphological evolution within the avian family Cettiidae revealed by multilocus analysis of a taxonomically densely sampled dataset. *BMC Evolutionary Biology* 11: 352.

Alström P, Jønsson K, Fjeldså J, Ödeen A, Ericson PGP, Irestedt M, 2015. Dramatic niche shifts and morphological change in two insular bird species. *Royal Society Open Science* 2: 140364.

Alström P, Rheindt FE, Zhang R, Zhao M, Wang J, Zhu X, Gwee CY, Hao Y, Ohlson J, Jia C, Prawiradilaga DM, Ericson PGP, Lei F, Olsson U, 2018. Complete species-level phylogeny of the leaf warbler (Aves: Phylloscopidae) radiation. *Molecular Phylogenetics and Evolution* 126: 141–152

Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J, 2004. Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences, USA* 101: 11040–11045.

Becker JJ, 1987. Neogene Avian Localities of North America. Smithsonian Institution Press, Washington, DC.

Bertola LD, Jongloed H, van der Gaag KJ, de Knifjj P, Yamagushi N, Hooghimstra H, Bauer H, Henschel P, White PA, Driscoll CA, Tende T, Ottosson U, Saidu Y, Vrieling K, de Iongh HH, 2016. Phylogeographic patterns in Africa and high resolution delineation of genetic clades in the Lion (*Panthera leo*). *Scientific Reports* 6: 30807.

Boles WE, 1999. A songbird (Aves: Passeriformes: Oriolidae) from the Miocene of Riversleigh, northwestern Queensland, Australia. *Alcheringa* 23: 51-56.

Brodkorb P, 1972. Neogene fossil jays from the Great Plains. *Condor* 74: 347-349.

Brown JL, 1987. *Helping and Communal Breeding in Birds: Ecology and Evolution*. Princeton, NJ: Princeton Univ. Press

Brown RM, Siler Cd, Oliveros CH, Esselstyn JA, Diesmos AC, Hosner PA, Linkem CW, Barley AJ, Oaks JR, Sanguila MB, Welton LJ, Blackburn DC, Moyle RG, Peterson AT, Alcala AC, 2013. Evolutionary processes of diversification in a model island archipelago. *Annual Review of Ecology, Evolution, and Systematics* 44: 411–435.

Billerman SM, Huber GH, Winkler DW, Safran RJ, Lovette IJ, 2011 Population genetics of a recent transcontinental colonization of South America by breeding Barn Swallows (*Hirundo rustica*). *Auk* 128: 506–513.

Christidis L, Rheindt F, Boles WE, Norman JA, 2010. Plumage patterns are good indicators of taxonomic diversity, but not of phylogenetic affinities, in Australian grasswrens *Amytornis* (Aves: Maluridae). *Molecular Phylogenetics and Evolution* 57: 868-877.

Cockburn A, 1998. Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology, Evolution, and Systematics* 29: 141–177.

Cockburn A, 2006. Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society B: Biological Sciences* 273: 1375–1383.

del Hoyo J, Collar NJ, 2016. *HBW and BirdLife International Illustrated Checklist of the Birds of the World. Volume 2: Passerines*. Lynx Edicions, Barcelona.

Dickinson EC, Christidis L, 2014. *The Howard & Moore Complete Checklist of the Birds of the World, 4th Edition, Vol. 2*. Aves Press, Eastbourne, U.K.

Droissart V, Dauby G, Hardy OJ, Deblauwe V, Harris DJ, Janssens S, Mackinder BA, Blach-Overgaard A, Sonké B, Sosef MS, Stévart T, Svenning J-C, Wieringa JJ, Couvreur TLP, 2018. Beyond trees: Biogeographical regionalization of tropical Africa. *Journal of Biogeography* 45: 1153-1167.

Drummond AJ, Suchard MA, Xie D, Rambaut A, 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969-1973.

Edwards EJ, Osborne CP, Strömberg CAE, Smith SA. C4 Grasses Consortium, 2010. The origins of C4 grasslands: Integrating evolutionary and ecosystem science. *Science* 328: 587-591.

Emlen ST, 1982. The evolution of helping. I: an ecological constraints model. *American Naturalist*

119:29–39.

Emlen ST, 1994. Benefits, constraints and the evolution of the family. *Trends in Ecology and Evolution* 9: 282–285.

Emlen ST,1997. *Predicting family dynamics in social vertebrates.* In *Behavioural Ecology: an Evolutionary Approach,* ed. JR Krebs, NB Davies, pp. 228–53. Oxford, UK: Blackwell Sci. 4th ed.

Flagstad Ø, Syvertsen PO, Stenseth NC, Jakobsen KS 2001. Environmental changes and rates of evolution: the phylogeographic pattern within the hartebeest complex as related to climatic variation. *Proceedings of the Royal Society B: Biological Sciences* 268, 667-677.

Fregin S, Haase M, Olsson U, Alström P, 2012. New insights into family relationships within the avian superfamily Sylvioidea (Passeriformes) based on seven molecular markers. *BMC Evolutionary Biology* 12, 157.

Fuchs J, Bowie RCK, Fjeldså J, Pasquet E, 2004. Phylogenetic relationships of the African bush-shrikes and helmet-shrikes (Passeriformes: Malaconotidae). *Molecular Phylogenetics and Evolution* 33: 428-439.

Fuchs J, Crowe TM, Bowie RCK, 2011. Phylogeography of the Fiscal Shrike (*Lanius collaris*): a novel pattern of genetic structure across the arid zones and savannas of Africa. *Journal of Biogeography* 38: 2210-2222.

Fuchs J, De Swardt DH, Oatley G, Fjeldså J, Bowie RCK, 2018. Habitat driven diversification, hybridization and cryptic diversity in the Fork-tailed Drongo (Passeriformes: Dicruridae: *Dicrurus adsimilis*). *Zoologica Scripta* 47: 266-284.

Fuchs J, Irestedt M, Fjeldså J, Couloux A, Pasquet E, Bowie RC, 2012. Molecular phylogeny of African bush-shrikes and allies: tracing the biogeographic history of an explosive radiation of corvoid birds. *Molecular Phylogenetics and Evolution* 64: 93–105.

Fuchs J, Fjeldså J, Bowie RCK, 2017. Diversification across major biogeographic breaks in the African Shining/Square-tailed Drongos complex (Passeriformes: Dicruridae). *Zoologica Scripta* 46: 27-41.

Fuchs J, Fjeldså J, Pasquet E, 2006. An ancient African radiation of corvoid birds (Aves :

Passeriformes) detected by mitochondrial and nuclear sequence data. *Zoologica Scripta* 35: 375-385.

Fuchs J, Johnson JA, Mindell DP, 2015. Rapid diversification of falcons (Aves : Falconidae) due to expansion of open habitats in the Late Miocene. *Molecular Phylogenetics and Evolution* 82: 166–182.

Gill F, Donsker D (Eds), 2017. IOC World Bird List (v 6.3).

Hall BP, Moreau RE, 1970. An *atlas of speciation in African passerine birds*. London, Trustees Brit. Mus. (Nat. Hist.).

