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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. mackinnoi*, *L. newtoni*).

Here, we present the first time-calibrated phylogeny of Laniidae, using mitochondrial and nuclear markers **for 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. anguimensis* was not sampled) and selected a broad representation of corvid 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 Corvidae fossils. The first fossil was *Kurrartapu johnguyeni* (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 World *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* $\gamma = -2.7156242042$, $p: 0.0033$; fossils with *L. c. marwitzi*: $\gamma = -2.473156$ $p: 0.00669$; rates without *L. c. marwitzi* $\gamma = -2.723424$, $p: 0.0032$; rates with *L. c. marwitzi*: $\gamma = -2.480653$ $p: 0.00557$), 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. collurio*/*L. 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.

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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 $\geq 70\%$, ≥ 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. marwitzii* 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 $\geq 70\%$ and ≥ 0.95 , respectively. Values are indicated when at least one of the two values was $\geq 70\%$ 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 $\geq 70\%$ and ≥ 0.95 , respectively. Values are indicated when at least one of the two values was $\geq 70\%$ 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 $\geq 70\%$ and ≥ 0.95 , respectively. Values are indicated when at least one of the two values was $\geq 70\%$ 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/ <i>Corvinella-Urolestes</i>	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 Hiddensee; 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.

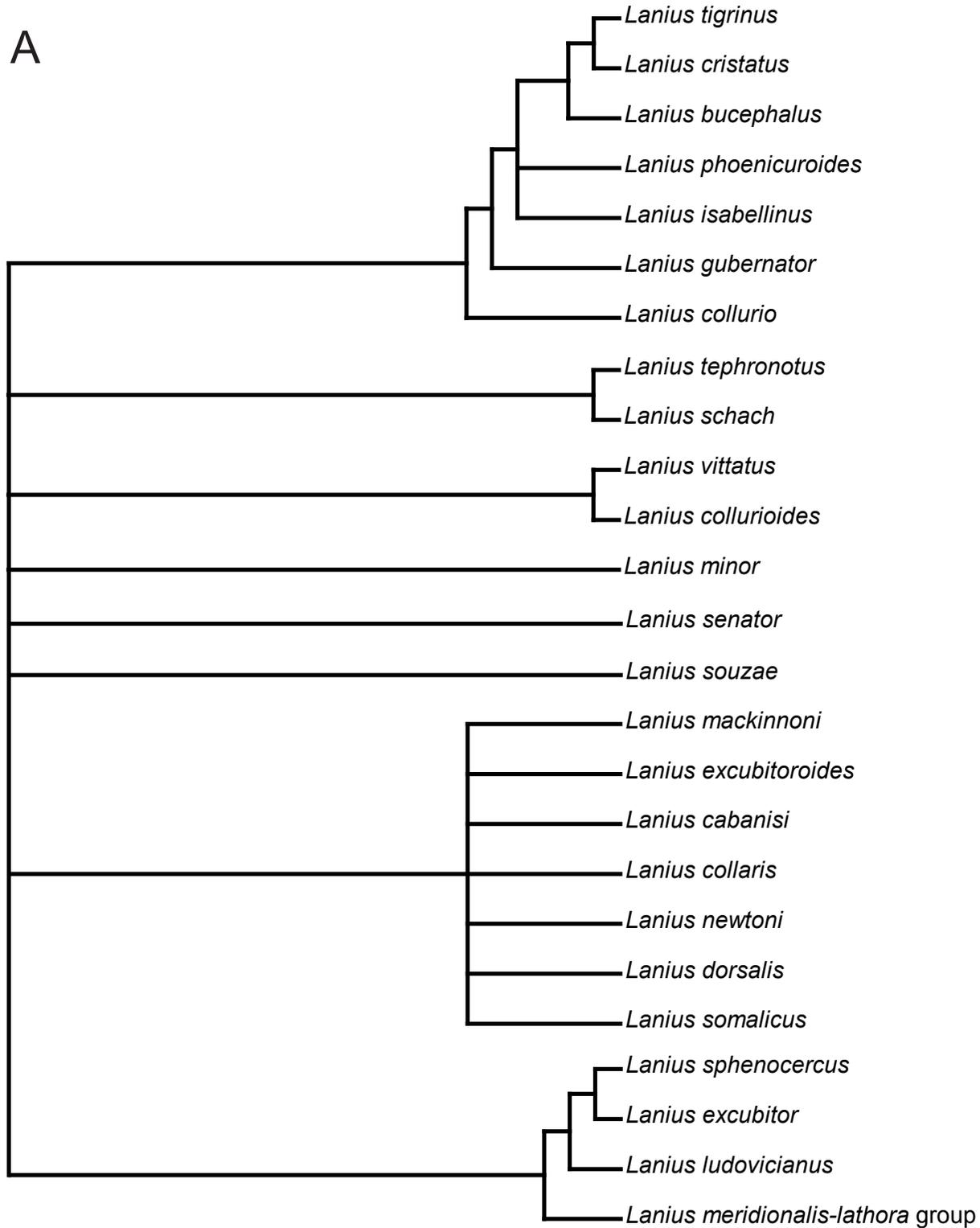
(XXXXXXX = sequences that will be deposited in GenBank when manuscript is accepted for publication)

