Citation for the published paper:
Per Alström, Keith N. Barnes, Urban Olsson, F. Keith Barker, Paulette Bloomer, Aleem Ahmed Khan, Masood Ahmed Qureshi, Alban Guillaumet, Pierre-André Crochet, Peter G. Ryan. (2013) Multilocus phylogeny of the avian family Alaudidae (larks) reveals complex morphological evolution, non-monophyletic genera and hidden species diversity. *Molecular Phylogenetics and Evolution*. Volume: 69, Number: 3, pp 1043-1056.
http://dx.doi.org/10.1016/j.ympev.2013.06.005.

Multilocus phylogeny of the avian family Alaudidae (larks) reveals complex morphological evolution, non-monophyletic genera and hidden species diversity

Per Alström[a,b,c*], Keith N. Barnes[c], Urban Olsson[d], F. Keith Barker[e], Paulette Bloomer[f], Aleem Ahmed Khan[g], Masood Ahmed Qureshi[g], Alban Guillaumet[h], Pierre-André Crochet[i], Peter G. Ryan[c]

[a] *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Chaoyang District, Beijing, 100101, P. R. China*

[b] *Swedish Species Information Centre, Swedish University of Agricultural Sciences, Box 7007, SE-750 07 Uppsala, Sweden*

[c] *Percy FitzPatrick Institute of African Ornithology, DST/NRF Centre of Excellence, University of Cape Town, Rondebosch 7700, South Africa*

[d] *Systematics and Biodiversity, Gothenburg University, Department of Zoology, Box 463, SE-405 30 Göteborg, Sweden*

[e] *Bell Museum of Natural History and Department of Ecology, Evolution and Behavior, University of Minnesota, 1987 Upper Buford Circle, St. Paul, MN 55108, USA*

[f] *Percy FitzPatrick Institute Centre of Excellence, Department of Genetics, University of Pretoria, Hatfield, 0083, South Africa*

[g] *Institute of Pure & Applied Biology, Bahauddin Zakariya University, 60800, Multan, Pakistan*

[h] *Department of Biology, Trent University, DNA Building, Peterborough, ON K9J 7B8, Canada*

[i] *CEFE/CNRS Campus du CNRS 1919, route de Mende, 34293 Montpellier, France*

* Corresponding author: *Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Chaoyang District, Beijing, 100101, P. R. China; E-mail: per.alstrom@slu.se*

ABSTRACT

The Alaudidae (larks) is a large family of songbirds in the superfamily Sylvioidea. Larks are cosmopolitan, although species-level diversity is by far largest in Africa, followed by Eurasia, whereas Australasia and the New World have only one species each. The present study is the first comprehensive phylogeny of the Alaudidae. It includes 83.5% of all species and representatives from all recognised genera, and was based on two mitochondrial and three nuclear loci (in total 6.4 kbp, although not all loci were available for all species). In addition, a larger sample, comprising several subspecies of some polytypic species was analysed for one of the mitochondrial loci. There was generally good agreement in trees inferred from different loci, although some strongly supported incongruences were noted. The tree based on the concatenated multilocus data was overall well resolved and well supported by the data. We stress the importance of performing single gene as well as combined data analyses, as the latter may obscure significant incongruence behind strong nodal support values. The multilocus tree revealed many unpredicted relationships, including some non-monophyletic genera (*Calandrella*, *Mirafra*, *Melanocorypha*, *Spizocorys*). The tree based on the extended mitochondrial data set revealed several unexpected deep divergences between taxa presently treated as conspecific (e.g. within *Ammomanes cinctura*, *Ammomanes deserti*, *Calandrella brachydactyla*, *Eremophila alpestris*), as well as some shallow splits between currently recognised species (e.g. *Certhilauda brevirostris–C. semitorquata–C. curvirostris*; *Calendulauda barlowi–C. erythrochlamys*; *Mirafra cantillans–M. javanica*). Based on our results, we propose a revised generic classification, and comment on some species limits. We also comment on the extraordinary morphological adaptability in larks, which has resulted in numerous examples of parallel evolution (e.g. in *Melanocorypha mongolica* and *M. leucoptera* [latter here proposed to be moved to *Alauda*]; *Ammomanopsis grayi* and *Ammomanes cinctura/deserti*; *Chersophilus duponti* and *Certhilauda* spp.; *Mirafra hova* [here proposed to be moved to *Eremopterix*] vs. several other *Mirafra* spp.), as well as both highly conserved plumages (e.g. within *Mirafra*) and strongly divergent lineages (e.g. *Mirafra hova* vs. *Eremopterix* spp.; *Calandrella cinerea* complex vs. *Eremophila* spp.; *Eremalauda dunni* vs. *Chersophilus duponti*; *Melanocorypha mongolica* and male *M. yeltoniensis* vs. other *Melanocorypha* spp. and female *M. yeltoniensis*). Sexual plumage dimorphism has evolved multiple times. Few groups of birds show the same level of disagreement between taxonomy based on morphology and phylogenetic relationships as inferred from DNA sequences.

Keywords: phylogeny; taxonomy; morphological evolution; nodal support

1. Introduction

The family Alaudidae, larks, comprises 97 species in 21 genera (Gill and Donsker, 2012; Spottiswoode et al., in press), including the Eurasian Skylark *Alauda arvensis* ("*the* lark"), which is familiar to many Europeans because of its widespread occurrence in agricultural land, local abundance, and beautiful song. Many other species of larks are well known for similar reasons. Larks are found on six continents, but the family's distribution and diversity is highly skewed. In terms of current distribution and diversity, the Alaudidae is primarily an African and secondarily a Eurasian family. Seventy-eight species occur in Africa, with 60 endemic to sub-Saharan Africa. Eurasia has 37 species, with one, *Mirafra javanica*, extending its range to Australia, as the only representative of this family on that continent (de Juana et al., 2004; Gill and Donsker, 2012). A single widespread species, the Horned Lark *Eremophila alpestris*, is native to the New World as well as much of the Palearctic. All 21 genera are represented in Africa, with 13 in Eurasia and one each in Australasia and the New World (de Juana et al., 2004; Gill and Donsker, 2012). In Africa, lark species richness is greatest in semi-arid and arid regions (Dean and Hockey, 1989). There are two primary centres of endemism, one in the north-east arid zone (Kenya, Ethiopia and Somalia), where 23 of the 34 species are endemic or near-endemic, and another one in the south-west arid zone (South Africa, Namibia and Botswana), where 26 of the 31 species are endemic or near-endemic (de Juana et al., 2004).

Most lark species share a similar plumage pattern: brownish or greyish above and paler below, with variously distinct darker streaking on the upperparts and breast. This pattern provides camouflage in the open, grassy or arid habitats where larks occur, and several authors have noted a positive correlation between the coloration of the upperparts of a species and the colour of the soil on which it lives (Bannerman, 1927; Guillaumet et al., 2008; Kleinschmidt, 1907, 1912; Meinertzhagen, 1951; Niethammer, 1940; Vaurie, 1951). In most species, there is no sexual dimorphism in plumage, although males average larger than females. However, in *Melanocorypha yeltoniensis* and the *Eremopterix* species, male and female plumages are strongly different (and in the former, males average 13–14% heavier than females; Cramp, 1988; de Juana et al., 2004). In contrast to their cryptic plumages, most species have well developed songs, and some species, e.g. *Alauda arvensis*, are renowned songsters. Most species also have elaborate song flights. Presumably in association with diet (e.g., many species consume seeds in addition to arthropod prey), bill morphology varies considerably among species, and in some species, also between the sexes (e.g. *Alauda razae* and the long-billed lark complex; Burton, 1971; Cramp, 1988; Donald et al., 2007; Ryan and Bloomer, 1999).

Morphologically, the family Alaudidae constitutes a well defined group, whose members share unique features of the syrinx (Ames, 1971) and tarsus (Rand, 1959). As a result, the limits of the family are not disputed, but the relationships between the larks and other taxa have long been uncertain. Linear classifications have generally placed them at the beginning of the oscine passerines (e.g. del Hoyo et al., 2004; Peters, 1960), whereas based on DNA-DNA hybridization they were placed in the superfamily Passeroidea (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990). However, recent studies based on sequence data have unanimously shown them to be part of the superfamily Sylvioidea, and together with the morphologically and ecologically radically different monotypic genus *Panurus* (Panuridae) forming a sister clade to the rest of the Sylvioidea (Alström et al., 2006; Ericson and Johansson, 2003; Fregin et al., 2012).

Traditionally, the designation of lark genera has been based on morphology. However, bill structure and plumage vary considerably with diet and habitat (e.g. Cramp, 1988; del Hoyo et al., 2004) and therefore are likely to be unreliable for phylogenetic assessment. Consequently, the number of genera and their composition have fluctuated dramatically over the years (e.g. Clancey, 1966, 1980; Dean et al., 1992; de Juana et al., 2004; Dickinson, 2003; Harrison, 1966; Macdonald, 1952a, b, 1953; Maclean, 1969; Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960; Roberts, 1940; Vaurie, 1951; Verheyen, 1958; Wolters, 1979). Certain genera, notably *Mirafra*, have acted as “dumping grounds”, while several monotypic genera (e.g. *Pseudalaemon*, *Lullula*, *Ramphocoris*), and enigmatic species (e.g. *Eremalauda dunni*, *Alauda razae*) and genera (e.g. *Alaemon*, *Chersomanes*) have defied consistent placement. Lark taxonomy has received much attention in Africa (Clancey, 1989; Lawson, 1961; Meinertzhagen, 1951; Winterbottom, 1957), and Eurasia (Dickinson and Dekker, 2001; Meinertzhagen, 1951; Vaurie, 1951, 1954). Recent studies based on molecular and/or vocal data have revealed considerable hidden diversity and taxonomic confusion in some taxa (Alström, 1998; Ryan et al., 1998; Ryan and Bloomer, 1999; Guillaumet et al., 2005, 2006, 2008), and it seems likely that the total number of recognised lark species is underestimated.

Previously, only one molecular phylogeny has been published, based on mitochondrial sequences from a small number of mostly African species (Tieleman et al., 2001). The present study is the first comprehensive phylogeny of the Alaudidae (although part of the data for the African and some of the Western Palearctic species have been analysed in an unpublished PhD thesis; Barnes, 2007). It is based on two mitochondrial and three nuclear loci (in total 6.4

kbp, although not all loci are available for all species), and includes representatives from all recognised genera and 86% of all species. We also analyse one mitochondrial locus for a larger sample, comprising multiple individuals and several subspecies of some polytypic species. These data provide the basis for a major reassessment of lark relationships and taxonomy, as well as the foundation for comments on the morphological evolution in this bird family.