Harris RB, Alström P, Ödeen A, Leache AD, 2018. Discordance between genomic divergence and phenotypic variation in a rapidly evolving avian genus (*Motacilla*). *Molecular Phylogenetics and Evolution* 120: 183–195.

Harris T, Franklin K, 2000. *Shrikes and Bush-shrikes: Including wood-shrikes, helmet-shrikes, flycatcher-shrikes, philentomas, batises and wattle-eyes*. Helm Editions, London.

Hassanin A, Delsuc F, Ropiquet A, Hammer C, Jansen van Vuuren B, Matthee C, Ruiz-Garcia M, Catzeflis F, Areskoug V, Nguyen TT, Couloux A, 2012. Pattern and timing of diversification of Cetartiodactyla (Mammalia, Laurasiatheria), as revealed by a comprehensive analysis of mitochondrial genomes. *Comptes Rendus Biologies* 335: 32-50.

Hatchwell BJ, Komdeur J, 2000. Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour* 59: 1079–1086.

Heled J, Drummond AJ, 2010. Bayesian inference of species trees from multilocus data. *Molecular Biology and Evolution* 27: 570-580.

Hockey PAR, Dean WRJ, Ryan PG. (eds) 2005 *Roberts birds of southern Africa,* 7th edn. Cape Town, South Africa: The Trustees of the John Voelcker Bird Book Fund.

Jønsson KA_Fabre, P-H F, Kennedy JD, Holt BG, Borregaard MK, Rahbek C, Fjeldså J, 2016. A supermatrix phylogeny of corvoid passerine birds (Aves: Corvides). *Molecular Phylogenetics and Evolution* 94: 87-94.

Jønsson KA, Fabre, P-H F, Fritz S, Etieenne RS, Ricklefs RE, Jørgensen TB, Fjeldså J, Rahbek C,

Ericson PGP, Woog F, Pasquet E, Irestedt M, 2012. Ecological and evolutionary determinants for the adaptive radiation of the Madagascan vangas. *Proceedings of the National Academy of Science of the United States of America* 109: 6620-6625.

Kessler E, 2013. Neogene songbirds (Aves, Passeriformes) from Hungary. *Hantkeniana* 8, 37-149,

Koenig WD, Pitelka FA, Carmen WJ, Mumme RL, Stanback MT, 1992. The evolution of delayed dispersal in cooperative breeders. *The Quarterly Review of Biology* 67:111–50.

Komdeur J, Richardson DS, Hatchwell B, 2008. *Kin-Recognition Mechanisms in Cooperative Breeding Systems: Ecological Causes and Behavioral Consequences of Variation.* In *Ecology of Social Evolution* (eds, Korb, J. Heinze, J. pp 175-193). Springer.

Lefranc N, Norfolk T, 1997. *Shrikes. A guide to the shrikes of the world*. Helm Editions, London.

Lerner HRL, Meyer M, James HF, Hofreiter M, Fleischer RC, 2011. Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian Honeycreepers. *Current Biology* 21: 1838-1844.

Ligon JD, Burt DB, 2004. *Evolutionary origins.* In *Cooperative breeding in birds* (eds, Koenig W. D.& Dickinson J. L.), pp. 5–34. Cambridge, UK: Cambridge University Press.

Ligon JD, Stacey PB, 1991. The origin and maintenance of helping in birds. *American Naturalist* 138: 254–258.

Linder HP, de Klerk HM, Born J, Burgess ND, Fjeldså J, Rahbek C, 2012. The partitioning of Africa: statistically defined biogeographical regions in sub-Saharan Africa. *Journal of Biogeography* 39: 1189-1205

Lorenzen ED, Arctander P, Siegismund HR, 2008, Three reciprocally monophyletic mtDNA lineages elucidate the taxonomic status of Grant's gazelles. *Conservation Genetics* 9: 593-601.

Lorenzen ED, Heller R, Siegismund HR, 2012. Comparative phylogeography of African savannah ungulates. *Molecular Ecology* 21: 3656-3670.

Matzke NJ, 2014. Model selection in historical biogeography reveals that founder-event speciation is a

crucial process in island clades. *Systematic Biology* 63: 951-970.

Mayr 1943. What genera belong to the family Prionopidae? *Ibis* 85: 216-218.

Mayr E, Greenway J C. 1960. *Check-list of the birds of the world*. Cambridge: Museum Comparative. Zoology 6: 309–364.

McCarthy EM, 2006. *Handbook of avian hybrids of the world*. Oxford University Press, Oxford

Miller MA, Pfeiffer W, Schwartz T., 2010. C*reating the CIPRES Science Gateway for inference of large phylogenetic trees*. Proceedings of the Gateway Computing Environments Workshop (GCE), (pp 1–8). LA, New Orleans.

Milne I, Lindner D, Bayer M, Husmeier D, McGuire G, Marshall DF, Wright F, 2009. *TOPALi* v2: a rich graphical interface for evolutionary analyses of multiple alignments on HPC clusters and multi-core desktops. *Bioinformatics* 25: 126-127.

Miranda Jr HC, Brooks DM, Kennedy RS, 2011. Phylogeny and taxonomic review of Philippine lowland scops-owls (Strigiformes): parallel diversification of highland and lowland clades. *The Wilson Journal of Ornithology* 123: 441-453.

Moodley Y, Bruford MW, 2007. Molecular biogeography: Towards an integrated framework for conserving Pan-African biodiversity. *PLoS One* 2, e454.

Moyle RG, Cracraft J, Lakim M, Nais J, Sheldon FH, 2006. Reconsideration of the phylogenetic relationships of the enigmatic Bornean Bristlehead (*Pityriasis gymnocephala). Molecular Phylogenetics and Evolution* 39: 893-898.

Moyle RG, Oliveros CH, Andersen MJ, Hosner PA, Benz BW, Manthey JD, Travers SL, Brown RM, Faircloth BC, 2016. Tectonic collision and uplift of Wallacea triggered the global songbird radiation. *Nature Communications* 7: 12709.

Mumme RL, 1992. Do helpers increase reproductive success—an experimental analysis in the Florida scrub jay. *Behavioral Ecology and Sociobiology* 31: 319–328.

Muwanika VB, Nyakaana S, Siegismund HR, Arctander P, 2003. Phylogeography and population

structure of the common warthog (*Phacochoerus africanus*) inferred from variation in mitochondrial DNA sequences and microsatellite loci. *Heredity* 91: 361-372.

Nguyen JMT, Worthy TH, Boles WE, Hand SJ, Archer M, 2013. A new cracticid (Passeriformes: Cracticidae) from the Early Miocene of Australia. *Emu* 113: 374-382

Oatley G. Simmons RE, Fuchs J, 2015. A molecular phylogeny of the harriers (Circus, Accipitridae) indicate the role of long distance dispersal and migration in diversification. *Molecular Phylogenetics and Evolution* 85: 150–160.