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

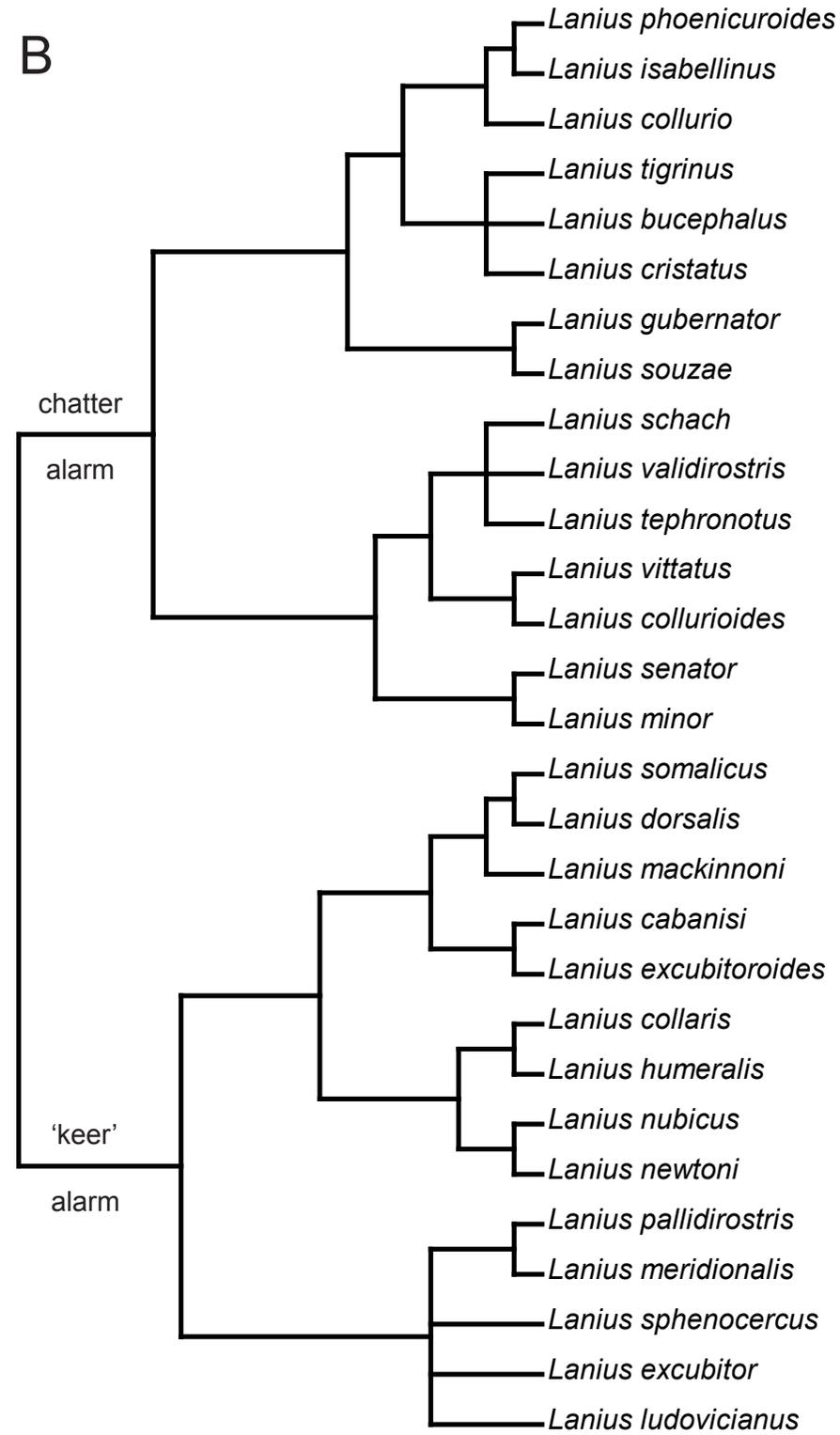
<i>Lanius excubitor</i>	Moscow, Russia	UWBM 57238	XXXXXXX	XXXXXXX	XXXXXXX
<i>Lanius excubitoroides</i>	Uganda	AH 1312	GU253548	XXXXXXX	GU253689
<i>Lanius giganteus</i>	[GenBank]	[GenBank]	JQ239201	—	—
<i>Lanius gubernator</i>	Nigeria	DZUG 2601	XXXXXXX	XXXXXXX	XXXXXXX
<i>Lanius humeralis</i>	Cameroon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