2. Material and methods

2. 1. Study group and sampling

Taxonomy follows Gill and Donsker (2012), except with respect to *Heteromirafra sidamoensis*, which we treat as conspecific with *H. archeri* based on Spottiswoode et al. (2013). We included 81 of the 97 species, representing all 21 genera. Eight African *Mirafra* spp., three African *Calandrella* spp. and the African *Alaemon hamertoni*, *Eremopterix leucotis* and *Spizocorys obbiensis*, as well as the Asian *Ammomanes phoenicura* and *Galerida deva* were missing.

Fresh tissue and blood samples, as well as a few feather samples, were collected by people with extensive field experience with these larks (mainly the authors of this study). Liver, heart and pectoral muscle were dissected for tissue samples, and stored in 20% dimethylsulphoxide (DMSO) and saturated salt (NaCl) (Amos and Hoezel, 1991) or ethanol. Blood samples were mixed immediately in a blood storage buffer (0.1M Tris-HCL, 0.04M EDTA.Na2, or 1.0M NaCl, 0.5% SDS). Samples were refrigerated as soon as possible. Feathers were kept at −20°C. Voucher specimens were deposited in various institutions (Appendix 1). For blood and feather samples, photographs were taken of some birds (Appendix 1 and 2). Unfortunately, a hard drive with photos of a large proportion of the species collected in Africa by KB, for which no specimens are available, has been lost.

2.2. DNA extraction and sequencing

Lab work was done mainly at the University of Pretoria (UP), University of Gothenburg (GU) and University of Minnesota (UMN). At UP DNA extractions followed standard procedures of chemical digestion, phenol/chloroform clean-up and ethanol precipitation (Sambrook et al., 1989) . DNA was eluted in Sabax® (Adcock Ingram) water and stored at -20°C. At GU and UMN, DNA was extracted using QIA Quick DNEasy Kit (Qiagen, Inc) according to the manufacturer's instruction, but with 30 µl 0.1% DTT added to the initial incubation step of the extraction of feathers.

We sequenced five loci: the main part of the mitochondrial cytochrome *b* gene and part of the flanking tRNA-Thr (together referred to as cyt*b*); the mitochondrial 16S rRNA; the nuclear ornithine decarboxylase (ODC) exon 6 (partial), intron 6, exon 7, intron 7 and exon 8 (partial); the entire nuclear myoglobin (myo) intron 2, and the nuclear recombination activating gene, parts 1 and 2 (RAG). At GU, amplification and sequencing of cyt*b* followed the protocols described in Olsson et al. (2005). At UP, cyt*b* was amplified and sequenced using primers L14841 and H15696 and L15408 and H15915 (Edwards et al., 1991; Kocher et al., 1989; Pääbo et al., 1988) with primer annealing at 50–52°C. Amplification and sequencing of cyt*b* at UMN, differing from the above primarily in the exact primers used, followed protocols described in Barker et al. (2008).

At UP, a 1702 base pairs (bp) segment of the 16S rRNA gene was amplified using the primers L2313 and H4015 (Lee et al., 1997); an internal primer L2925 (Tieleman et al., 2003) was used for sequencing. For 16S the PCR protocol was identical to that for cyt*b*, except for the modification of the primer annealing temperature (58°C, 30s). Amplification and sequencing followed the protocols described in Olsson et al. (2005) for myo, Allen & Omland (2003) for ODC, and Barker et al. (2004) for RAG.

DNA was also extracted from toepad samples of two *Pinarocorys* species, for which no fresh DNA was available. For extraction, PCR-amplification, and sequencing procedures for these, the procedures described in Irestedt et al. (2006) were followed, with specially designed primers (Supplementary Table 1).

2.3. Phylogenetic analyses

We followed a hierarchical sampling scheme prioritizing mtDNA sampling for all species, and nuclear loci for a subset of samples, representing major lineages of larks (e.g., Wiens et al. 2005). The following sequence data were included in the analyses: cyt*b* for all species; 16S for nearly all African species and a few Eurasian species; and between one to three nuclear loci for most species. In addition, we analysed 142 cyt*b* haplotypes, including some sequences from GenBank, comprising several subspecies of polytypic species. For one species, only cyt*b* was available, and for 20 species, only cyt*b* and 16S were available. See Appendix 1 and Fig. 1 for details regarding coverage of loci across the taxa. All new sequences have been deposited in GenBank (Appendix 1).

Sequences were aligned using Muscle (Edgar, 2004) in Seaview 4.3.4 (Gouy, 2012; Gouy et al., 2010); some manual adjustment was done for the non-coding sequences. For the nuclear loci, heterozygous sites were coded as ambiguous. Trees were estimated by Bayesian inference (BI) using MrBayes 3.2 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) as follows: (1) All loci were analysed separately (single-locus analyses, SLAs). (2) Sequences were also concatenated, partitioned by locus (in total 5 partitions), using rate multipliers to allow different rates for different partitions (Nylander et al., 2004; Ronquist and Huelsenbeck, 2003). We also ran analyses where, in addition to the five locus-specific partitions, the coding sequences were partitioned by codon (in total 9 partitions). (3) All analyses were run under the best-fit models according to the Bayesian Information Criterion (BIC), calculated in jModeltest 0.1.1 (Posada, 2008a, b), as well as (4) using the "mixed" command to sample across the GTR model space in the Bayesian MCMC (Huelsenbeck et al. 2004), and assuming rate variation across sites according to a discrete gamma distribution with four rate categories (Γ; Yang, 1994) and an estimated proportion of invariant sites (I; Gu et al., 1995). For cyt*b*, 16S and RAG, the model selected by the BIC was the general time-reversible (GTR) model (Lanave et al., 1984; Rodríguez et al., 1990; Tavaré, 1986) + Γ + I. For myo and ODC, the HKY model (Hasegawa et al., 1985) + Γ was chosen by the BIC. Ambiguous base pairs and indels were treated as missing data, but indels were plotted on the trees *a posteriori*. *Panurus biarmicus* and *Prinia bairdii* were chosen as outgroups based on the results of Alström et al. (2006), Johansson et al. (2008) and Fregin et al. (2012), except in the SLA of 16S, for which *Cisticola brachyptera*, *Prinia bairdii*, *Acrocephalus arundinaceus* and *Aegithalos concinnus* were used as outgroups (three latter downloaded from GenBank), as no 16S sequences were available for *P. biarmicus*. Default priors in MrBayes were used. Four Metropolis-coupled MCMC chains with incremental heating temperature 0.1 or 0.05 were run for 5–40×10^6 generations and sampled every 1000 generations. Convergence to the stationary distribution of the single chains was inspected in Tracer 1.5.0 (Rambaut and Drummond, 2009) using a minimum threshold for the effective sample size. The joint likelihood and other parameter values reported large effective sample sizes (>1000). Good mixing of the MCMC and reproducibility was established by multiple runs from independent starting points. Topological convergence was examined by eye and by the average standard deviation of split frequencies (<0.005). The first 25% of generations were discarded as "burn-in", well after stationarity of chain likelihood values had been established, and the posterior probabilities were calculated from the remaining samples (pooled from the two simultaneous runs).

The cyt*b* data set with multiple subspecies was analysed in BEAST version 1.7.4 (Drummond and Rambaut, 2007, 2012). XML files for the BEAST analyses were generated in BEAUti version 1.7.4 (Rambaut and Drummond, 2012). Analyses were run under the GTR + Γ model (cf. Weir and Schluter, 2008), using a "birth-death incomplete sampling" prior, and (a) a fixed clock rate of 2.1%/MY (Weir and Schluter, 2008) or (b) an uncorrelated lognormal relaxed clock (Drummond et al., 2006) with the same mean rate. Other priors were used with default values. For these analyses, 30×10^6 generations were run, sampled every 1000 generations. Every analysis was run twice. The MCMC output was analysed in Tracer version 1.5.0 (Rambaut and Drummond, 2009) to evaluate whether valid estimates of the posterior distribution of the parameters had been obtained. The first 25% of the generations were discarded as "burn-in", well after stationarity of chain likelihood values had been established. Trees were summarized using TreeAnnotator version 1.7.4 (Rambaut and Drummond, 2012), choosing "Maximum clade credibility tree" and "Mean heights", and displayed in FigTree version 1.3.1 Rambaut (2009).

The concatenated data were analysed by maximum likelihood bootstrapping (MLBS) and parsimony bootstrapping (PBS). MLBS (1000 replicates) was conducted with RAxML-HPC2 version 7.3.2 (Stamatakis, 2006; Stamatakis et al., 2008) on the Cipres portal (Miller et al., 2010). The data were partitioned by locus, and as per default GTRCAT was used for the bootstrapping phase, and GTRGAMMA for the final tree inference. PBS was performed in PAUP* version 4.0b10 (Swofford, 2001) on the complete dataset, using a heuristic search strategy, 1000 replicates, starting trees obtained by stepwise addition (random addition sequence, 10 replicates), TBR branch swapping, and MulTrees option not in effect (only one tree saved per replicate).

2.4. Summary of abbreviations

BI – Bayesian inference; cyt*b* – cytochrome *b* gene and part of the flanking tRNA-Thr; MLBS – maximum likelihood bootstrapping; myo – myoglobin intron 2; ODC – ornithine decarboxylase (mainly) introns 6–7; PBS – parsimony bootstrapping; PP – posterior probability; RAG – recombination activating gene, parts 1 and 2; SLA – single-locus analysis.

3. Results

3.1. Sequence characteristics

We obtained a contiguous ≤1002 bp of cyt*b*, ≤1016 bp of 16S, ≤729 bp of myo, ≤712 bp of ODC and ≤2878 bp of RAG. No unexpected stop codons or indels that would indicate the presence of nuclear pseudogenes were found in the coding sequences, although two three-bp and one six-bp indels were found in the aligned RAG sequences. The aligned cyt*b* sequences comprised 1002 characters, of which 439 (43.8%) were parsimony informative; 16S 1016 characters, 146 (14.4 %) parsimony informative; myo 761 characters, 115 (15.1 %) parsimony informative; ODC 746 characters, 148 (19.8 %) parsimony informative; and RAG 2878 characters, 218 (7.6 %) parsimony informative. The total dataset comprised 6403 characters, of which 1066 (16.6 %) were parsimony informative. The cyt*b* dataset comprising multiple samples for many species included 450 parsimony-informative characters (44.9%).

3.2. Concatenated multilocus analyses

The tree based on the concatenated multilocus data (Fig. 1) was overall well resolved and well supported by the data. There were three strongly supported primary clades (A–C), of which A and B were inferred to be sisters with high support. Clade A contained the mainly or entirely Palearctic genera *Calandrella* (“short-toed larks”), *Melanocorypha*, *Eremophila* (“horned larks”), *Galerida* (“crested larks”), *Alauda* (“skylarks”), *Lullula* (Woodlark), *Chersophilus* (Dupont’s Lark) and *Eremalauda* (Dunn’s Lark; Sahara/Arabia), as well as the Afrotropical *Spizocorys* and *Pseudalaemon* (Short-tailed Lark). Clade B included the Afrotropical-Oriental *Mirafra* (bushlarks) and Afrotropical *Calendulauda* and *Heteromirafra*. Clade C comprised the Afotropical *Certhilauda* (“long-billed larks”), *Chersomanes* (Spike-heeled Lark), *Pinarocorys* (“thrush-like larks”) and *Ammomanopsis* (Gray’s Lark), the single Malagasy *Mirafra* (Madagascar Lark), the Palearctic-Afrotropical-Oriental *Eremopterix* (“sparrow-larks”), *Ammomanes* (“desert larks”) and *Alaemon* (“hoopoe-larks”), and the Palearctic *Ramphocoris* (Thick-billed Lark).