Olsson U, Alström P, Svensson L, Aliabadian M, Sundberg P, 2010. The *Lanius excubitor* (Aves, Passeriformes) conundrum – Taxonomic dilemma when molecular and non-molecular data tell different stories. *Molecular Phylogenetics and Evolution* 55: 347-57.

Olsson U, Yosef R, Alström P, Collinson M, 2013. Assessment of species limits in African 'brown buntings' (*Emberiza*, Passeriformes) based on mitochondrial and nuclear sequence data. *Ibis* 155: 534-543.

Osborne CP, Beerling DJ, 2006. Nature's green revolution: the remarkable evolutionary rise of C4 plants. *Philosophical Transactions of the Royal Society B: Biological Sciences* 361: 173–194.

Panov EN 1995. Superspecies of shrikes in the Former USSR. *Proceedings of the Western. Foundation of Vertebrate Zoology* 6: 26-33.

Panov EN, 2011. The True Shrikes (Laniidae) of the World: Ecology, Behavior and Evolution. Pensoft, Sofia and Moscow.

Paradis E, Claude J, Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289-290.

Peters JL, 1960. *Check-List of Birds of the World A continuation of the work of James L. Peters Volume IX*. G. J. C. J. Mayr E., Cambridge, Massachusetts.

Pybus OG, Harvey PH, 2000. Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society B* 267: 2267-2272.

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available via http://www.R-project.org/

Rabosky DL, 2006a. Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* 60: 1152-1164.

Rabosky DL, 2006b. LASER: a maximum likelihood toolkit for detecting temporal shifts in diversification rates from molecular phylogenies. *Evolutionary Bioinformatics Online* 2:257-260.

Rabosky DL, 2014. Automatic detection of key innovations, rate shifts, and diversity-dependence on phylogenetic trees. *PLoS ONE* 9: e89543.

Rabosky DL, Grundler MC, Anderson CJ, Title PO, Shi JJ, Brown JW, Huang H, Larson JG. 2014. BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. Methods in Ecology and Evolution 5: 701-707.

Raikow RJ, Polumbo PJ, Borecky SR, 1980. Appendicular myology and relationships of the shrikes. *Annals of the Carnegie Museum of Natural History* 49: 131-152.

Rambaut A, Suchard MA, Xie D, & Drummond AJ, 2014. Tracer v1.7, Available from http://beast.bio.ed.ac.uk/Tracer

Rand AL, 1959. Tarsal scutellation of song birds as a taxonomic character. *Wilson Bulletin* 71: 274-277.

Reddy S, Driskell A, Rabosky DL, Hackett SJ, Schulenberg TS, 2012. Diversification and the adaptive radiation of the vangas of Madagascar. *Proceedings of the Royal Society of London B: Biological Sciences* 279: 2062-2071.

Ree RH, Moore BR, Webb CO, Donoghue MJ. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* 59: 2299-2311

Ree RH, Sanmartín I, 2018. Conceptual and statistical problems with the DEC+J model of founder event speciation and its comparison with DEC via model selection. *Journal of Biogeography* 45:741-749.

Ree RH, Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57: 4-14.

Revell LJ, 2012. *phytools*: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 3: 217-223.

Rohland N, Pollack JL, Nagel D, Beauval C, Airvaux J, Pääbo S,Hofreiter M, 2005. The population history of extant and extinct hyenas. *Molecular Biology and Evolution* 22: 2435-2443.

Rolland J, Jiguet F, Jønsson KA, Condamine FL,Morlon H, 2014. Settling down of seasonal migrants promotes bird diversification. *Proceedings of the Royal Society B: Biological Sciences* 281: 20140473.

Ronquist F, Teslenko M, van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP, 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539-542.

Selander RK, 1964. Speciation in wrens of the genus *Campylorhychus*. *University of California Publications in Zoology* 74: 1–224.

Sibley CG, Ahlquist JE, 1990. *Phylogeny and Classification of Birds: A study in Molecular Evolution*. Yale University Press, New Haven, Connecticut.

Stamatakis A, 2006. RAxML-VI-HPC: Maximum Likelihood-based phylogenetic analyses with thousands of Taxa and mixed models. *Bioinformatics* 22: 2688-2690.

Stamatakis A, Hoover P, Rougemont J, 2008. A Rapid bootstrap algorithm for the RAxML Web-Servers. *Systematic Biology* 75: 758-771.

Shultz A.J., Burns K.J., 2013. Plumage evolution in relation to light environment in a novel clade of Neotropical tanagers. *Molecular Phylogenetics and Evolution* 66: 112-125.

Stresemann E, 1927. Die Wanderungen der Rotschwanz-Wiirger (Formenkreis *Lanius cristatus*). *Journal für Ornithologie* 75: 68-87.

Strömberg CAE, 2011. Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences* 39: 517-544

Yosef R, International Shrike Working Group, 2008. Family Laniidae. In J. Del Hoyo. A. Elliott, D.A. Christie (Eds) Handbook of the Birds of the World. Vol. 13 Penduline tits to Shrikes (pp. 732-796). Lynx Edicions, Barcelona.

Yu Y, Harris AJ, Blair C, He X, 2015. RASP (Reconstruct Ancestral State in Phylogenies): a tool for historical biogeography. *Molecular Phylogenetics and Evolution* 87: 46-49.

Voelker G, Bowie RC, Klicka J, 2013. Gene trees, species trees and Earth history combine to shed light on the evolution of migration in a model avian system. *Molecular Ecology* 22: 3333–3344.

Winger BM, Barker FK, Ree RH, 2014. Temperate origins of long-distance seasonal migration in New World songbirds. *Proceedings of the National Academy of Sciences* 111: 12115–12120.

Wolters HE, 1975–1982. *Die Vogelarten der Erde*. Paul Parey, Hamburg and Berlin.

Zack S, Ligon JD, 1985a. Cooperative breeding in Lanius shrikes. I. Habitat and demography of two sympatric species. *The Auk* 102: 754-765

Zack S, Ligon JD, 1985b. Cooperative breeding in Lanius shrikes. II. Habitat and demography of two sympatric species. *The Auk* 102: 766-773

Zhang Z, Ramstein G, Schuster M, Li C, Contoux C, Yan Q, 2014. Aridification of the Sahara desert caused by Tethys Sea shrinkage during the Late Miocene. *Nature* 513: 401-404.

Zhang W, Lei F-M, Liang G, Yin Z-H, Zhao H-F, Wang H-J, Krištín A. 2007. Taxonomic status of eight Asian shrike species (*Lanius*): phylogenetic analysis based on Cyt *b* and CoI gene sequences. *Acta Ornithologica* 42: 173–180.

Zhen Y, Harrigan RJ, Ruegg KC, Anderson EC, Ng TC, Lao S, Lohmueller KE, Smith TB, 2017. Genomic divergence across ecological gradients in the Central African rainforest songbird (*Andropadus virens*). *Molecular Ecology* 26: 4966–4977.

Figure 1. Relationships among *Lanius* species according to Panov (A, op cit. in Harris and Franklin 2000), based on morphology and B) Harris and Franklin (2000) based on communication characters.