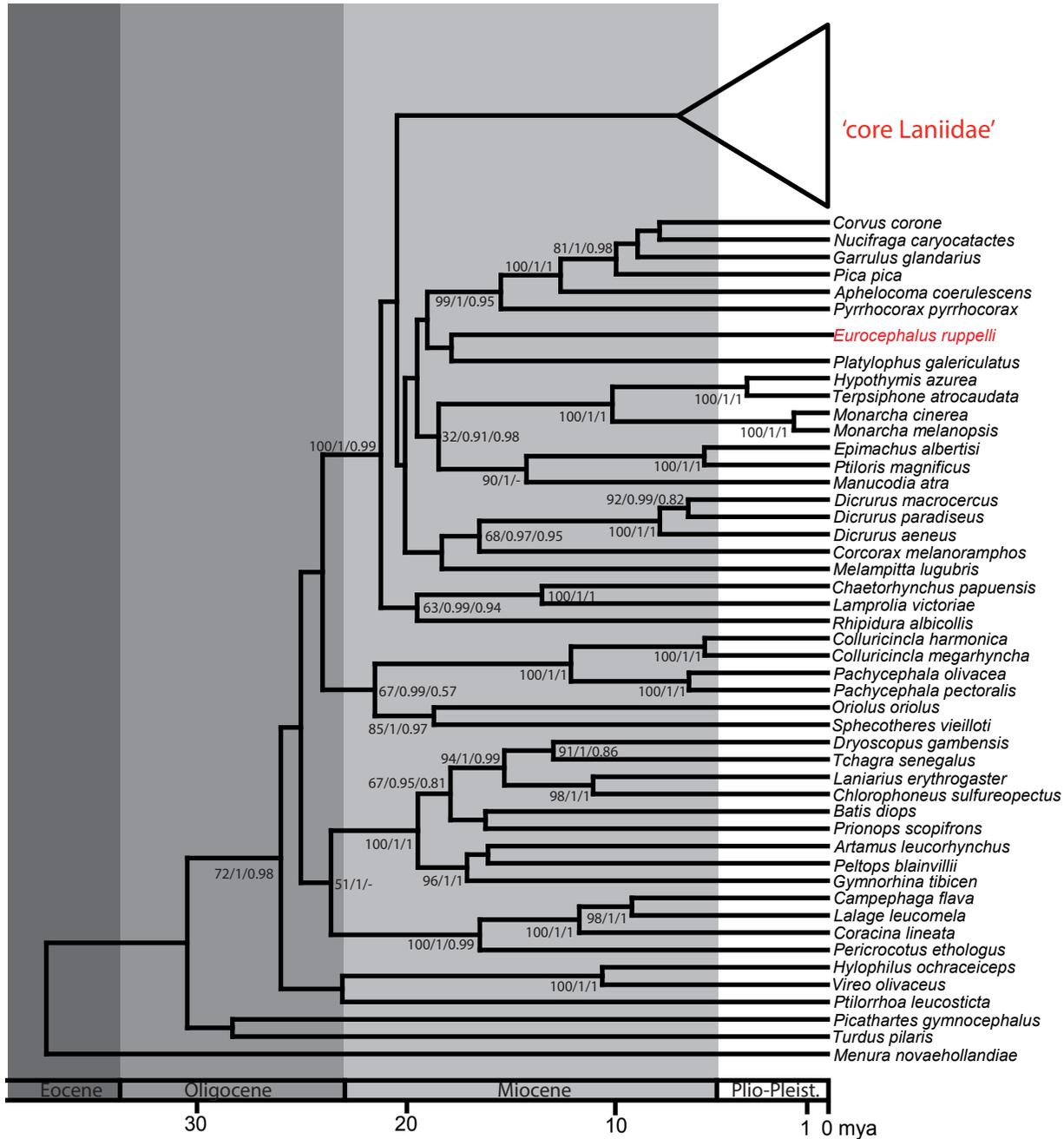
A



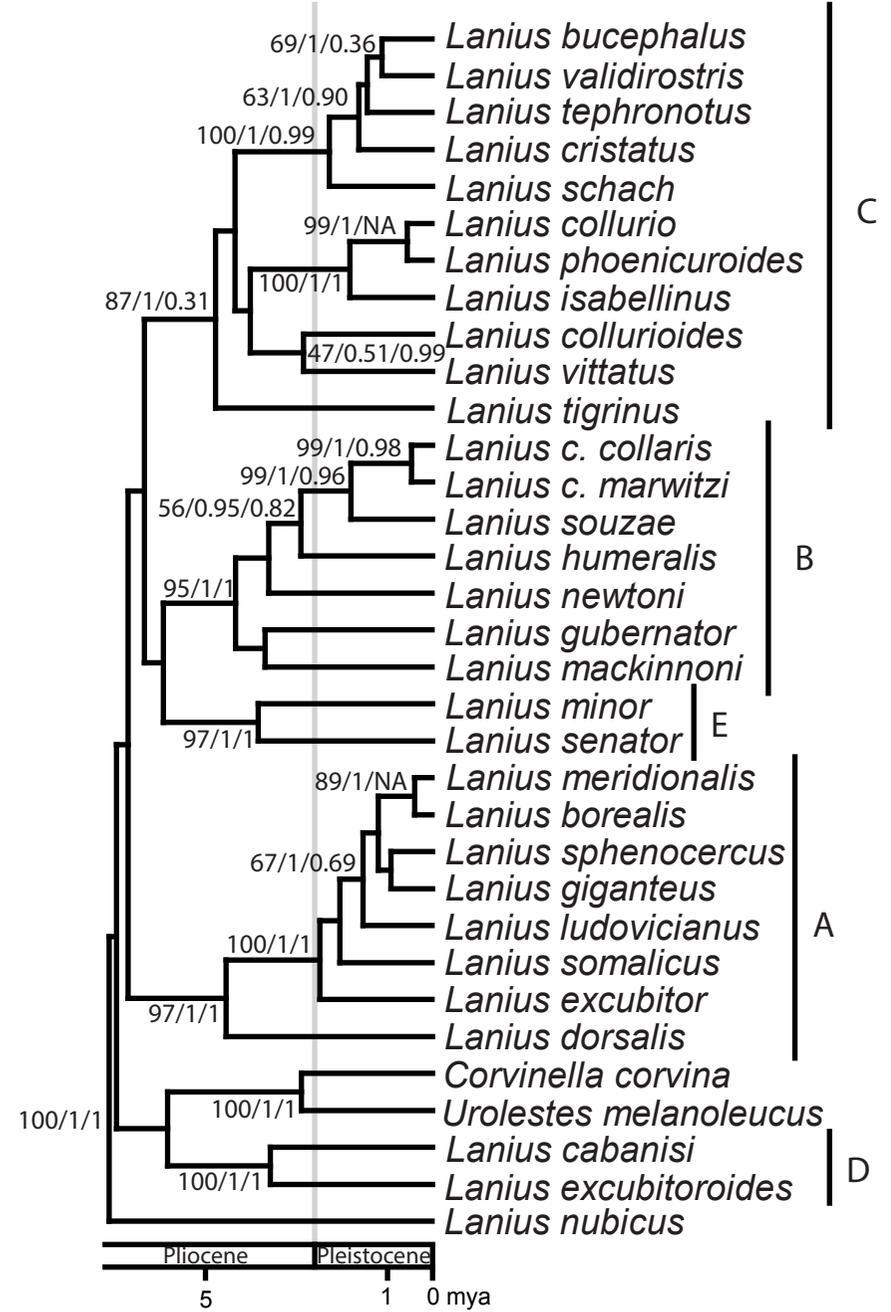
B



A)