Clade A could be subdivided into the strongly supported A1 and A2 (although A1 was contradicted by ODC; see *3.2*). Clade A1 contained *Calandrella*, *Melanocorypha*, *Eremophila* and the two monotypic genera *Eremalauda* and *Chersophilus*. The genus *Calandrella* was non-monophyletic, as some of its members (A1a) formed the sister clade to *Eremalauda/Chersophilus* (A1b), whereas the other members of this genus (A1d) were most closely related to *Eremophila* (A1e). Also the genus *Melanocorypha* was non-monophyletic, as five of its species were in clade A1c, whereas the sixth species (*M. leucoptera*) was in A2b. Clade A2 comprised, in addition to the single *Melanocorypha* species, the genera *Galerida* (A2a), *Alauda* (A2b) and *Spizocorys*, as well as the two monotypic genera *Pseudalaemon* and

Lullula (A2c); *Pseudalaemon* was nested among the *Spizocorys* species, whereas *Lullula* was sister to the others in clade A2c. The Palearctic A2a and A2b were sisters, separated from the Afrotropical (except *Lullula*) A2c.

Clade B could be separated into B1 and B2, both of which were strongly supported by the data. B1 included all *Mirafra* species (Africa and Asia) except the Malagasy *M. hova* and, as sister to these, the genus *Heteromirafra*. The *Mirafra* species formed four well supported clades (B1a–B1d). The rather poorly resolved clade B2 only contained the genus *Calendulauda*. Within this clade, clades B2a and B2b were well supported.

Clade C could be subdivided into the well supported clades C1 and C2. Clade C1 contained *Eremopterix* and *Mirafra hova* (C1a); the genus *Eremopterix* was non-monophyletic, although this was poorly supported, with conflicting reconstructions in different SLAs (see *3.3*). Clade C1b comprised *Ammomanes*, *Pinarocorys* and the monotypic *Ramphocoris*. In clade C2, *Certhilauda* (C2a), *Chersomanes* (C2b) and the monotypic genus *Ammomanopsis* formed a clade that was in effect trichotomous, with *Alaemon alaudipes* strongly supported as sister to these taxa.

3.3. Single-locus analyses

The trees based on single-locus analyses (SLAs) of single sequences per species varied in resolution: 77.8% of the nodes in the ingroup were bifurcating in the cyt*b* tree, 78% in the 16S tree, 72.6% in the ODC tree, 56.8% in the myo tree and 94.6% in the RAG tree (Supplementary Fig. 1; see also Fig. 1, where SLAs are shown in pie charts). Only the cyt*b* tree contained the complete set of species. There were a number of topological conflicts, which received ≥0.95 posterior probability (PP) in different SLAs (indicated by red pie wedges in Fig. 1): (1) *Calandrella raytal* and *C. rufescens* were sisters in the cyt*b* (PP 0.97) and myo (PP 1.00) trees, whereas *C. raytal* and *C. cheleensis* were sisters according to ODC (PP 1.00) (data incomplete for other loci); (2) RAG supported clade A1 (PP 1.00), whereas ODC supported a clade comprising A1d, A1e and A2 (PP 0.97) (other loci unresolved; however, the extended cyt*b* dataset inferred a clade with A1a–A1c + A2 with PP 0.99; cf. Fig. 2); (3) cyt*b*, myo and RAG supported a sister relationship between clades A and B (PP 0.79, 0.93 and 0.97, respectively; cyt*b* was raised to 1.00 in the extended dataset, cf. Fig. 2), and myo and RAG supported clade C (PP 0.91 and 1.00, respectively), whereas clade C1 was part of the A+B clade according to ODC (PP 0.98); (4) *Mirafra passerina* formed a clade with *M. cheniana*, *M. cantillans* and *M. javanica* in the 16S tree (PP 0.95), whereas it was sister to *M. williamsi* in the ODC tree (PP 1.00) (cyt*b* unresolved, myo and RAG incomplete); (5) clades

B1a–B1c formed a clade according to 16S, myo and ODC (PP 0.96, 1.00 and 0.98, respectively; cyt*b* unresolved), whereas RAG supported *M. apiata* from clade B1d as sister to clade B1c (PP 1.00); (6) *Calendulauda barlowi*, *C. erythrochlamys* and *C. burra* formed a clade according to cyt*b* (PP 0.97), whereas 16 S supported *C. barlowi*, *C. erythrochlamys* and *C. albescens* as a clade (PP 0.99) (data incomplete for other loci); (7) *Mirafra hova* was part of a clade containing all *Eremopterix* species except *E. australis* in the cyt*b* tree (PP 0.99), whereas *E. australis*, not *M. hova*, was sister to the other *Eremopterix* species in the 16S (PP 0.99) and RAG trees (PP 0.97; only *E. leucopareia* included of "other" *Eremopterix*), and according to ODC, *M. hova* and *E. australis* were more closely related to clade C1b (PP 0.96) than to the two other *Eremopterix* species included (*E. leucopareia*, *E. nigriceps*).

3.4. Indels

Several clades were supported by apparently synapomorphic indels in the alignments of 16S, myo and ODC (Fig. 1). All of these indels supported clades that received high PPs. In addition, the sister relationship between *Mirafra hova* and *Eremopterix australis* inferred by ODC but not by any other SLA or analysis of concatenated sequences (see *3.2*), was supported by three unique indels: a 4 bp deletion in the myo alignment and two 2 bp insertions in the ODC alignment.

3.5. Extended cytochrome b dataset

The dated tree containing multiple cyt*b* sequences for many species, including several subspecies (Fig. 2), basically agreed with the cyt*b* tree with single individuals of each species. Some nodes with PP ≤0.95 in the latter tree received PPs ≥0.95 in the extended dataset (indicated by footnote numbers in Fig. 1). The youngest split between widely sympatric, reproductively isolated sister species (the Asian *Melanocorypha maxima* and *M. mongolica*; de Juana et al., 2004) was dated to 3.0 million years ago (MYA) (95% HPD 2.0–4.1 MYA) (indicated by red line in Fig. 2). The most recent split between marginally sympatric, reproductively isolated species (*Galerida cristata* and *G. macrorhyncha*; Guillaumet et al., 2005, 2006, 2008) was estimated to 1.9 MYA (95% HPD 1.3–2.7 MYA; indicated by orange line in Fig. 2). A few allo-/parapatric taxa treated as separate species were inferred to be considerably younger than this (youngest pair, *Certhilauda brevirostris–C. semitorquata*, dated to 0.8 MYA, 95% HPD 0.4–1.3 MYA; indicated by purple line in Fig. 2). In contrast, several allo-/parapatric taxa treated as conspecific (in one case even consubspecific) were inferred to have diverged much longer ago. The deepest split, between *Calandrella b.*

brachydactyla/C. b. rubiginosa and *C. b. dukhunensis*, which were not even inferred to be sisters, was dated to 6.0 MYA (95% HPD 4.6–7.5 MYA; indicated by blue line in Fig. 2).

4. Discussion

4.1. Phylogeny

4.1.1. Large-scale topology

This is the first comprehensive molecular study of relationships in the family Alaudidae. The only previously published study (Tieleman et al., 2003) was based on cyt*b* and 16S for 22 species. However, nearly all of the cyt*b* and all of the 16S sequences of the African and some of the Western Palearctic species presented in this study, as well as some RAG sequences for exemplars from major lineages, were analysed in an unpublished PhD thesis (Barnes, 2007). The findings of this thesis formed the basis of several novel generic allocations presented in handbooks over the last decade (de Juana et al., 2004; Hockey et al. 2005). The phylogenetic hypothesis in Fig. 1 is mostly well resolved and well supported by the data, although some clades (notably A2c, B1a, B2 and C1a) include several polytomies or poorly supported nodes. The primary clades A–C, as well as the sister relationship between A and B, are strongly supported.

4.1.2. Clade A

Although clade A1 is strongly supported by the concatenated data (PP 1.00, MLBS 93%, PBS 89%), it is only recovered in one SLA (RAG) and is strongly contradicted by the SLA of ODC and by the analysis of the extended cyt*b* dataset. Moreover, the topologies of the ODC and cyt*b* trees differ from each other, resulting in three strongly supported incongruent topologies. Accordingly, clade A1 should be considered highly uncertain despite the high statistical support. This underscores the importance of critical evaluation of results, rather than just accepting high support at face value. It is possible that a species tree approach could have reconciled the incongruence among the gene trees, if it was caused by hemiplasy (reviewed by Avise and Robinson, 2008; Degnan and Rosenberg, 2009; Edwards, 2009; Liu et al., 2009). However, our data are not suitable for species tree analysis, as most species are just represented by single samples, and not all loci are available for all species. In contrast to clade A1, clade A2 is recovered with high confidence.

Within clade A1, the unexpected sister relationships between the two monotypic genera *Chersophilus* and *Eremalauda* (A1b) and between this clade and the *Calandrella rufescens-cheleensis-raytal-athensis* complex (A1a) are well supported by the data. The strongly supported sister relationship between the *Calandrella cinerea-brachydactyla-acutirostris* complex (A1d) and *Eremophila* (A1e) is equally surprising. All of these relationships are recovered in SLAs of two unlinked loci and are not contradicted by any other SLAs, and the A1d+A1e clade also receives support from an indel in the ODC alignment. Accordingly, these relationships all seem robust. *Eremalauda dunni* often has been placed in *Ammomanes* (Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960; Wolters, 1979 [subgenus *Eremalauda*]), but a close relationship with the type species of this genus (*A. cinctura*; clade C1b) is strongly refuted by the present study. Meinertzhagen's (1951) placement of *Chersophilus* in *Certhilauda* (together with e.g. *Alaemon* and *Chersomanes*), based on especially bill structure and behaviour, is strongly rejected by our data.

A close relationship between *Galerida*, *Alauda* and *Melanocorypha leucoptera* (clade A2a+b) is supported by all loci. *Melanocorypha leucoptera* is firmly nested in this clade, and hence far removed from the other *Melanocorypha* (A1c). The sister relationship with *Alauda* receives high PP and moderate bootstrap support, although this is only supported by ODC in the SLAs. This is further supported by a closer resemblance to *Alauda* than to *Melanocorypha* or *Galerida* in morphology, vocalizations, behaviour and ecology (de Juana et al., 2004; P.A. and Krister Mild, unpublished), although – as has repeatedly been revealed by the present study –morphological similarity can be an extremely poor indicator of relationship among larks (see also *4.4*, below). *Galerida magnirostris* and *G. modesta* have been placed in the monotypic genera *Calendula* (Pätzold, 2003; Wolters, 1979) and *Heliocorys* (Wolters, 1979), respectively.