Figure 2. A) Majority Clade Credibility tree results from the partitioned Bayesian analyses of the concatenated data set (cytochrome b, MB, ODC) using BEAST v1.8.0 and calibrated using three fossils. Numbers close to the nodes refer to maximum likelihood bootstrap support/concatenated BEAST posterior probabilities/species tree probabilities. Values are indicated when at least one the three values were ≥70%, ≥0.95 and ≥0.95, respectively. B) Topology of the 'core Laniidae'.

Figure 3. Results of the biogeographic analyses using the DEC model in RASP v4 (Yu et al. 2015). Pie charts next to the nodes represent the probability of each ancestral area. Ancestral area codes are: A, Ethiopian; B, Western Palearctic; C, Eastern Palearctic; D, Oriental (including Australasia); E, Nearctic. A) Reconstructions on the MCC tree using fossils as calibration; B) reconstructions on the MCC tree using substitution rates as a calibration. The map shows the boundaries of the bioregions used for the biogeographic analyses (note that only bioregions where Laniidae occurs are coded).

Figure 4. Character evolution for A) social and B) migratory behaviours. Reconstructions were performed using stochastic mapping, as implemented in PHYTOOLS (Revell 2012). The reconstruction represents one random simulation (out of 100). The tree shown is the MCC tree calibrated with three fossils with only the members of the 'core Laniidae' included. Analyses were performed on the MCC tree with only the members of the 'core Laniidae' included. Pie charts at nodes represent the maximum likelihood probability of the ancestral state reconstructed using *ace* (Paradis et al. 2004).

Figure 5. A) Lineage specific diversification rates dynamics of the 'core Laniidae' through time. The BAMM (Rabosky 2014) and BAMMTOOLS (Rabosky et al. 2014) analyses were run under the '*speciationextinction*' model, assuming a sampling probability of 1 (since we sampled all recognized species) and defaults priors. The tree shown is the MCC tree calibrated with three fossils with only the members of the 'core Laniidae' included and *L. c. marwitzi* not recognized as a species. B) Diversification rates through time plot.

Figure S1. 50% majority consensus tree resulting from Bayesian analyses of cytochrome *b*. Numbers close to the nodes refer to maximum likelihood bootstrap support and Bayesian posterior probabilities when ≥70% and ≥0.95, respectively. Values are indicated when at least one the two values was ≥70% or ≥0.95, respectively.

Figure S2. 50% majority consensus tree resulting from Bayesian analyses of Myoglobin intron 2. Numbers close to the nodes refer to maximum likelihood bootstrap support and Bayesian posterior probabilities when ≥70% and ≥0.95, respectively. Values are indicated when at least one the two values was ≥70% or ≥0.95, respectively.

Figure S3. 50% majority consensus tree resulting from Bayesian analyses of the ODC exon 6 to 8 gene region, including introns. Numbers close to the nodes refer to maximum likelihood bootstrap support and Bayesian posterior probabilities when ≥70% and ≥0.95, respectively. Values are indicated when at least one the two values was ≥70% or ≥0.95, respectively.

Figure S4. Species tree topology obtained using the algorithm implemented in *BEAST. Bayesian posterior probabilities when ≥0.95, respectively. The tree was calibrated with the substitution rates from Lerner et al. (2011).

Table 1. Divergence times (in million years ago) for the 'core Laniidae' primary lineages. Divergence times were obtained using either calibrations based on substitution rates from Lerner *et al.* (2011) or fossil data. Numbers between brackets represents the 95% Highest Posterior Density.

Divergence	Fossils	Substitution rates
'core Laniidae'/Sister-group	20.6 (18.0-23.2)	26.6 (22.1-31.4)
'core Laniidae'	7.2 (6.1-8.5)	9.1 (7.5-11.0)
clade A	4.6 (3.6-5.8)	5.9 (4.4-7.4)
clade B	4.4 (3.5-5.4)	5.8 (4.3-6.9)
clade D/*Corvinella-Urolestes*	5.9 (4.6-7.2)	7.5 (5.8-9.4)
clade C	4.9 (3.9-6.0)	6.1 (4.8-7.5)
clade E	3.9 (2.6-5.1)	5.0 (3.4-6.7)

Supplementary Table 1. **Genetic samples and sequences.** Taxonomy follows Dickinson and Christidis (2014). Samples from mistnetted birds are identified with ring number or our database ID (DZUG = Department of Biology and Environmental Science, University of Gothenburg); museum samples with catalogue number and institutional acronym, where AH = Andreas Helbig collection, Vogelwarte Hiddenzee; FMNH = Field Museum, Chicago; MNHN = Muséum National d'Histoire Naturelle, Paris; NHM = Natural History Museum at Tring (UK); NHMO = Natural History Museum, University of Oslo, Norway; NMBV = National Museum, Bloemfontein, South Africa; NRM = Natural History Museum, Stockholm; LSUMZ = Louisiana State University Museum of Natural Science; UWBM = University of Washington Burke Museum; and ZMUC = Zoological Museum, University of Copenhagen.

(XXXXXXX = sequences that will be deposited in GenBank when manuscript is accepted for publication)