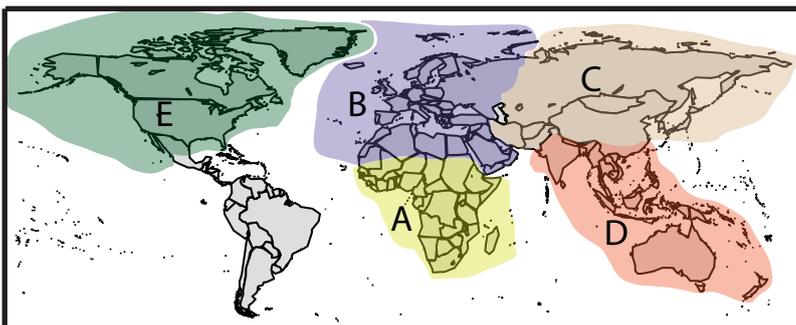
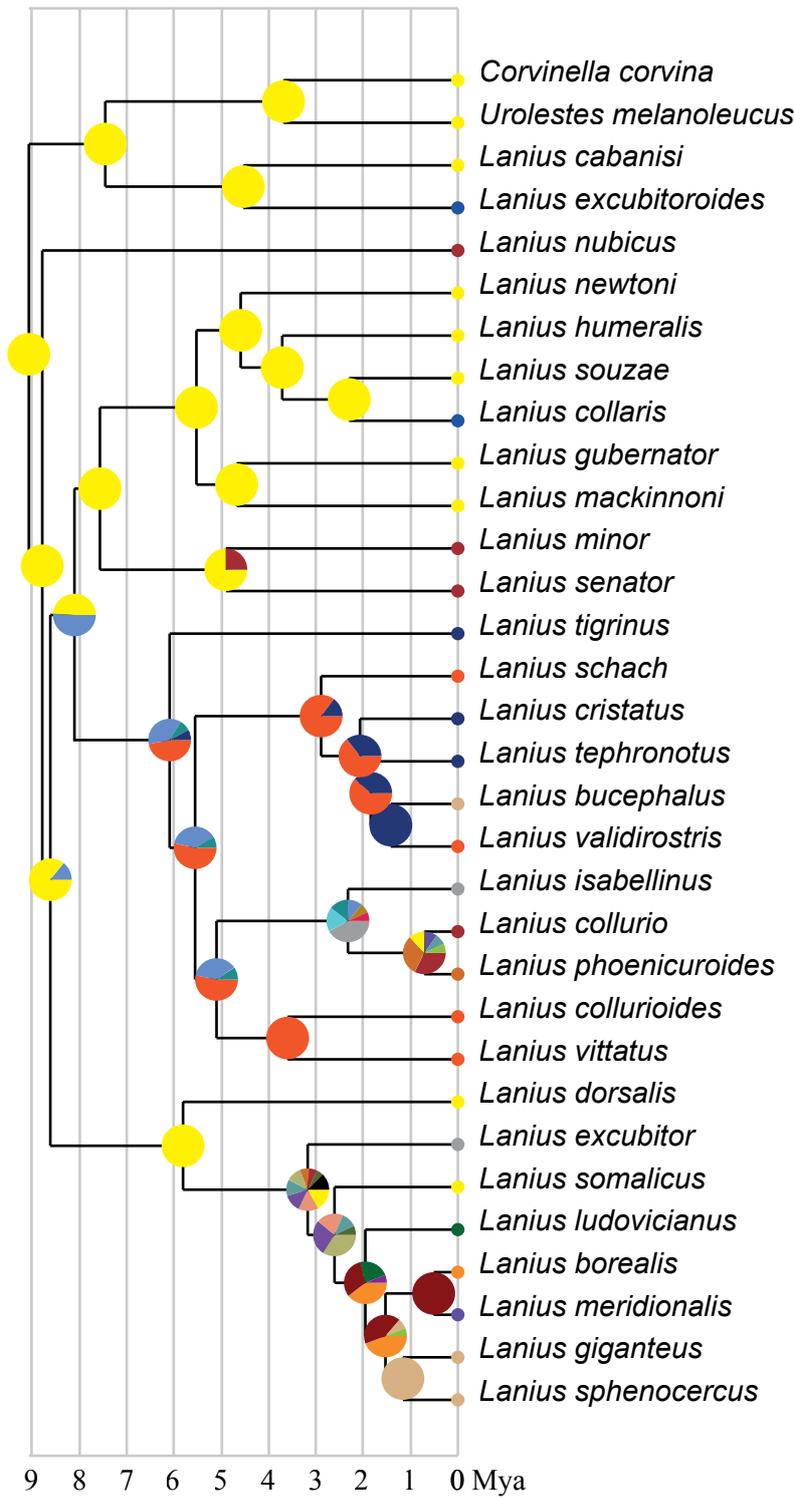
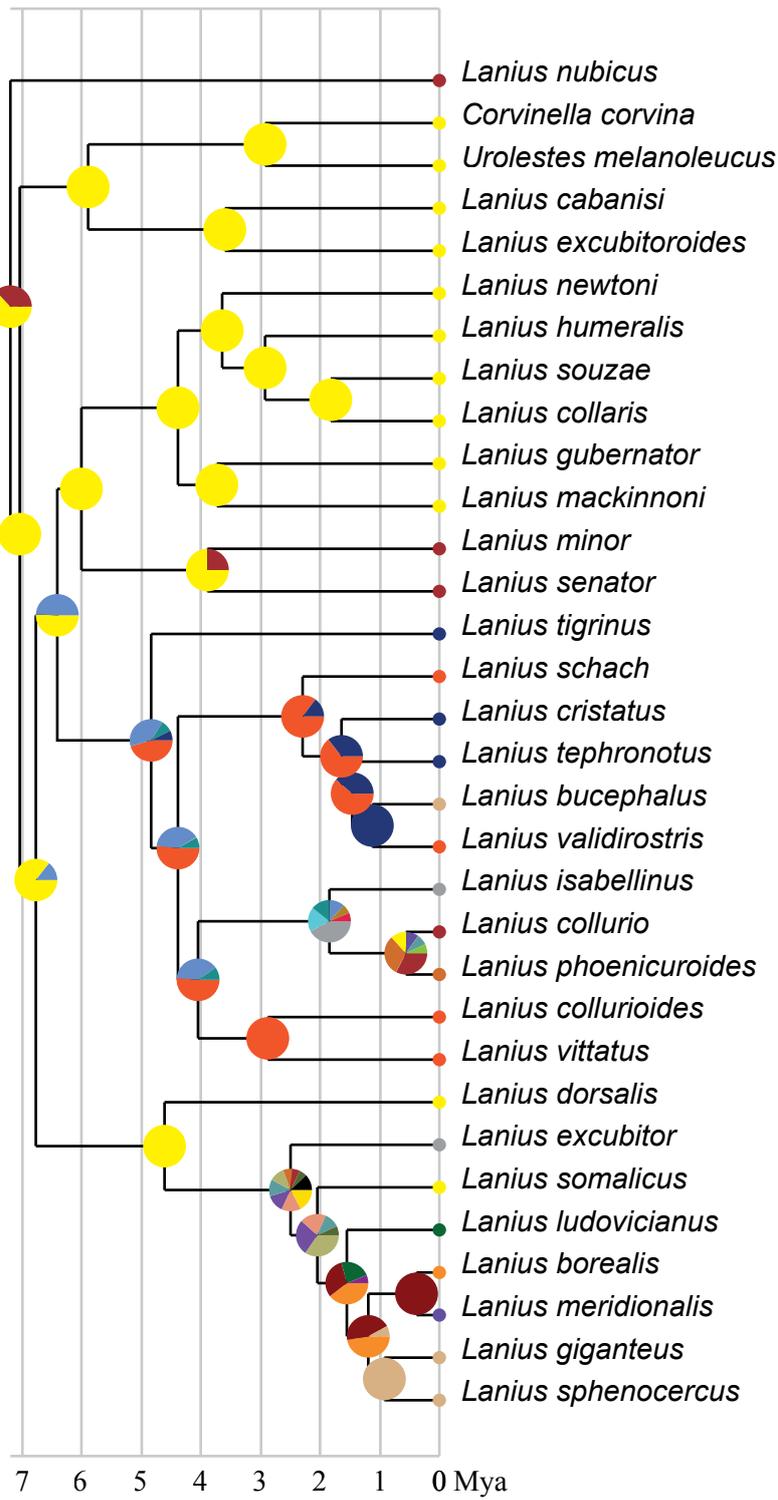