The generic affinity of the Raso Island (Cape Verde) endemic *Alauda razae* has long been unsettled. This species has been placed in *Spizocorys* (Boyd Alexander, 1898), *Calandrella* (Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960; Vaurie, 1959), *Alaudala* (Wolters, 1979), *Alauda* (Dean et al., 1992; Dickinson, 2003; de Juana et al., 2004; Gill and Donsker, 2012; Hall, 1963), and Voous (1977) argued that its affinities are with African larks (e.g. *Pseudalaemon*). Hazevoet (1989, 1995) supported the placement in *Alauda* based on similarities with that genus in song, calls and displays (including song-flight). The molecular data corroborate this. However, our data are inconclusive with respect to the relationships among the three species of *Alauda*, although MLBS (72%) and PBS (67%) suggest that *A. arvensis* and *A. gulgula* are sisters.

The clade containing the five *Spizocorys* species (A2c) and the Short-tailed Lark *Pseudalaemon fremantlii* is strongly supported, although for half of these only cyt*b* and 16S are available. The latter is usually placed in a monotypic genus (Dean et al., 1992; de Juana et al., 2004; Dickinson, 2003; Gill and Donsker, 2012; Pätzold, 2003; Peters, 1960; Wolters, 1979), whereas *S. starki* has variously been placed in *Calandrella* (Meinertzhagen, 1951; Peters, 1960; Wolters, 1979) or *Eremalauda* (Dean, 1989; Dean et al., 1992; Dickinson, 2003). The placement of *S. starki* in *Spizocorys* by de Juana et al. (2004) and Hockey et al. (2005) was based on unpublished mitochondrial DNA data from Barnes (2007). Also *S. fringillaris* has been placed in a monotypic genus, *Botha* (Wolters, 1979; Pätzold, 2003). Meinertzhagen (1951) placed *S. fringillaris*, *S. conirostris*, *S. sclateri* and *S. personata* in *Calandrella*. Our data refute a close relationship between any of the *Spizocorys* species and *Calandrella* or *Eremalauda*.

The sister relationship between the sub-Saharan *Spizocorys/Pseudalaemon* and Western Palearctic monotypic genus *Lullula* is well supported. Previous authors have debated whether *Lullula* should be recognised or synonymised with *Alauda* (de Juana et al., 2004; Harrison, 1966; Meinertzhagen, 1951), and Tieleman et al. (2003) inferred a sister relationship between *Lullula* and *Alauda arvensis* based on cyt*b* and 16S. However, the present study refutes a close relationship between *Lullula* and *Alauda*.

4.1.3. Clade B

The sister relationship between the *Mirafra*/*Heteromirafra* clade (B1) and the *Calendulauda* clade (B2) is strongly supported (albeit only inferred by two SLAs, one with PP <0.95, one with PP ≥0.95), as is the sister relationship between *Mirafra* and *Heteromirafra*. The close relationship between the two major clades was partly unexpected, although three of the *Calendulauda* species have previously been placed in *Mirafra* (see below). A close affinity between *Mirafra* and *Heteromirafra* has formerly been assumed (Dean et al., 1992), and the latter genus has been synonymized with the former (Pätzold, 2003).

Within *Mirafra*, the four clades B1a–B1d are recovered with a high degree of confidence. The close relationship between the five Asian species in clade B1a is unsurprising, as they are all morphologically very similar, and four of them have been treated as conspecific (see *4.3*). However, the relationships among these are mostly unsupported, and only cyt*b* provides slight resolution in the SLAs. Clade B1b comprises a mix of African and Asian/Australasian taxa, including the extremely widespread *M. cantillans* and *M. javanica* (see *4.3*). The close relationship between these two, which have previously been considered conspecific (see *4.3*), and *M. cheniana*, *M. passerina* and *M. williamsi* has been suggested based on morphological similarity (de Juana et al., 2004; Wolters, 1979). Clades B1c and B1d contain exclusively African species, and the sister species *M. africana* and *M. hypermetra*, as well as *M. apiata* and *M. fasciolata*, have been considered to be conspecific or form superspecies (see *4.3*), so their close associations were expected. In contrast, the predicted close relationship between *M. rufocinnamomea*/*M. angolensis* and the *M. apiata* complex (Dean et al., 1992; de Juana et al., 2004; Pätzold, 2003) is unsupported, and the close association (subgenus *Corypha*) between these and *M. africana* and *M. hypermetra* (and *M. somalica* and *M. sharpii*, which were not included here) is only partly supported (*M. africana*, *M. hypermetra*, *M. apiata* and *M. fasciolata*; clade B1d).

Clades B2a and B2b are both strongly supported (though only cyt*b* and 16S are available for all but one of these species), although all of the relationships within clade B2a except the sister relationship between *C. barlowi* and *C. erythrochlamys* are effectively unresolved. The taxonomic history of the taxa in clade B2a is checkered. Two or three of the species *C. albescens*, *C. barlowi* and *C. erythrochlamys* have been treated as conspecific (see *4.3*), and they have variously been placed in *Certhilauda* (Dean et al., 1992; Dickinson, 2003; Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960) or *Calendulauda* (de Juana et al., 2004; Wolters, 1979). *C. burra* has been placed in *Ammomanes* (Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960), *Certhilauda* (Dean et al., 1992; Dickinson, 2003) or *Calendulauda* (de Juana et al., 2004; Wolters, 1979). The four remaining species in clade B2 (*C. africanoides*, *C. alopex*, *C. poecilosterna*, *C. sabota*) have all been placed in the genus *Mirafra* (Dean et al., 1992; Dickinson, 2003; Pätzold, 2003; Peters, 1960), or, the two latter, in *Sabota* (Wolters, 1979), but they were moved to *Calendulauda* by de Juana et al. (2004) based on unpublished genetic data from Barnes (2007).

4.1.4. Clade C

Clades C1 and C2 are both strongly supported by the data. Their sister relationship seems fairly robust (SLAs: 16S PP 0.94, myo PP 0.92, RAG PP 1.00), although it is strongly contradicted by ODC, according to which clade C1 was part of clade A+B (PP 0.99). Clade C1a is also strongly supported (PP 1.00; four SLAs PP 1.00 for all included species). Within C1a, a clade comprising five species of *Eremopterix* is well supported, although the relationships among these are effectively unresolved. The proposed close (superspecies) relationships between *E. signatus* and *E. verticalis* and between *E. leucopareia* and *E. griseus*, respectively (Dean et al., 1992), are neither supported nor rejected. The positions of *E. australis* and *Mirafra hova* in relation to each other and to the other five *Eremopterix* species is highly uncertain: the inclusion of *M. hova* in this clade is most unexpected (see *4.4*).

The surprising mix of three morphologically divergent genera (see *4.4*) in clade C1b is well supported by the data, as are the sister relationships of the two *Ammomanes* species and of the two *Pinarocorys* species. In contrast, the sister relationship between *Ramphocoris* and *Ammomanes* receives varying support in different analyses of the concatenated data: PP 0.86, MLBS 99% and PBS 67%. At any rate, the suggested close affinity between *Ramphocoris* and *Melanocorypha* (Dean et al., 1992; Meinertzhagen, 1951; Voous, 1977; Pätzold, 2003) is strongly rejected. The same applies to the suggestion that *Pinarocorys* be synonymized with *Mirafra* (Meinertzhagen, 1951; Peters, 1960).

Clade C2 contains a heterogeneous collection of species, which separate into three main lineages that in effect form a trichotomy. One of these (C2a) contains the *Certhilauda* species, of which five (all except *C. chuana*) have previously been treated as conspecific (see *4.3*). The suggestion that *C. chuana* be placed in *Mirafra* (Pätzold, 2003; Peters, 1960) is strongly rejected. One (Peters, 1960) or both (Pätzold, 2003) of the two species of *Chersomanes* (C2b), which have frequently been treated as conspecific (see *4.3*), have also been placed in the genus *Certhilauda*. *Ammomanopsis grayi* has usually been placed in *Ammomanes* (Dean et al., 1992; Dickinson, 2003; Pätzold, 2003; Meinertzhagen, 1951; Peters, 1960; Wolters, 1979), but was moved to the monotypic genus *Ammomanopsis* by de Juana et al. (2004) and Hockey et al. (2005), based on unpublished genetic data from Barnes (2007). The present study corroborates the more distant relationship with *Ammomanes*. *Alaemon alaudipes* is strongly supported as sister to the rest of clade C1; it would be interesting to confirm whether the Lesser Hoopoe Lark *Alaemon hamertoni* (not sampled in this study) is part of this clade.

4.2 Taxonomic implications at the generic level

Our findings highlight the large number of relationships suggested by molecular data that conflict with previous morphology-based classifications (e.g. Dickinson, 2003; Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960; Sibley & Monroe, 1990; Wolters, 1979; cf. Fig. 3). The treatments by de Juana et al. (2004), Hockey et al. (2005) and Gill and Donsker (2012) are more closely aligned with our findings because they were partly based on mitochondrial data from Barnes (2007) that is only now being published here.

Harrison (1966) suggested, based on a detailed study of morphological characters, that *Galerida*, *Lullula* and *Pseudalaemon* be synonymized with *Alauda*. At the time, three of the species presently placed in *Galerida*, i.e. *G. deva* (not included in the present study), *G. magnirostris* and *G. modesta*, were placed in monotypic genera (*Spizalauda*, *Calendula* and *Heliocorys*, respectively), and *A. razae* was placed in a monotypic *Spizocorys*. The present study supports Harrison's (1966) proposal only if *Spizocorys* also is included in *Alauda*, i.e. the entire clade A2 is referred to as *Alauda*. However, we prefer to retain *Galerida*, *Alauda*, *Lullula* and *Spizocorys*. There is no support for upholding the monotypic genus *Pseudalaemon*, so we synonymize this with *Spizocorys*. *Melanocorypha leucoptera* has been considered to form a superspecies with *M. mongolica* based on plumage similarity and parapatric distributions (Cramp, 1988; Glutz von Blotzheim and Bauer, 1985). However, as the molecular data suggest that *M. leucoptera* is not closely related to the other *Melanocorypha* species (including the type species of the genus, *M. yeltoniensis*), it should be removed from this genus. Its affinity with *Alauda* is strongly supported in the concatenated analysis, although, as has been pointed out above, this might rest entirely on ODC. As a close relationship with *Alauda* is indicated also by morphological, vocal, behavioural and ecological data (de Juana et al., 2004; P.A. and Krister Mild, unpublished), we propose that it be treated as *Alauda leucoptera*.