Scientific name	Origin	Sample ID	GenBank accession numbers		
			cytb	*myo*	*ODC*
Aphelocoma coerulescens	[GenBank]	[GenBank]	U77335	AY395580	HQ123974
Artamus leucoryn[1]	[GenBank]	[GenBank]	JQ864485	FJ821079	JN614602
Batis diops	[GenBank]	[GenBank]	JQ239204	JQ744696	JQ744986
Campephaga flava	[GenBank]	[GenBank]	JN614872	EF052822	JQ744961
Chaetorhynchus papuensis	[GenBank]	[GenBank]	KP036754	EU726214	EU726224
Chlorophoneus sulfureopectus	Nigeria	DZUG 5370	XXXXXXX	AY529912	EU380413
Colluricincla harmonica	[GenBank]	[GenBank]	FJ821113	EU273396	EU273356
Colluricincla megarhyncha	[GenBank]	[GenBank]	FJ821114	FJ821081	EU273357
Coracina lineata	Numfor, Indonesia	DZUG 5364	XXXXXXX	XXXXXXX	XXXXXXX
Corcorax melanorhamphos	[GenBank]	[GenBank]	AY064274	AY064737	JN614621
Corvinella corvina	Ghana	LSUMZ 39260	XXXXXXX	XXXXXXX	XXXXXXX
Corvus corone orientalis	Uzbekistan	DZUG 726	HE805708	EU739909	XXXXXXX
Dicrurus aeneus	[GenBank]	[GenBank]	JQ864497	KX134188	KJ455775
Dicrurus macrocercus	[GenBank]	[GenBank]	GU253469	EF449733	GU253661
Dicrurus paradiseus	[GenBank]	[GenBank]	JQ864502	KX134189	KJ455778
Drepanornis albertisi	[GenBank]	[GenBank]	U15205	AY064735	EU380436
Dryoscopus gambensis	Nigeria	DZUG 5365	XXXXXXX	AY529918	XXXXXXX
Eurocephalus ruppelli	Kenya	ZMUC 135521	XXXXXXX	XXXXXXX	XXXXXXX
Garrulus glandarius	[GenBank]	[GenBank]	JN018413	KY492647	KJ455799
Gymnorhina tibicen	[GenBank]	[GenBank]	AF197867	AY064741	KC162665
Hylophilus ochraceiceps	[GenBank]	[GenBank]	FJ899419	EU272100	EU272109
Hypothymis azurea	[GenBank]	[GenBank]	AF096467	EF052768	EU726223
Lalage leucomela	[GenBank]	[GenBank]	FJ821124	FJ821088	EU380438
Lamprolia victoriae	[GenBank]	[GenBank]	KP036722	KP070395	EU726225
Laniarius erythrogaster	Nigeria	DZUG 5371	XXXXXXX	XXXXXXX	XXXXXXX
Lanius borealis	[GenBank]	[GenBank]	JQ239201	GU253676	–
Lanius bucephalus	Japan	DZUG 2958	XXXXXXX	XXXXXXX	XXXXXXX
Lanius c. collaris	South Africa	MNHN Uncat CV33927	XXXXXXX	EF635053	XXXXXXX
Lanius c. marwitzi	Tanzania	ZMUC 74.738	XXXXXXX	HQ996802	XXXXXXX
Lanius cabanisi	Tanzania	ZMUC 72.579	GU253470	XXXXXXX	XXXXXXX
Lanius collurio	Sweden	DZUG 5203	XXXXXXX	EF635052	XXXXXXX
Lanius collurioides	Myanmar	DZUG 5368	XXXXXXX	XXXXXXX	XXXXXXX
Lanius cristatus	China	DZUG 5372	XXXXXXX	XXXXXXX	XXXXXXX
Lanius dorsalis	Tanzania	ZMUC 74.741	GU253474	XXXXXXX	XXXXXXX

Lanius excubitor	Moscow, Russia	UWBM 57238	XXXXXXX	XXXXXXX	XXXXXXX
Lanius excubitoroides	Uganda	AH 1312	GU253548	XXXXXXX	GU253689
Lanius giganteus	[GenBank]	[GenBank]	JQ239201	–	–
Lanius gubernator	Nigeria	DZUG 2601	XXXXXXX	XXXXXXX	XXXXXXX
Lanius humeralis	Cameroon	MNHN Uncat 02-26	AF094614	HQ996754	FJ358081
Lanius isabellinus	Mongolia	DZUG 2235	XXXXXXX	XXXXXXX	XXXXXXX
Lanius ludovicianus	USA	JK96002	XXXXXXX	XXXXXXX	XXXXXXX
Lanius mackinnoni	Congo Kinshasa	ZMUC 128585	GU253558	XXXXXXX	GU253687
Lanius meridionalis	Spain	NRM 20076378	GU253529	XXXXXXX	GU253669
Lanius minor	[GenBank]	[GenBank]	GU253559	EF635054	GU253688
Lanius newtoni	Sao Tome	DZUG 102	XXXXXXX	XXXXXXX	XXXXXXX
Lanius nubicus	[GenBank]	[GenBank]	GU253560	EF635056	GU253690
Lanius phoenicuroides	Kazakhstan	DZUG 5375	XXXXXXX		
Lanius schach	Yunnan, China	SWFU01005	XXXXXXX	XXXXXXX	XXXXXXX
Lanius senator	Spain	DZUG 1451	XXXXXXX	XXXXXXX	XXXXXXX
Lanius somalicus	Kenya	NHM 1971.16.182	GU253562	XXXXXXX	GU253682
Lanius souzae	Malawi	FMNH 441063	XXXXXXX	HQ996805	XXXXXXX
Lanius sphenocercus	Primorsk, Russia	UWBM 75445	GU253564	XXXXXXX	GU253681
Lanius tephronotus	Tibet, China	NHMO-BI-7753	GU253566	XXXXXXX	XXXXXXX
Lanius tigrinus	Primorsk, Russia	UWBM 71869	XXXXXXX	XXXXXXX	XXXXXXX
Lanius validirostris	Philippines	ZMUC 116777	XXXXXXX	HQ996789	XXXXXXX
Lanius vittatus	India	DZUG 2342	XXXXXXX	XXXXXXX	XXXXXXX
Lophorina magnifica	[GenBank]	[GenBank]	AY228092	EU726219	EU726229
Manucodia ater	[GenBank]	[GenBank]	AY443250	EU726218	EU726228
Melampitta lugubris	[GenBank]	[GenBank]	AY443253	EU726213	EU726221
Menura novaehollandiae	[GenBank]	[GenBank]	AY542313	EU739986	JN614589
Monarcha cinerascens	Numfor, Indonesia	DZUG 122	XXXXXXX	XXXXXXX	XXXXXXX
Monarcha melanopsis	[GenBank]	[GenBank]	FJ821128	FJ821092	EU272114
Nucifraga caryocatactes	[GenBank]	[GenBank]	KJ456365	AY395590	JQ024107
Oriolus oriolus	[GenBank]	[GenBank]	JQ864511	AY228329	KF690789
Pachycephala olivacea	[GenBank]	[GenBank]	FJ821133	FJ821097	EU273365
Pachycephala pectoralis	[GenBank]	[GenBank]	FJ821134	EU273407	KF916463
Peltops blainvillii	[GenBank]	[GenBank]	FJ821135	KF690880	KF690808
Pericrocotus ethologus	Vietnam	DZUG 4426	XXXXXXX	EF052844	XXXXXXX
Pica pica	[GenBank]	[GenBank]	JQ393835	AY395592	JQ024108
Picathartes gymnocephalus	[GenBank]	[GenBank]	JN614899	EU740018	GU816900
Platylophus galericulatus	captive	ZMUC 139719	XXXXXXX	XXXXXXX	XXXXXXX
Prionops scopifrons	Kenya	ZMUC 117529	XXXXXXX	AY529932	JQ744960
Ptilorrhoa leucosticta	[GenBank]	[GenBank]	FJ821140	EF441261	EF441255
Pyrrhocorax pyrrhocorax	[GenBank]	[GenBank]	JQ864523	AY395595	KJ455909
Rhipidura albicollis	Thailand	DZUG 106	XXXXXXX	JN614746	JN614618
Sphecotheres vieilloti	[GenBank]	[GenBank]	JN614878	FJ821107	JN614606
Tchagra senegalus	Nigeria	DZUG 84	XXXXXXX	AY529937	XXXXXXX
Terpsiphone atrocaudata	Japan	DZUG 5369	XXXXXXX	XXXXXXX	XXXXXXX
Turdus pilaris	[GenBank]	[GenBank]	EU154656	EU154767	EU154882
Urolestes melanoleucus	South Africa	NMBV06236	XXXXXXX	XXXXXXX	XXXXXXX
Vireo olivaceus	[GenBank]	[GenBank]	JQ239201	EU272101	EU272110