B)



A) Fossils

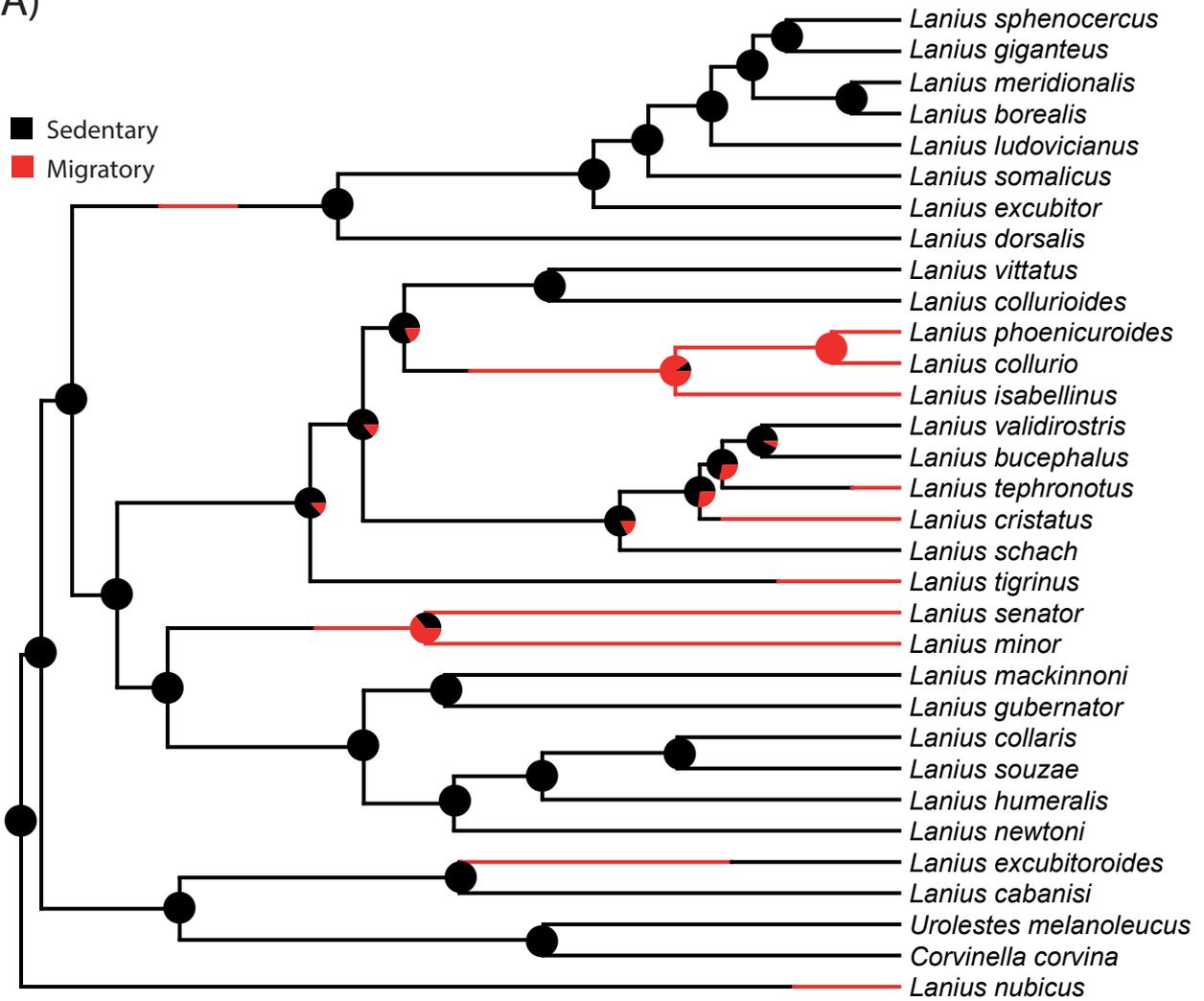
B) Substitution rates



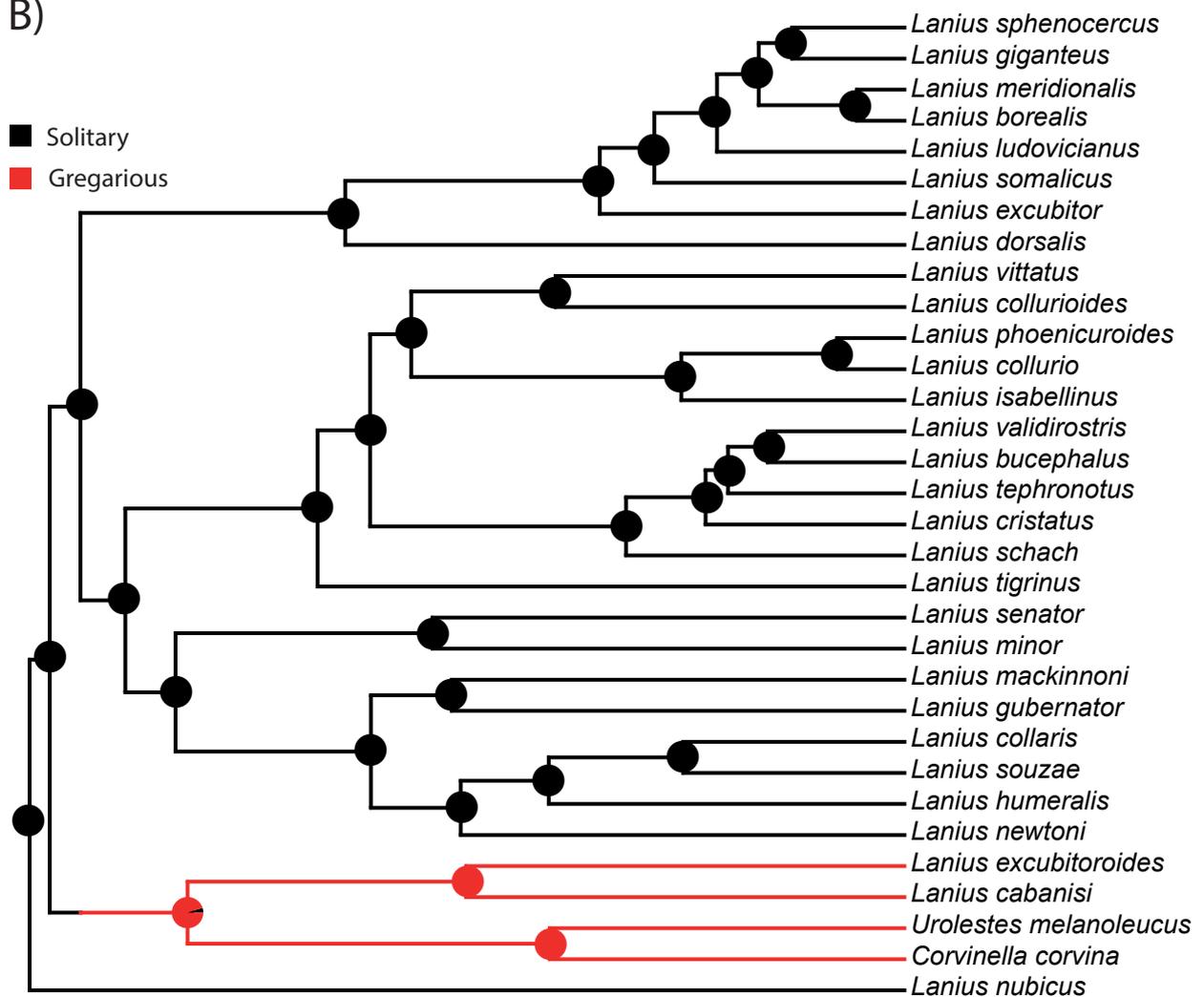
LEGEND

A	E	*	AE
B	ABCD	ABCE	BC