The non-monophyly of *Calandrella* is strongly supported by our data. The type species of this genus, *C. brachydactyla*, is in clade A1d. Accordingly, the species in this clade should retain the generic name *Calandrella*. For clade A1a, the generic name *Alaudala* Horsfield and Moore, 1856 is available (type species: *Calandrella raytal*), and we propose that this name be used for the species in this clade, i.e. *A. rufescens*, *A. cheleensis*, *A. raytal* and *A. athensis* (as was already done by Wolters, 1979, except for the last one, which was placed in the genus *Calandrella*).

Mirafra hova is firmly anchored in clade C1a, together with *Eremopterix*. Although it is uncertain whether it is sister to all *Eremopterix*, to all *Eremopterix* except *E. australis*, or to *E. australis*, we propose that it be recognised as *Eremopterix hova*.

4.3. Taxonomic implications at the species level

Although the main focus of this paper is not on species level taxonomy, some of the results provide important contributions to ongoing debates about species limits, and some reveal previously unknown deep divergences. We do not advocate the use of cut-of values in genetic divergence as taxonomic yardsticks, but instead support an integrative approach based on independent data, whatever species concept is adopted. As dating based on the molecular clock is uncertain (e.g. García-Moreno, 2004; Lovette, 2004; Penny, 2005; but see Weir and

Schluter, 2008, whose average rate we have adopted), we emphasize the relative ages of different clades more than the actual ages inferred.

Guillaumet et al. (2005, 2006, 2008) discovered two primary clades within *Galerida cristata*, which had reached reciprocal monophyly in mtDNA and showed evidence of strong reproductive isolation in their narrow contact zone in Morocco. These were later recognised as separate species, *Galerida cristata sensu stricto* and *G. macrorhyncha* (Gill and Donsker, 2012). The split between these clades is here estimated to be approximately two thirds of that between the youngest widely sympatric reproductively isolated sister species. As all available *G. macrorhyncha* sequences are from Morocco, at the western edge of the purported range of the taxon *randoni* (Cramp, 1988; de Juana, 2004), and as there are no samples from or close to the Algerian type localities of *randoni* and *macrorhyncha*, more research is needed on the circumscription and nomenclature of these taxa.

Guillaumet et al. (2008) showed using cyt*b* sequences that the subspecies *Galerida theklae praetermissa* (Ethiopia) and *G. t. ellioti* (Somalia) are deeply diverged from the northwest African subspecies, and also fairly distinct from each other. Using mainly the same data, the present study infers the split between the populations from northwest Africa and the Horn of Africa to be approximately the same as that between the youngest widely sympatric reproductively isolated species pair. The separation between the two Horn of Africa taxa is inferred to be similar to that between the reproductively isolated, marginally sympatric *G. cristata* and *G. macrorhyncha*. A taxonomic revision is evidently called for, including sequence data for the taxa in the Horn of Africa for which no molecular data are available (*G. t. harrarensis*, *G. t. mallablensis*, *G. t. huriensis*), and additional data on the Horn of Africa *G. t. huei*, for which a short cyt*b* fragment indicated substantial divergence from *praetermissa* (Guillaumet et al., 2008).

The taxonomy of the *Calandrella rufescens*-*C. cheleensis*-*C. athensis*-*C. raytal* complex has been much debated (e.g. Dickinson, 2003; Dickinson and Dekker, 2001; de Juana et al., 2004; Gill and Donsker, 2012; Hall & Moreau, 1970; Meinertzhagen, 1951; Peters, 1960; Sibley and Monroe, 1990; Stepanyan, 1967; Wolters, 1979), although there is no consensus among authors regarding the taxonomy of these species. The present study supports the idea that *cheleensis* and *athensis* are specifically different from *C. rufescens minor*, although the limited taxonomic sampling does not permit a proper taxonomic revision. That *C. raytal* is nested within this complex was an unexpected new finding, although Meinertzhagen (1951) treated it as conspecific with *C. rufescens* (including *C. cheleensis*). Although the sister relationship between *C. raytal* and *C. rufescens* was strongly supported in the concatenated analysis, this was only inferred in SLAs of cyt*b* and myo, whereas ODC strongly supported a sister relationship between *C. raytal* and *C. cheleensis*, so additional data would be required to elucidate the precise position of *C. raytal*.

Calandrella brachydactyla has been treated as a subspecies of *C. cinerea* (e.g. Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960; Stepanyan, 1990; Vaurie, 1959), but is nowadays usually considered a separate species (e.g. Cramp, 1988; Dean et al., 1992; de Juana et al., 2004; Dickinson, 2003; Gill and Donsker, 2012; Glutz von Blotzheim and Bauer, 1985; Hall and Moreau, 1970; Sibley and Monroe, 1990; Wolters, 1979). Meinertzhagen (1951) included also *C. acutirostris* in *C. cinerea sensu lato*. The results from the present study confirm deep splits between *C. cinerea*, *C. brachydactyla* and *C. acutirostris*, adding further support to the treatment of these as different species. However, completely unexpectedly, they also suggest a deep separation between *C. brachydactyla rubiginosa/C. b. longipennis* from Morocco and Kazakhstan, respectively, and *C. b. dukhunensis* from Mongolia, and strongly support a sister relationship between the latter and *C. acutirostris*. As these results are only based on mitochondrial DNA, a more comprehensive study is needed before any taxonomic revision can be undertaken.

The genus *Eremophila* comprises only two species. *Eremophila bilopha* is restricted to North Africa and the Middle East, whereas *E. alpestris* is the most widely distributed of all lark species, breeding on five continents, and is the only lark native to the New World (de Juana et al., 2004). Morphological variation is pronounced in *E. alpestris*, with 40–42 subspecies recognised (de Juana et al., 2004; Peters, 1960). The present study includes just a small portion of this variation, but nevertheless indicates that *E. alpestris* is probably better treated as multiple species. That our sample of the Central Asian *E. a. brandti* is inferred to be more closely related to the two North American samples than to the other Eurasian taxa is totally unexpected, and requires confirmation. If corroborated by independent data, this implies a complex biogeographical history for this species group.

The widespread *M. cantillans*, which ranges from west Africa to India, and the similarly widely distributed *M. javanica*, from Myanmar to Australia (de Juana et al., 2004) have previously been considered conspecific (Dickinson and Dekker, 2001; Pätzold, 2003; Peters, 1960; Vaurie, 1951; reviewed in first reference). The close relationship between these two is confirmed by the present study. Both species are monophyletic in the cyt*b* tree, although their separation is comparatively recent (1.2 MYA; 0.7–1.7 MYA, 95% HPD), only slightly more than one third of the age of the youngest widely sympatric species pair. These taxa have apparently spread over a vast area in a very short time, and are in the early stages of the speciation process. Although the extended cyt*b* tree suggests that they are independently evolving lineages, additional sampling might reveal incomplete sorting of haplotypes, and the ODC sequences do not sort according to species. Independent data are needed to corroborate our results.

Mirafra affinis, *M. erythrocephala* and *M. microptera* were previously treated as subspecies of *Mirafra assamica* (reviews in Alström, 1998; Dickinson and Dekker, 2001). Alström (1998) proposed that these four (using the name *M. marionae* for *M. erythrocephala*) were better treated as separate species, based on pronounced differences in especially vocalizations and display-flights. This is corroborated by the evidence presented here (and has been accepted by most recent authors, e.g. de Juana et al., 2004; Dickinson, 2003; Gill and Donsker, 2012). Although the relationships among these species are largely unsupported, our data suggest that *M. erythroptera* is nested within the *M. assamica* complex, and that *M. microptera* is sister to the others. The splits among these species are inferred to be at least twice as old as the oldest widely sympatric sister pair in the entire study.

Mirafra apiata and *M. fasciolata* were traditionally treated as conspecific (e.g. Dean et al., 1992; Pätzold, 2003; Peters, 1960; Wolters, 1979), but have recently been suggested to be separate species (de Juana et al., 2004; Hockey et al., 2005) based on limited unpublished genetic data. The present study confirms that these two taxa have been separated for a long time.

Calendulauda albescens, *C. barlowi* and *C. erythrochlamys* have been treated as conspecific (under the first name; Peters, 1960; Wolters, 1979), or *C. erythrochlamys* has been split off as a separate species (Dean et al., 1992; Sibley and Monroe, 1990). Ryan et al. (1998) suggested, based on a study of cyt*b*, morphology and song, that three species should be recognized, and this has been followed by most subsequent authors (Dickinson, 2003; de Juana et al., 2004; Gill and Donsker, 2012; Hockey et al., 2005). The relationships among these are uncertain, as cyt*b* and 16S support different topologies in relation to *C. burra*. The extended cyt*b* dataset suggests deep splits among *C. albescens*, *C. burra* and *C. barlowi/C. erythrochlamys*, considerably older than the split between the widely sympatric *Melanocorypha maxima* and *M. mongolica*, adding further support to the treatment of these as separate species. However, the divergence between *C. barlowi* and *C. erythrochlamys* is the second most recent of all pairs treated as different species. Accordingly, in the absence of other data, whether *C. barlowi* should be given species status or treated as a subspecies of *C. erythrochlamys* (by priority) is an open question. The same applies to *C. alopex*, which is often considered a subspecies of *C. africanoides* (e.g. Dean et al., 1992; Pätzold, 2003; Peters, 1960), although the divergence between these two is slightly deeper than between *C. barlowi* and *C. erythrochlamys*.

Ammomanes deserti is widely distributed across North Africa to western India, with 23–24 subspecies recognised (de Juana et al., 2004; Peters, 1960). Although the present study only covers a tiny fraction of the geographical variation, it nevertheless infers four deeply-diverging cyt*b* lineages, suggesting that *A. deserti* is in need of further study and taxonomic revision. Additionally, *A. cinctura*, which occurs from the Cape Verde islands through North Africa to southwest Pakistan, with three subspecies recognised (de Juana et al., 2004; Peters, 1960) shows an unexpected deep cyt*b* divergence between samples of the same subspecies (*arenicolor*) from Morocco and Saudi Arabia. More extensive sampling of this species also is warranted.

Five *Certhilauda* species (all except *C. chuana*) previously have been treated as conspecific under the name *C. curvirostris* (Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960; Wolters, 1979), although they have recently been split based on differences in mitochondrial DNA (Ryan and Bloomer, 1999; followed by Dickinson, 2003; de Juana et al., 2004; Gill and Donsker, 2012; Hockey et al., 2005). The divergence between *C. subcoronata* and *C. benguelensis* is substantial (despite limited morphological differentiation), as is the difference between these two and the three other species in this complex. In contrast, the separation between *C. brevirostris*, *C. semitorquata* and *C. curvirostris* is much more recent. Divergence between the two former taxa is the shallowest of all taxa currently treated as different species, yet they have divergent ranges, separated by a population of *C. subcoronata*. These three taxa are in the early stages of the speciation process, and their taxonomic ranking is therefore open to different interpretations.