[1] This species is usually referred to as *Artamus leucorhynchus*, but original spelling *Artamus leucoryn* used by Dickinson and Christidis (2014)

A

- *Lanius tigrinus*
- *Lanius cristatus*
- *Lanius bucephalus*
- *Lanius phoenicuroides*
- *Lanius isabellinus*
- *Lanius gubernator*
- *Lanius collurio*
- *Lanius tephronotus*
- *Lanius schach*
- *Lanius vittatus*
- *Lanius collurioides*
- *Lanius minor*
- *Lanius senator*
- *Lanius souzae*
- *Lanius mackinnoni*
- *Lanius excubitoroides*
- *Lanius cabanisi*
- *Lanius collaris*
- *Lanius newtoni*
- *Lanius dorsalis*
- *Lanius somalicus*
- *Lanius sphenocercus*
- *Lanius excubitor*
- *Lanius ludovicianus*
- *Lanius meridionalis-lathora* group

B

- *Lanius phoenicuroides*
- *Lanius isabellinus*
- *Lanius collurio*
- *Lanius tigrinus*
- *Lanius bucephalus*
- *Lanius cristatus*
- *Lanius gubernator*
- *Lanius souzae*
- *Lanius schach*
- *Lanius validirostris*
- *Lanius tephronotus*
- *Lanius vittatus*
- *Lanius collurioides*
- *Lanius senator*
- *Lanius minor*
- *Lanius somalicus*
- *Lanius dorsalis*
- *Lanius mackinnoni*
- *Lanius cabanisi*
- *Lanius excubitoroides*
- *Lanius collaris*
- *Lanius humeralis*
- *Lanius nubicus*
- *Lanius newtoni*
- *Lanius pallidirostris*
- *Lanius meridionalis*
- *Lanius sphenocercus*
- *Lanius excubitor*
- *Lanius ludovicianus*

chatter
alarm

'keer'
alarm

A)

'core Laniidae'

Corvus corone
Nucifraga caryocatactes
Garrulus glandarius
Pica pica
Aphelocoma coerulescens
Pyrrhocorax pyrrhocorax
Eurocephalus ruppelli
Platylophus galericulatus
Hypothymis azurea
Terpsiphone atrocaudata
Monarcha cinerea
Monarcha melanopsis
Epimachus albertisi
Ptiloris magnificus
Manucodia atra
Dicrurus macrocercus
Dicrurus paradiseus
Dicrurus aeneus
Corcorax melanoramphos
Melampitta lugubris
Chaetorhynchus papuensis
Lamprolia victoriae
Rhipidura albicollis
Colluricincla harmonica
Colluricincla megarhyncha
Pachycephala olivacea
Pachycephala pectoralis
Oriolus oriolus
Sphecotheres vieilloti
Dryoscopus gambensis
Tchagra senegalus
Laniarius erythrogaster
Chlorophoneus sulfureopectus
Batis diops
Prionops scopifrons
Artamus leucorhynchus
Peltops blainvillii
Gymnorhina tibicen
Campephaga flava
Lalage leucomela
Coracina lineata
Pericrocotus ethologus
Hylophilus ochraceiceps
Vireo olivaceus
Ptilorrhoa leucosticta
Picathartes gymnocephalus
Turdus pilaris
Menura novaehollandiae

81/1/0.98
100/1/1
99/1/0.95
100/1/1
100/1/1
100/1/1
100/1/0.99
32/0.91/0.98
90/1/-
92/0.99/0.82
68/0.97/0.95
100/1/1
100/1/1
63/0.99/0.94
100/1/1
100/1/1
100/1/1
67/0.99/0.57
85/1/0.97
94/1/0.99
91/1/0.86
67/0.95/0.81
98/1/1
100/1/1
96/1/1
98/1/1
100/1/1
100/1/0.99
72/1/0.98
51/1/-
100/1/1

Eocene | Oligocene | Miocene | Plio-Pleist.
30 | 20 | 10 | 1 | 0 mya

B)

Lanius bucephalus
Lanius validirostris
Lanius tephronotus
Lanius cristatus
Lanius schach
Lanius collurio
Lanius phoenicuroides
Lanius isabellinus
Lanius collurioides
Lanius vittatus
Lanius tigrinus
Lanius c. collaris
Lanius c. marwitzi
Lanius souzae
Lanius humeralis
Lanius newtoni
Lanius gubernator
Lanius mackinnoni
Lanius minor
Lanius senator
Lanius meridionalis
Lanius borealis
Lanius sphenocercus
Lanius giganteus
Lanius ludovicianus
Lanius somalicus
Lanius excubitor
Lanius dorsalis
Corvinella corvina
Urolestes melanoleucus
Lanius cabanisi
Lanius excubitoroides
Lanius nubicus

C
B
E
A
D

69/1/0.36
63/1/0.90
100/1/0.99
99/1/NA
100/1/1
47/0.51/0.99
87/1/0.31
99/1/0.98
99/1/0.96
56/0.95/0.82
95/1/1
97/1/1
89/1/NA
67/1/0.69
100/1/1
97/1/1
100/1/1
100/1/1
100/1/1

Pliocene | Pleistocene
5 | 1 | 0 mya

A) Fossils

B) Substitution rates

LEGEND

A)

- ■ Sedentary
- ■ Migratory

Lanius sphenocercus
Lanius giganteus
Lanius meridionalis
Lanius borealis
Lanius ludovicianus
Lanius somalicus
Lanius excubitor
Lanius dorsalis
Lanius vittatus
Lanius collurioides
Lanius phoenicuroides
Lanius collurio
Lanius isabellinus
Lanius validirostris
Lanius bucephalus
Lanius tephronotus
Lanius cristatus
Lanius schach
Lanius tigrinus
Lanius senator
Lanius minor
Lanius mackinnoni
Lanius gubernator
Lanius collaris
Lanius souzae
Lanius humeralis
Lanius newtoni
Lanius excubitoroides
Lanius cabanisi
Urolestes melanoleucus
Corvinella corvina
Lanius nubicus

B)

- ■ Solitary
- ■ Gregarious

Lanius sphenocercus
Lanius giganteus
Lanius meridionalis
Lanius borealis
Lanius ludovicianus
Lanius somalicus
Lanius excubitor
Lanius dorsalis
Lanius vittatus
Lanius collurioides
Lanius phoenicuroides
Lanius collurio
Lanius isabellinus
Lanius validirostris
Lanius bucephalus
Lanius tephronotus
Lanius cristatus
Lanius schach
Lanius tigrinus
Lanius senator
Lanius minor
Lanius mackinnoni
Lanius gubernator
Lanius collaris
Lanius souzae
Lanius humeralis
Lanius newtoni
Lanius excubitoroides
Lanius cabanisi
Urolestes melanoleucus
Corvinella corvina
Lanius nubicus