C	BCE	ABD	BCD
D	ABC	ABE	BD
AB	AD	AC	BE
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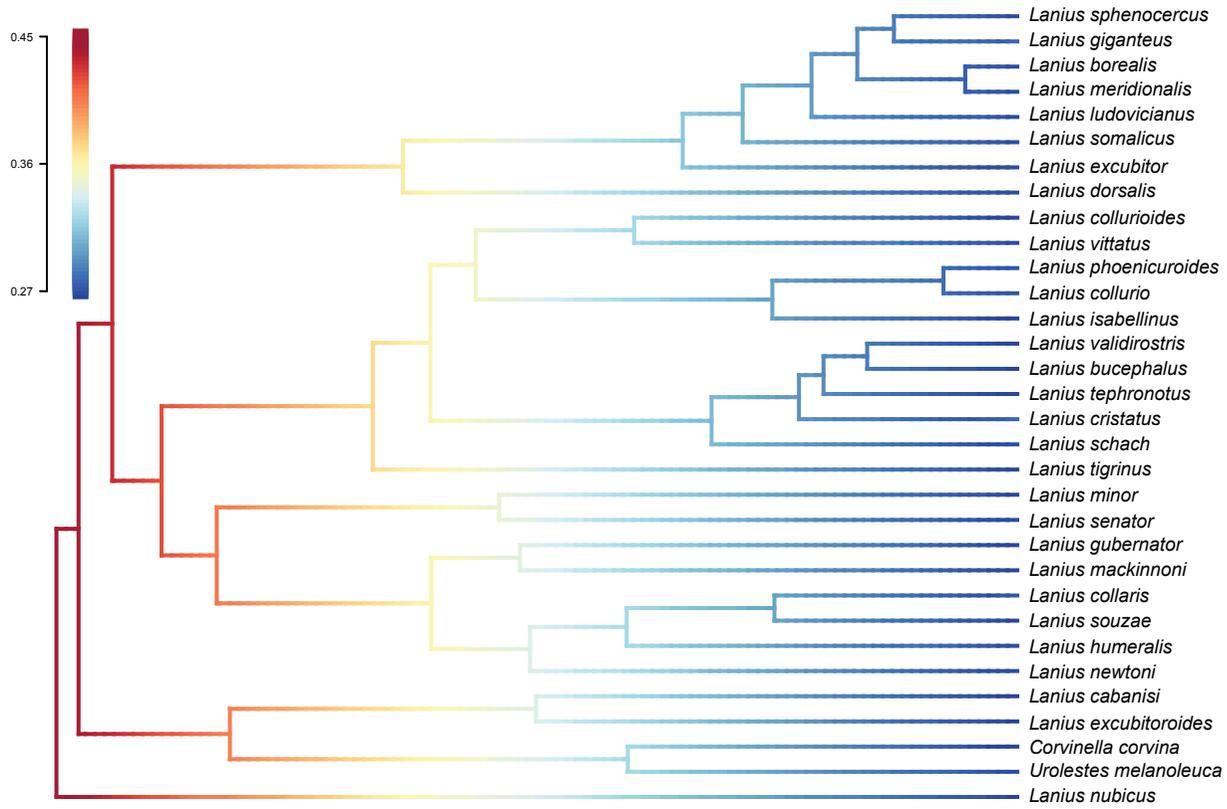
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