The two *Chersomanes* species (C2b) were previously often considered conspecific (Dean et al., 1992; Pätzold, 2003), but were separated by de Juana et al. (2004) based on unpublished genetic differences, widely disjunct distributions and differences in sexual plumage dimorphism (slight in *beesleyi*, absent in *albofasciata*). This separation has since been questioned (Donald and Collar 2011), but the present study confirms their long separation, adding further support to their treatment as separate species (although better coverage of northern populations of *albofasciata* is desirable).

4.4. Strongly heterogeneous morphological evolution

Larks provide extraordinary examples of the effects of natural selection on phenotypes, and few groups of birds show the same level of disagreement between taxonomy, based on morphology, and phylogenetic relationships as inferred by DNA. Although the present study does not examine morphological divergence quantitatively, it nevertheless indicates multiple examples of highly conserved phenotypes as well as dramatic morphological divergence in certain lineages and instances of parallel evolution (Fig. 3). Traits related to feeding, such as size and shape of bill, appear to be particularly labile, with striking differences between some sister species as well as, conversely, close similarities among distantly related species. For larks, which inhabit mostly open habitats, cryptic plumages are evidently important. Consequently, the strength of streaking and colour shades above appear to be particularly adaptable, reflecting the amount of vegetation cover (aridity) and substrate colour more than phylogeny.

The similarities in size, structure and plumage between the two distantly related clades of traditional *Calandrella* (here recognized as *Calandrella* and *Alaudala*; cf. de Juana et al., 2004; Fig. 3) are likely the result of either retained plesiomorphies or parallel evolution. The similarity between the north African/west Asian *Eremalauda dunni* and Afrotropical *Spizocorys starki*, between the Western Palearctic *Chersophilus* and Afrotropical *Certhilauda*, and between the north African/west Asian *Ammomanes* and Afrotropical *Ammomanopsis* (cf. de Juana et al., 2004; Fig. 3) provide examples of close morphological similarity evolving independently in similar environments. In contrast, the dissimilarity between *Ammomanopsis* and its closest relatives, *Chersomanes* and *Certhilauda*, suggests strong divergence in the former.

The sister relationship between the genera *Calandrella* (as redefined here) and *Eremophila* suggests remarkable plumage divergence in the latter lineage (which is one of the most aberrant of all larks; cf. de Juana et al., 2004 and Fig. 3). Similarly, the close relationship between *Alaudala* (as redefined here; clade A1a) and the two monotypic genera *Eremalauda* and *Chersophilus* reveal extraordinary changes in both structure (especially bill) and plumage among sister taxa (cf. de Juana et al., 2004; Fig. 3). Meinertzhagen's (1951) inappropriate placement of *Chersophilus*, *Pseudalaemon*, *Calendulauda*, *Alaemon*, *Chersomanes* and *Certhilauda* in one genus based on bill structure and behaviour (notably strong digging with the bill when feeding, and fast running) is a striking example of a misclassification caused by the strong lability and adaptability of bill morphology in larks.

Within the true *Melanocorypha* clade (A1c), there is much variation, especially with respect to plumage (cf. de Juana et al., 2004; Fig. 3). *M. yeltoniensis* is one of the few larks with pronounced sexual dimorphism in plumage: females have cryptic, plesiomorphic, plumages reminiscent of *M. bimaculata* and *M. calandra*, whereas males are practically all black in the breeding season (somewhat more cryptic in the non-breeding season); also the size differences between females and males are pronounced. The plumage similarity between *M. mongolica* and *Alauda leucoptera* (previously *M. mongolica*), which has been assumed to be due to close relationship (e.g. Pätzold, 2008; Wolters, 1979) is apparently due to parallel evolution.

Apart from *Melanocorypha yeltoniensis*, the sparrow-larks *Eremopterix* spp. are the only larks with strong sexual plumage dimorphism, and the male plumages are contrastingly patterned in black and white on the head and underparts, except in *E. australis*, which lacks white (cf. de Juana et al., 2004; Fig. 3). However, the strongly supported inclusion of the Madagascar endemic *Mirafra hova* in this clade, and hence its suggested transfer to *Eremopterix*, is most remarkable in view of its strikingly different plumage from all plumages of other *Eremopterix* species and close similarity to some *Mirafra* species (cf. de Juana et al., 2004; Fig. 3). The uncertainty regarding its position in the tree in relation to *E. australis* (and hence also the other *Eremopterix* species) precludes reconstruction of the evolution of sexual dimorphism and typical male *Eremopterix* plumage.

Apart from the species with strong sexual dimorphism in plumage, *Melanocorypha yeltoniensis* and the sparrow-larks *Eremopterix* spp. (except *E. hova*), slight plumage differences between the sexes is present in *Eremophila* spp., *Alauda leucoptera*, *Ramphocoris clotbey* and *Pinarocorys erythropygia* (de Juana et al., 2004), showing that sexual plumage dimorphism has evolved multiple times.

The molecular data suggest that the similarities between *Galerida theklae* and *G. malabarica*, which have often been treated as conspecific (e.g. Dean et al., 1992; Hall and Moreau, 1970; Howard and Moore, 1994), are due to parallel evolution, although retention of plesiomorphies cannot be eliminated based on the available data. In contrast, the divergent morphology of the Cape Verde endemic *Alauda razae* (not shown) compared to the other species of *Alauda* (cf. de Juana et al., 2004) has misled earlier workers regarding its generic affinities (Boyd Alexander, 1898; Meinertzhagen, 1951; Pätzold, 2003; Peters, 1960; Vaurie, 1959; Voous, 1977; Wolters, 1979). This disparity agrees with the rapid morphological evolution typical of many small island populations (Grant, 1998).

Within the *Spizocorys* clade there is considerable variation (cf. de Juana et al., 2004; Fig. 3), especially with respect to pigmentation, head pattern (notably *S. personata*) and bill size/shape (especially *S. fremantlii*), which has confused earlier taxonomists. The morphological similarity between *Spizocorys* and *Calandrella* (which led Meinertzhagen, 1951, to unite these genera) is apparently the result of parallel evolution. Conversely, based on morphology (cf. de Juana et al., 2004; Fig. 3), the close relationship between *Spizocorys* and the monotypic *Lullula* is totally unexpected. Similarly, the close relationship between *Ramphocoris*, *Pinarocorys* and *Ammomanes* is highly surprising when viewed from a purely morphological perspective; in particular the bill morphology of *Ramphocoris* is unique among the larks (cf. de Juana et al., 2004; Fig. 3).

In the *Mirafra/Heteromirafra* clade (B1), plumage variation mainly concerns colour tones and strength of streaking, whereas the variation in bill morphology is more pronounced (cf. de Juana et al., 2004; Fig. 3). Morphological divergence has apparently been extremely slow over substantial time periods in some clades, e.g. in the five species in the *M. assamica*-*M. erythroptera* compex (clade B1a), which until recently was usually treated as two species, but which was here inferred to have been separated for millions of years. Conversely, in the closely related *Calendulauda* clade (B2), the variation in plumage and structure is so pronounced (cf. de Juana et al., 2004; Fig. 3) that the species placed in this genus have previously been placed in five different genera. Even within clade B2a, the variation in plumage and bill size is marked.

5. Conclusions

Our analyses support the contention that incomplete data sets, especially those where one or a few loci have been consistently sampled from all taxa, can provide robust, well-resolved hypotheses of relationship (Wiens et al., 2005; Wiens and Morrill, 2011; but see Lemmon et al., 2009). Overall, our concatenated tree shows little conflict with individual gene trees, but a few specific relationships do show evidence of conflict, possibly due to differential lineage sorting. This highlights the continued importance of performing single gene as well as combined data analyses, since the latter may obscure significant incongruence behind strong nodal support values. The multilocus tree inferred here revealed many unpredicted relationships, including some non-monophyletic genera. The dated cyt*b* tree indicated some unexpectedly deep divergences between taxa currently regarded as subspecies and one non-monophyletic species, as well as some comparatively shallow splits between currently recognised species. The phylogeny indicates multiple examples of parallel morphological evolution, probably resulting from variation in selective forces (both natural and sexual) associated with the broad array of open habitats where larks occur. In contrast to the overall rather conserved plumage evolution in larks, some close relatives show dramatic differences in plumage and bill structure, with the latter appearing to be particularly labile. Future work should focus on quantifying rates of evolution in these traits in the context of our robust phylogenetic framework. Few groups of birds show the same level of disagreement between morphologically-based taxonomy and phylogenetic relationships as inferred using DNA data.

6. Acknowledgements

We are most grateful to the following colleagues and institutions for providing samples and/or for assistance in the field: Raül Aymí, Neil and Liz Baker, John Bates, Oleg Belyalov, Geoff Carey, Callan Cohen, Nigel Collar, Miles Coverdale, Edward Gavrilov, Andrew Grieve, Cornelis Hazevoet, Daniel Hooper, Nick Horrocks, Björn Johansson, Joris Komen, Andrew Lassey, Paul Leader, Dave Moyer, H. Nikolaus, Trevor Price, Hadoram Shirihai, Claire Spottiswoode, Martin Stervander, Lars Svensson, Irene Tieleman, Per Undeland, Jo Williams, Bill Zetterström; Leon Bennun and George Amutete and the Kenyan National Museum; Leo Joseph and the Australian National Wildlife Collection; Michel Louette and the Royal Museum for Central Africa, Tervuren; Göran Frisk, Ulf Johansson and Peter Nilsson and the Swedish Museum of Natural History; Silke Fregin and Martin Haase and the Vogelwarte Hiddensee, Ernst Moritz Arndt University of Greifswald; Jan Lifjeld and the National Centre for Biosystematics, Natural History Museum, Oslo; John Bates and the Field Museum of Natural History, Chicago; Jean-Marc Pons and the Muséum National d'Histoire Naturelle, Paris; and Sharon Birks and the University of Washington Burke Museum. Our sincerest thanks also to Wayne Delport, Lisel Solms and Isa-Rita Russo for assistance in the lab, and to Shimiao Shao for submitting the sequences to GenBank. We also thank Josep del Hoyo, Andrew Elliott and Lynx Edicions for permitting the use of paintings of larks from the Handbook of the Birds of the World, and to Anders Rådén for assistance in their scanning. We are indebted to Jornvall Foundation, Riksmusei Vänners Linnaeus award and the Chinese Academy of Sciences Visiting Professorship for Senior International Scientists (No. 2011T2S04) (all to P.A.); to the Pakistan Science Foundation (research project No. PSF/Res. / P-BZU/Bio(340); to A.A.K and M.A.Q.); and to University of Cape Town and South African National Research Foundation (to P.B. and P.G.R.). Collections in Morocco were facilitated and funded in part by the International Foundation for the Development and Conservation of Wildlife (IFCDW). We are most grateful to Margaret Koopman at the Niven Library, Percy FitzPatrick Institute of African Ornithology, for locating important references; to Krister Mild and Jan Sundler for various assistance; to Normand David for his expert advice on the ending of the name *Eremopterix hova*; and to two anonymous reviewers for comments on the manuscript.