100/1 — *Lanius collurio*
100/1 — *Lanius phoenicuroides*
— *Lanius isabellinus*
— *Lanius collurioides*
83/0.99 — *Lanius vittatus*
— *Lanius tigrinus*
87/1 95/1 — *Lanius cristatus*
— *Lanius validirostris*
— *Lanius bucephalus*
— *Lanius tephronotus*
100/1 — *Lanius schach*
— *Corvinella corvina*
88/0.99 — *Urolestes melanoleucus*
93/0.98 — *Lanius meridionalis*
— *Lanius borealis*
68/0.95 — *Lanius sphenocercus*
71/0.84 — *Lanius giganteus*
— *Lanius ludovicianus*
87/0.90 — *Lanius somalicus*
— *Lanius excubitor*
91/1 — *Lanius dorsalis*
100/1 — *Lanius c. marwitzi*
86/0.99 — *Lanius c. collaris*
— *Lanius souzae*
— *Lanius humeralis*
— *Lanius newtoni*
— *Lanius gubernator*
— *Lanius mackinnoni*
— *Lanius cabanisi*
85/1 — *Lanius excubitoroides*
— *Lanius minor*
— *Lanius senator*
100/1 — *Lanius nubicus*
— *Monarcha melanopsis*
100/1 — *Monarcha cinerea*
— *Hypothymis azurea*
98/1 — *Terpsiphone atrocaudata*
— *Drepanornis albertisi*
— *Lophorina magnifica*
86/0.99 — *Corvus corone*
— *Nucifraga caryocatactes*
— *Pica pica*
96/1 85/0.91 — *Aphelocoma coerulescens*
— *Garrulus glandarius*
— *Pyrrhocorax pyrrhocorax*
— *Picathartes gymnocephalus*
— *Platylophus galericulatus*
— *Eurocephalus ruppeli*
— *Manucodia ater*
— *Melampitta lugubris*
— *Vireo olivaceus*
95/1 — *Hylophilus ochraceiceps*
— *Ptilorrhoa leucosticta*
— *Pericrocotus ethologus*
— *Rhipidura albicollis*
— *Oriolus oriolus*
— *Dicrurus paradiseus*
— *Dicrurus macrocercus*
100/1 — *Dicrurus aeneus*
— *Corcorax melanoramphos*
— *Laniarius erythrogaster*
— *Tchagra senegalus*
— *Chlorophoneus sulfureopectus*
— *Dryoscopus gambensis*
— *Artamus leucorhyn*
— *Peltops blainvillii*
— *Gymnorhina tibicen*
— *Batis diops*
— *Campephaga flava*
92/1 — *Lalage leucomela*
97/1 — *Coracina lineata*
— *Chaetorhynchus papuensis*
— *Prionops scopifrons*
— *Lamprolia victoriae*
— *Colluricincla harmonica*
99/1 — *Colluricincla megarhyncha*
96/1 — *Pachycephala olivacea*
100/1 — *Pachycephala pectoralis*
— *Turdus pilaris*
— *Sphecotheres vieilloti*
-/0.97 — *Menura novaehollandiae*

0.1 substitution / site

85/0.99 *Lanius c. collaris*
Lanius c. marwitzi
Lanius souzae
Lanius mackinnoni
Lanius humeralis
Lanius newtoni
Lanius excubitor
Lanius meridionalis
Lanius ludovicianus
Lanius sphenocercus
Lanius somalicus
Lanius dorsalis
89/1 *Lanius cabanisi*
Lanius excubitoroides
Corvinella corvina
98/1 *Urolestes melanoleucus*
Lanius collurioides
Lanius vittatus
81/0.99 *Lanius bucephalus*
Lanius validirostris
Lanius collurio
Lanius tigrinus
Lanius tephronotus
Lanius senator
Lanius schach
Lanius nubicus
Lanius minor
Lanius isabellinus
Lanius gubernator
Lanius cristatus
86/0.96
100/1 *Monarcha melanopsis*
Monarcha cinerea
100/1 *Hypothymis azurea*
100/1 *Terpsiphone atrocaudata*
Chaetorhynchus papuensis
Lamprolia victoriae
70/1 *Rhipidura albicollis*
Drepanornis albertisi
96/1 *Lophorina magnifica*
93/1 *Manucodia ater*
63/0.99
82/0.96 *Corvus corone*
Nucifraga caryocatactes
87/0.98 *Pica pica*
97/0.98 *Garrulus glandarius*
Aphelocoma coerulescens
94/0.99 *Pyrrhocorax pyrrhocorax*
64/0.98 *Dicrurus paradiseus*
Dicrurus macrocercus
97/1 *Dicrurus aeneus*
Corcorax melanoramphos
Eurocephalus ruppelli
Platylophus galericulatus
Vireo olivaceus
94/1 *Hylophilus ochraceiceps*
Oriolus oriolus
Sphecotheres vieilloti
Colluricincla harmonica
100/1 *Colluricincla megarhyncha*
Pachycephala olivacea
95/1 96/1 *Pachycephala pectoralis*
Melampitta lugubris
Laniarius erythrogaster
Dryoscopus gambensis
Tchagra senegalus
73/1 *Chlorophoneus sulfureopectus*
Batis diops
Artamus leucorhyn
Prionops scopifrons
80/0.99 *Gymnorhina tibicen*
Peltops blainvillii
Campephaga flava
100/1 *Lalage leucomela*
85/0.98 *Coracina lineata*
68/1 *Pericrocotus ethologus*
100/1 *Picathartes gymnocephalus*
Ptilorrhoa leucosticta
Turdus pilaris
Menura novaehollandiae

0.01

Lanius excubitor
Lanius borealis
88/1
70/0.96
Lanius ludovicianus
Lanius sphenocercus
Lanius meridionalis
93/1
79/1
Lanius somalicus
Lanius dorsalis
Lanius gubernator
Lanius c. marwitzi
Lanius c. collaris
Lanius humeralis
69/1
Lanius souzae
Lanius newtoni
Lanius mackinnoni
Lanius minor
Lanius senator
92/1
Corvinella corvina
Urolestes melanoleucus
96/1
Lanius cabanisi
Lanius collurio
Lanius isabellinus
79/0.59
Lanius tephronotus
Lanius vittatus
67/1
Lanius bucephalus
Lanius validirostris
89/1
Lanius schach
Lanius nubicus
Lanius tigrinus
91/1
Lanius collurioides
Lanius excubitoroides
Lanius cristatus
100/1
Monarcha melanopsis
Monarcha cinerea
100/1
99/1
Hypothymis azurea
Terpsiphone atrocaudata
100/1
Dicrurus paradiseus
52/0.95
Dicrurus macrocercus
Dicrurus aeneus
99/1
Melampitta lugubris
97/1
Corvus corone
Garrulus glandarius
Nucifraga caryocatactes
Pica pica
Aphelocoma coerulescens
Pyrrhocorax pyrrhocorax
Drepanornis albertisi
Lophorina magnifica
100/1
Manucodia ater
67/1
Chaetorhynchus papuensis
Lamprolia victoriae
100/1
Eurocephalus ruppelli
Platylophus galericulatus
Corcorax melanoramphos
Rhipidura albicollis
Colluricincla harmonica
Colluricincla megarhyncha
96/1
81/1
Pachycephala olivacea
Pachycephala pectoralis
100/1
Coracina lineata
Lalage leucomela
86/1
Campephaga flava
98/1
Pericrocotus ethologus
Oriolus oriolus
Sphecotheres vieilloti
Chlorophoneus sulfureopectus
Laniarius erythrogaster
94/1
Tchagra senegalus
Dryoscopus gambensis
97/0.98
Prionops scopifrons
Artamus leucorhyn
Gymnorhina tibicen
89/1
66/0.97
Peltops blainvillii
Batis diops
Picathartes gymnocephalus
Vireo olivaceus
Hylophilus ochraceiceps
99/1
Ptilorrhoa leucosticta
Turdus pilaris
Menura novaehollandiae