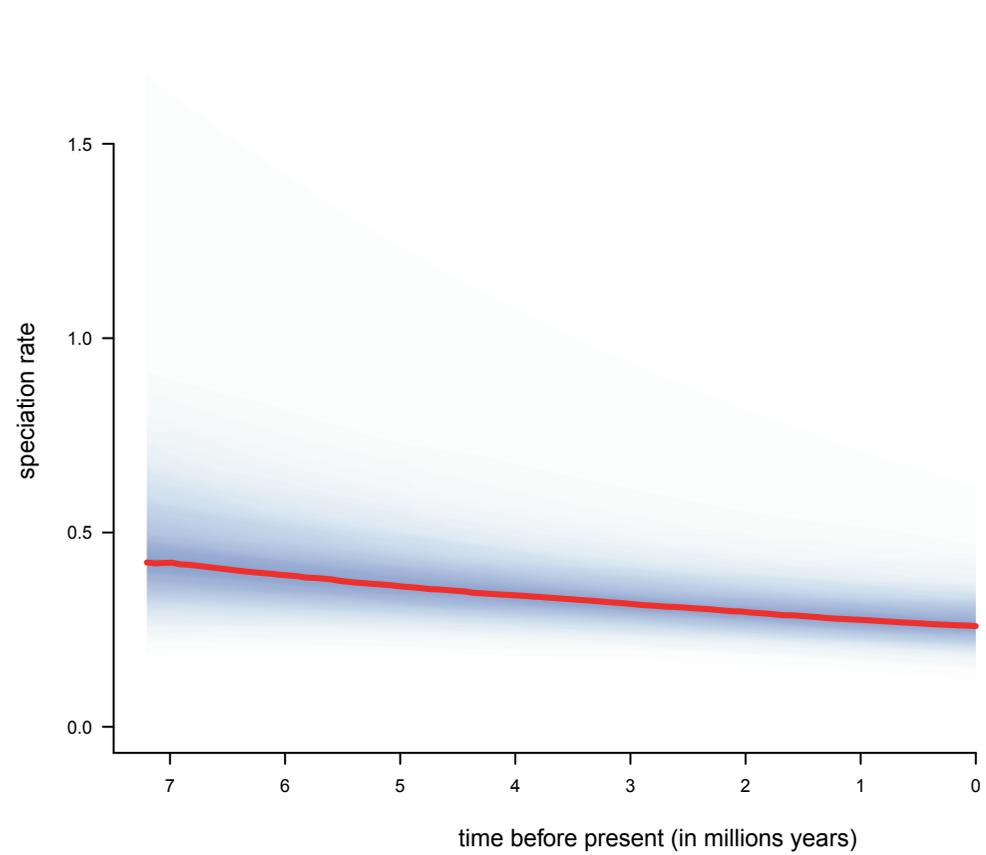
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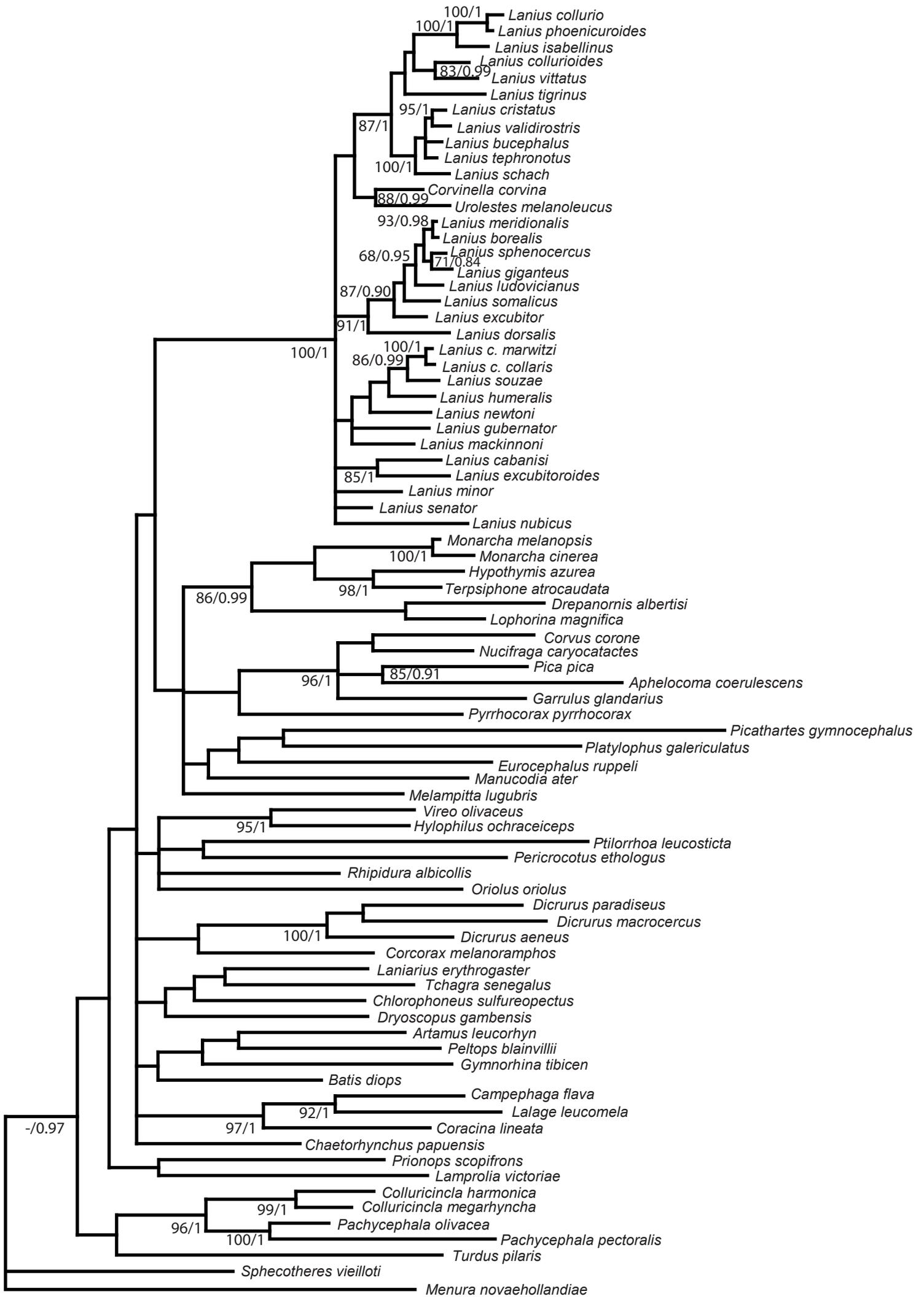