References

Allen, E.S., Omland, K.E., 2003. Novel intron phylogeny supports plumage convergence in orioles (*Icterus*). Auk 120, 961–969.

Alström, P., 1998. Taxonomy of the *Mirafra assamica* complex. Forktail 13, 97–107.

Alström, P., Ericson, P.G.P., Olsson, U., Sundberg, P., 2006. Phylogeny and classification of the avian superfamily Sylvioidea. Mol. Phylogenet. Evol. 38, 381–397.

Ames, P.L., 1971. The morphology of the syrinx in passerine birds. Peabody Mus. Nat. Hist. Bull. 37, 1–241.

Amos, B., Hoezel, A.R., 1991. Long-term preservation of whale skin for DNA analysis. Report of the International Whaling Commision 13, 99–04.

Avise, J.C., Robinson, T.J., 2008. Hemiplasy: a new term in the lexicon of phylogenetics. Syst. Biol. 57, 503–507.

Bannerman, D.A., 1927. Report on the birds collected and observed during the British Museum Expedition to Tunisia in 1925. Ibis 3 (suppl.), 1–208.

Barker, F.K., Cibois, A., Schikler, P., Feinstein, J., Cracraft, J., 2004. Phylogeny and diversification of the largest avian radiation. Proc. Natl. Acad. Sci. USA 101, 11040–11045.

Barker, F.K., 2004. Monophyly and relationships of wrens (Aves: Troglodytidae): a congruence analysis of heterogeneous mitochondrial and nuclear DNA sequence data. Mol. Phylogenet. Evol. 31, 486–504.

Barker, F.K., Vandergon, A.J., Lanyon, S.M., 2008. Assessment of species limits among yellow-breasted meadowlarks (*Sturnella* spp.) using mitochondrial and sex-linked markers. Auk 125, 869–879.

Barnes, K.N., 2007. The Phylogenetics and Evolution of Africa’s Larks. Unpublished PhD thesis. University of Cape Town, Cape Town.

Alexander, B. 1898. An ornithological expedition to the Cape Verde islands. Ibis 13, 74–118.

Burton, P.J.K., 1971. Sexual size dimorphism in *Alauda razae*. Bull. Brit. Orn. Club 91, 108–109.

Clancey, P.A., 1966. Subspeciation in southern African populations of Sabota Lark *Mirafra sabota* Smith. Ostrich 37, 207–213.

Clancey, P.A. (Ed.), 1980. S.A.O.S. Checklist of Southern African Birds. Southern African Ornithological Society, Johannesburg.

Clancey, P.A., 1989. Taxonomic and distributional findings on some birds from Namibia. Cimbebasia 11, 111–133.

Cramp, S. (Ed.), 1988. The birds of the Western Palearctic, Vol. V. Oxford University Press, Oxford.

Dean, W.R.J., 1989. A review of the genera *Calandrella*, *Spizocorys* and *Eremalauda* (Alaudidae). Bull. Brit. Orn. Club 109, 95–100.

Dean, W.R.J., Fry, C.H., Keith, S., Lack, P. 1992. Family Alaudidae: Larks. In Keith, S., Urban, E.K., Fry, C.H. (Eds.), The Birds of Africa, vol. 4. Academic Press, London, pp. 13–124.

Dean, W.R.J., Hockey, P.A.R., 1989. An ecological perspective of lark (Alaudidae) distribution and diversity in the southwest-arid zone of Africa. Ostrich 60, 27–34.

Degnan, J.H., Rosenberg N.A., 2009. Gene tree discordance, phylogenetic inference, and the multispecies coalescent. Trends Ecol. Evol. 24, 332–340.

Dickinson, E. (Ed.), 2003. The Howard and Moore Complete Checklist of the Birds of the World, third ed. Helm, London.

Dickinson, E.C., Dekker, R.W.R.J., 2001. Systematic notes on Asian birds. 11. A preliminary review of the Alaudidae. Zool. Verh. Leiden 335, 61–84.

de Juana, E., Suárez, F., Ryan, P., Alström, P. & Donald, P., 2004. Family Alaudidae (Larks), in: del Hoyo, J., Elliott, A. & Christie, D.A. (Eds.), Handbook of the Birds of the World, vol. 9. Lynx Edicions, Barcelona, pp. 496–601.

del Hoyo, J., Elliott, A. & Christie, D.A. (Eds.), Handbook of the Birds of the World, vol. 9. Lynx Edicions, Barcelona.

Donald. P.F., Collar, N.J., 2011. Is Beesley’s Lark a species? Bull. Afr. Bird Club 18, 168–173.

Donald, P.F., Hille, S., de l. Brooke, M., Taylor, R., Wells, C.E., Bolton, M., Marlow, T. 2007. Sexual dimorphism, niche partitioning and social dominance in the feeding ecology of the critically endangered Raso Lark *Alauda razae*. Ibis 149, 848–852.

Drummond, A.J., Rambaut, A., 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7, 214.

Drummond, A.J., Rambaut, A., 2012. BEAST, Version 1.7.4. Available at http://beast.bio.ed.ac.uk.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J., Rambaut, A., 2006. Relaxed phylogenetics and dating with confidence. PLoS Biol. 4**,** e88.

Edgar, R.C., 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32, 1792–1797.

Edwards, S.V., Arctander, P., Wilson, A.C., 1991. Mitochondrial resolution of a deep branch in the genealogical tree for perching birds. Proc. Roy. Soc. Lond. B 243, 99–107.

Edwards S.V., 2009. Is a new and general theory of molecular systematics emerging? Evolution 63, 1–19.

Ericson, P.G.P., Johansson, U.S., 2003. Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. Mol. Phylogenet. Evol. 29, 126–138.

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 Evol. Biol. 12, 157.

García-Moreno, J., 2004. Is there a universal mtDNA clock for birds? J. Avian Biol. 35, 465–468.

Gill, F., Donsker, D. (Eds.), 2012. IOC World Bird Names, version 3.1. Available at http://www.worldbirdnames.org [Accessed 25 June, 2012].

Glutz von Blotzheim, U. N., Bauer, K. M. (Eds.), 1985. Handbuch der Vögel Mitteleuropas, band 10. Aula-Verlag, Wiesbaden.

Gouy, M. 2012. Seaview, Version 4.3.4. Available at: http://pbil.univ-lyon1.fr/software/seaview.html.

Gouy, M., Guindon, S., Gascuel., O., 2010. SeaView version 4: a multiplatform graphical user interface for sequence alignment and phylogenetic tree building. Mol. Biol. Evol. 27, 221–224.

Grant, P.R. (Ed.), 1998. Evolution on islands. Oxford University Press, Oxford.

Gu, X., Fu, Y.-X., Li, W.-H., 1995. Maximum likelihood estimation of the heterogeneity of substitution rate among nucleotide sites. Mol. Biol. Evol. 12, 546–557.

Guillaumet, A., Crochet, P.A., Godelle, B., 2005. Phenotypic variation in *Galerida* larks in Morocco: the role of history and natural selection. Mol. Ecol. 14, 3809–3821.

Guillaumet, A., Pons, J.M., Godelle, B., Crochet, P.A., 2006. History of the Crested Lark in the Mediterranean region as revealed by mtDNA sequences and morphology. Mol. Phylogenet. Evol. 39, 645–656.

Guillaumet, A., Crochet, P.A., Pons, J.-M., 2008. Climate-driven diversification in two widespread *Galerida* larks. BMC Evol. Biol. 8, 32.

Hall, B.P., 1963. The status of *Spizocorys razae* Alexander. Bull. Brit. Orn. Cl. 83, 133–134.

Hall, B.P., Moreau, R.E., 1970. An atlas of speciation in African passerine birds. Trustees of the British Museum (Natural History), London.

Harrison, C.J.O., 1966. The validity of some genera of larks (Alaudidae). Ibis 108, 573–583.

Hasegawa, M., Kishino, Y., Yano, T. 1985. Dating of the human–ape splitting by a molecular clock of mitochondrial DNA. J. Mol. Evol. 22, 160–174.

Hockey, P.A.R., Dean, W.R.J., Ryan, P.G. (Eds.), 2005. Roberts Birds of southern Africa, seventh edition. The Trustees of the John Voelcker Bird Book Fund, Cape Town.

Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: Bayesian inference of phylogeny. Bioinformatics 17, 754–755.

Huelsenbeck, J.P., Larget, B., Alfaro, M.E., 2004. Bayesian phylogenetic model selection using reversible jump Markov chain Monte Carlo. Mol. Biol. Evol. 21, 1123–1133.

Irestedt, M., Ohlson, J.I., Zuccon, D., Källersjö, M., Ericson, P.G.P., 2006. Nuclear DNA from old collections of avian study skins reveals the evolutionary history of the Old World suboscines (Aves, Passeriformes). Zool. Scr. 35, 567–580.

Johansson, U.S., Fjeldså, J., Bowie, R.C.K., 2008. Phylogenetic relationships within Passerida (Aves: Passeriformes). Mol. Phylogenet. Evol. 48, 858–876.

Johansson, U.S., Fjeldså, J., Lokugalappatti,L.G.S., Bowie, R.C.K., 2007. A nuclear DNA phylogeny and proposed taxonomic revision of African greenbuls (Aves, Passeriformes, Pycnonotidae). Zool. Scr. 36, 417–427.

Kleinschmidt, O. 1907. Flückigers Sammelreisen in Algerien. III. Die Haubenlerchen. Falco, pp. 8–21.

Kleinschmidt, O. 1912. Die von Flückiger in Algerien gesammelten Vogelarten. Falco, pp. 43–48, plus Tafel 1.

Kocher, T.D., Thomas, W.K., Meyer, A., Edwards, S.V., Pääbo, S., Villablanca, F.X., Wilson, A.C., 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Natl. Acad. Sci. USA 86, 6196–6200.

Lanave, C., Preparata, C., Saccone, C., Serio, G., 1984. A new method for calculating evolutionary substitution rates. J. Mol. Evol. 20, 86–93.

Lawson, W.J., 1961. The races of the Karoo Lark, *Certhilauda albescens* (Lafresnaye). Ostrich 32, 64–74.

Lee, K., Feinstein, J., Cracraft, J. 1997. The phylogeny of Ratite birds: Resolving conflicts between molecular and morphological datasets, in: Mindell D.P. (Ed.), Avian Molecular Evolution and Systematics. Academic Press, San Diego, pp 213–147.

Lemmon, A.R., Brown, J.M., Stanger-Hall, K., Lemmon, E.M., 2009. The effect of ambiguous data on phylogenetic estimates obtained by maximum likelihood and Bayesian inference. Syst. Biol., 58, 130–145.