0.01 substitution / site

Lanius c. collaris — 0.98
Lanius c. marwitzi — 0.96
Lanius souzae
Lanius humeralis
Lanius mackinnoni
Lanius newtoni
Lanius gubernator
Lanius minor — 1
Lanius senator
Lanius cabanisi — 1
Lanius excubitoroides
Corvinella corvina
Urolestes melanoleucus — 1
Lanius bucephalus
Lanius validirostris
Lanius cristatus
Lanius tephronotus — 0.99
Lanius schach
Lanius collurioides
Lanius vittatus — 0.99
Lanius collurio
Lanius isabellinus — 1
Lanius tigrinus
Lanius nubicus
Lanius meridionalis
Lanius sphenocercus
Lanius ludovicianus
Lanius excubitor
Lanius somalicus — 1
Lanius dorsalis
Platylophus galericulatus
Eurocephalus ruppelli
Corvus corone
Nucifraga caryocatactes
Garrulus glandarius — 0.98
Pica pica — 1
Aphelocoma coerulescens
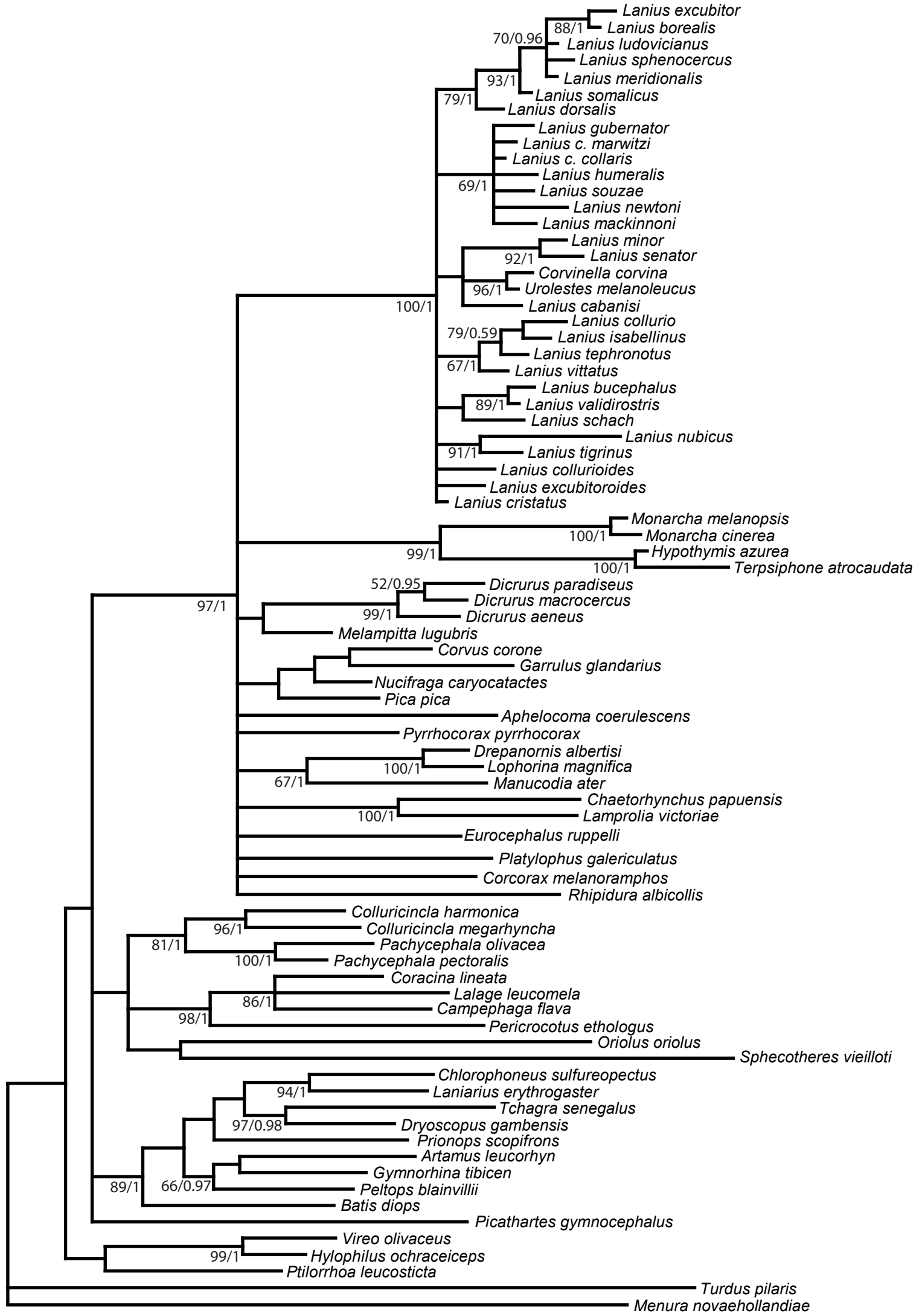*Pyrrhocorax pyrrhocorax* — 0.95
Dicrurus macrocercus
Dicrurus paradiseus
Dicrurus aeneus — 1
Corcorax melanoramphos — 0.95
Melampitta lugubris
Hypothymis azurea
Terpsiphone atrocaudata — 1
Monarcha cinerea
Monarcha melanopsis — 1
Epimachus albertisi
Ptiloris magnificus — 1
Manucodia atra
Chaetorhynchus papuensis
Lamprolia victoriae — 1
Rhipidura albicollis
Colluricincla harmonica
Colluricincla megarhyncha — 1
Pachycephala olivacea — 1
Pachycephala pectoralis
Oriolus oriolus
Sphecotheres vieilloti
Campephaga flava
Lalage leucomela — 1
Coracina lineata — 1
Pericrocotus ethologus — 0.99
Hylophilus ochraceiceps
Vireo olivaceus — 1
Chlorophoneus sulfureopectus
Laniarius erythrogaster — 1
Dryoscopus gambensis — 0.99
Tchagra senegalus
Batis diops
Prionops scopifrons
Artamus leucorhynchus
Peltops blainvillii
Gymnorhina tibicen — 1
Ptilorrhoa leucosticta
Turdus pilaris
Picathartes gymnocephalus
Menura novaehollandiae

0.99
0.98
0.97
1
1

1