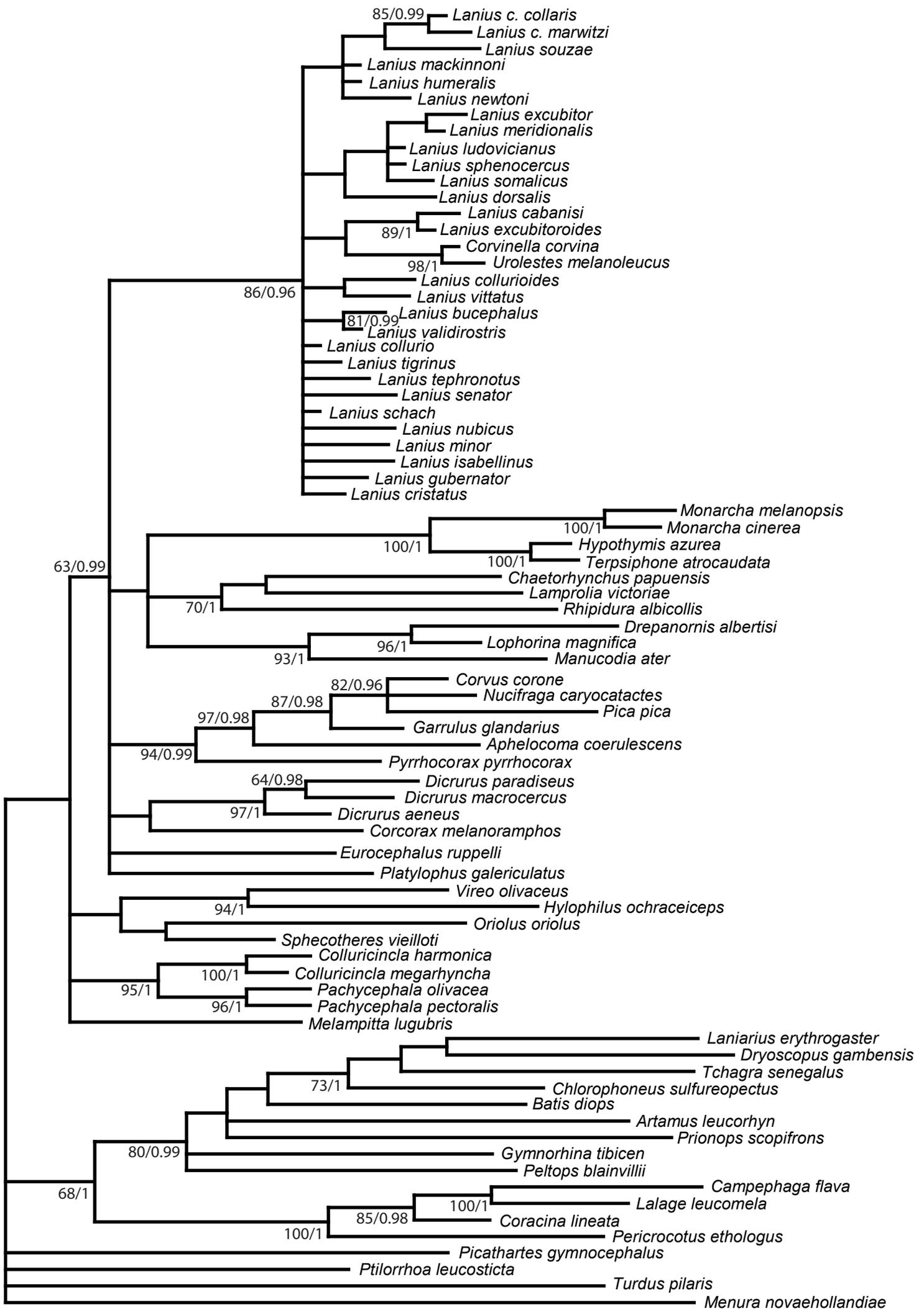
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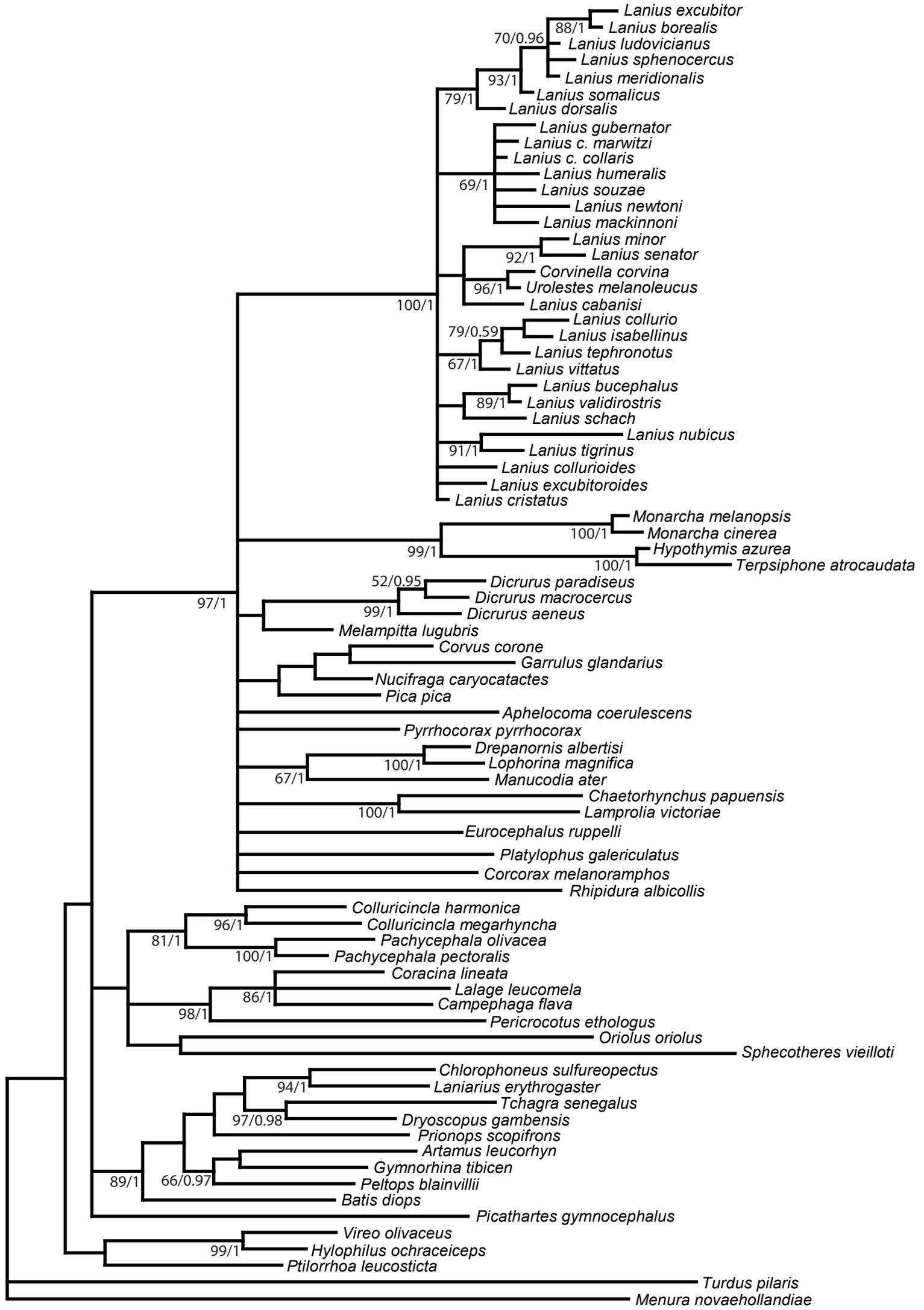


B)









0.01 substitution / site