Liu L., Yu L., Kubatko L., Pearl D.K., Edwards S.V., 2009. Coalescent methods for estimating phylogenetic trees. Mol. Phylogenet. Evol. 53, 320–328.

Lovette, I.J., 2004. Mitochondrial dating and mixed-support for the '2% rule' in birds. Auk 121, 1–6.

Mackworth-Praed, C.W., Grant, C.H.B., 1955. Birds of Eastern and North Eastern Africa, vol. 2. Longmans, Green and Co., London.

Macdonald, J.D., 1952a. Notes on the Long-bill Lark *Certhilauda curvirostris*. Ibis 94, 122–127.

Macdonald, J.D., 1952b. Notes on the taxonomy of the clapper larks of South Africa. Ibis 94, 629–635.

Macdonald, J.D., 1953. Taxonomy of the Karoo and Red-back Larks of western South Africa. Bull. Brit. Mus. Nat. Hist. Zool. 1, 319–350.

Maclean, G.L., 1969. South African Lark genera. Cimbebasia (Series A) 1, 79–94.

Meinertzhagen, R., 1951. A review of the Alaudidae. Proc. Zool. Soc. Lond. 121, 81–132.

Miller, M.A., Pfeiffer, W., and Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees in Proceedings of the Gateway Computing Environments Workshop (GCE), 14 Nov. 2010, New Orleans, LA, pp. 1–8.

Niethammer, G., 1940. Die Schutzanpassung der Lerchen, in: Hoesch, W. and Niethammer, G. (Eds.), Die Vogelwelt Deutsch-Süd-west-afrika. J. Ornithol., 88 (Sonderheft), 75–83.

Nylander, J.A.A., Ronquist, F., Huelsenbeck, J.P., Nieves-Aldrey, J.L., 2004. Bayesian phylogenetic analysis of combined data. Syst. Biol. 53, 47–67.

Olsson, U., Alström, P., Ericson. P.G.P, Sundberg, P., 2005. Non-monophyletic taxa and cryptic species–evidence from a molecular phylogeny of leaf-warblers (*Phylloscopus*, Aves). Mol. Phylogenet. Evol. 36, 261–276

Pääbo, S., Gifford, J.A., Wilson, A.C., 1988. Mitochondrial DNA sequences from a 7000-year old brain. Nucleic Acids Research 16, 9775–9786.

Pätzold, R., 2003. Kompendium der Lerchen *Alaudidae*. Jan Schimkat Medienpublizistik, Dresden.

Penny, D., 2005. Evolutionary biology – relativity for molecular clocks. Nature 436, 183–184.

Peters, J.L., 1960. Family Alaudidae, in: Mayr, E., Greenway, J.C., Jr. (Eds.), Check-list of Birds of the World, vol. IX. Museum of Comparative Zoology, Cambridge, Mass, pp. 3–80.

Posada, D., 2008a. jModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25, 1253–1256.

Posada, D, 2008b. jModeltest. version 0.1.1. Available at https://code.google.com/p/jmodeltest2.

Rambaut A. 2009. FigTree, Vversion 1.3.1. Available from http://tree.bio.ed.ac.uk/software/figtree.

Rambaut, A., Drummond, A.J., Xie, W., 2012. BEAUti, version 1.7.4. Available at http://beast.bio.ed.ac.uk.

Rambaut, A., Drummond, A.J., 2009. Tracer, version 1.5. Available at http://beast.bio.ed.ac.uk.

Rambaut, A., Drummond, A.J., 2012. TreeAnnotator., version 1.7.4. Available at http://beast.bio.ed.ac.uk.

Rand, A.L., 1959. Tarsal scutellation of song birds as a taxonomic character. Wilson Bull. 71, 274–277.

Rasmussen, P.C., Anderton, J.C. 2012. Birds of South Asia: the Ripley guide, second ed. Lynx Edicions, Barcelona.

Roberts, A., 1940. The birds of South Africa. HF & G. Witherby, London.

Ronquist, F., Huelsenbeck, J.P., 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.

Rodríguez, J., Oliver, L., Marín, A., Medina, R., 1990. The general stochastic model of nucleotide substitution. J. Theoret. Biol. 142, 485–501.

Ryan, P.G., Bloomer, P. 1999. The Long-billed Lark complex: a species mosaic in south-western Africa. Auk 116, 194-208.

Ryan, P.G., Hood, I., Bloomer, P., Komen, J., Crowe, T.M., 1998. Barlow's Lark: a new species in the Karoo Lark *Certhilauda albescens* complex of southwest Africa. Ibis 140, 605–619.

Sambrook, J., Fritsch, E.E., Maniatis, T. 1989. Molecular cloning: A laboratory manual, 2nd ed., vol. 3. Cold Spring Harbor Laboratory, Cold Spring Harbor, New York.

Shirihai, H., 1996. The birds of Israel. Academic Press, London and San Diego.

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

Sibley, C.G., Monroe, B.L., Jr., 1990. Distribution and taxonomy of birds of the World. Yale University Press, New Haven.

Spottiswoode, C.N., Olsson, U., Mills, M.S.L., Cohen, C., Francis, J.E., Toye, N., Hoddinott, D., Dagne, A., Wood, C., Donald, P.F., Collar, N.J., Alström, P., 2013. Rediscovery of a long-lost lark reveals the conspecificity of endangered *Heteromirafra* populations in the Horn of Africa. J. Ornithol.

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 fast bootstrapping algorithm for the RAxML web-servers. Syst. Biol. 57, 758–771.

Stepanyan, L.S,. 1967. Calandrella cheleënsis SWINHOE a valid species. Acta Orn. 10, 97–107.

Swofford, D.L., 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0b10. Sinauer Associates, Sunderland, MA.

Tavaré, S., 1986. Some probabilistic and statistical problems on the analysis of DNA sequences. Lec. Math. Life Sci. 17, 57–86.

Tieleman, B.I., Williams, J.B., Bloomer, P., 2002. Adaptation of metabolism and evaporative water loss along an aridity gradient. Proc. Roy. Soc. Lond. B 270, 207–214.

Vaurie, C., 1951. A study of Asiatic larks. Notes from the Walter Koelz collections number 11. Bull. Am. Mus. Nat. Hist. 97, 435–526 .

Vaurie, C., 1954. Systematic Notes on Palearctic birds. No. 7. Alaudidae and Motacillidae (genus *Anthus*). Amer. Mus. Novit. No. 1672, 1–13.

Vaurie, C., 1959. The birds of the palearctic fauna. Passeriformes. Witherby, London.

Verheyen, R., 1958. Contribution a l'anatomie de base et la systematique des Alaudidae (Passeriformes). Alauda 26, 1–25.

Voous, K.H., 1977. List of recent Holarctic bird species, second ed. British Ornithologists' Union, London.

Weir, J.T., Schluter, D., 2008. Calibrating the avian molecular clock. Mol. Ecol. 17, 2321–2328.

Wiens, J.J., Fetzner, J.W., Parkinson, C.L., Reeder, T.W., 2005. Hylid frog phylogeny and sampling strategies for speciose clades. Syst. Biol. 54, 719–748.

Wiens, J.J., Morrill, M.C., 2011. Missing data in phylogenetic analysis: reconciling results from simulations and empirical data. Syst. Biol. 60, 719–731.

Winterbottom, J.M., 1957. The problem of status of the Dusky Bush Lark *Mirafra nigricans*. Ostrich 28, 240–241.

Wolters, H.E., 1979. Die Vogelarten der Erde. Paul Parey, Hamburg and Berlin.

Yang, Z., 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. J. Mol. Evol. 39, 306–314.

Fig. 1. Majority rule (50%) consensus tree of Alaudidae based on concatenated nuclear ODC, myoglobin and RAG1+2 and mitochondrial cytochrome *b* (cyt*b*) and 16S sequences, inferred by Bayesian inference, analysed in five partitions (one per locus; all mixed+Γ+I). Colours of names indicate position incongruent with current taxonomy (Gill and Donsker, 2012). Labelled bars denote clades discussed in text. Pie charts indicate posterior probabilities (PP) in single-locus analyses (see explanation in upper left corner). Support values are indicated at the nodes, in the order PP / maximum likelihood bootstrap (MLBS) / parsimony bootstrap (PBS); an asterisk represents support 1.0 / 100%. Red values indicate strongly supported clades that are considered uncertain despite high statistical support (see text). Coloured boxes to the right indicate sequences available for each species (see explanation in upper left corner). [1] "Strong conflict" means PP ≥0.95 for alternative relationship than the one in this figure. [2] Strongly contradicted in analysis of extended cyt*b* dataset (cyt*bE*; Fig. 2). [3] PP ≥0.95 in cyt*bE*. [4] *M. yeltoniensis* + *M. calandra* are supported as sisters with PP 1.00 in SLA of RAG, whereas *M. mongolica* is outside *Melanocorypha* clade (not strongly supported). [5] MLBS and PBS infers *A. arvensis* + *A. gulgula* with 72% and 67%, respectively. [6] PP 0.66 in cyt*bE*. [7] PP 0.81 in cyt*bE*. Encircled numbers at nodes represent indels: (1) + 1 bp myo; (2) – 1 bp ODC; (3) – 1 bp, – 5 bp ODC; (4) + 1 bp 16S, myo; (5) + 1 bp ODC (and *H. ruddi*); (6) + 11 bp 16S; (7) + 2 bp ODC; (8) + 1 bp ODC; (9) – 4 bp myo; (10) – 1 bp myo, ODC, + 4 bp myo.

Fig. 2. Chronogram for Alaudidae based on cytochrome *b* sequences and a relaxed molecular clock (2.1%/MY), inferred by Bayesian inference. Blue bars at nodes represent 95% highest posterior density intervals for the node ages. Posterior probabilities are indicated at the nodes; an asterisk represents posterior probability 1.00; only values ≥0.95 are indicated. Species for which no subspecific names are given are regarded as monotypic. Coloured lines indicate age of youngest widely sympatric, reproductively isolated sister pair (red); youngest marginally sympatric, reproductively isolated sister pair (orange); youngest allo-/parapatric sister pair treated as separate species according to Gill and Donsker (2012) (purple); and oldest divergence between taxa treated as conspecific according to Gill and Donsker (2012) (blue). The names of the species concerned are the same colours as the lines.

Fig. 3. Morphological variation in some larks. Same tree as in Figure 1. Different colours of names indicate genera as defined by Peters (1960) based on morphology; monotypic genera are shown in black. Revised names compared to Gill and Donsker (2012) are indicated by *.

Supplementary Fig. 1. Cytochrome *b* gene tree inferred by Bayesian inference under the mixed+Γ+I model, partitioned by codon. Values at nodes are posterior probabilities. Only taxa for which more than one sample are available have sample identifiers.

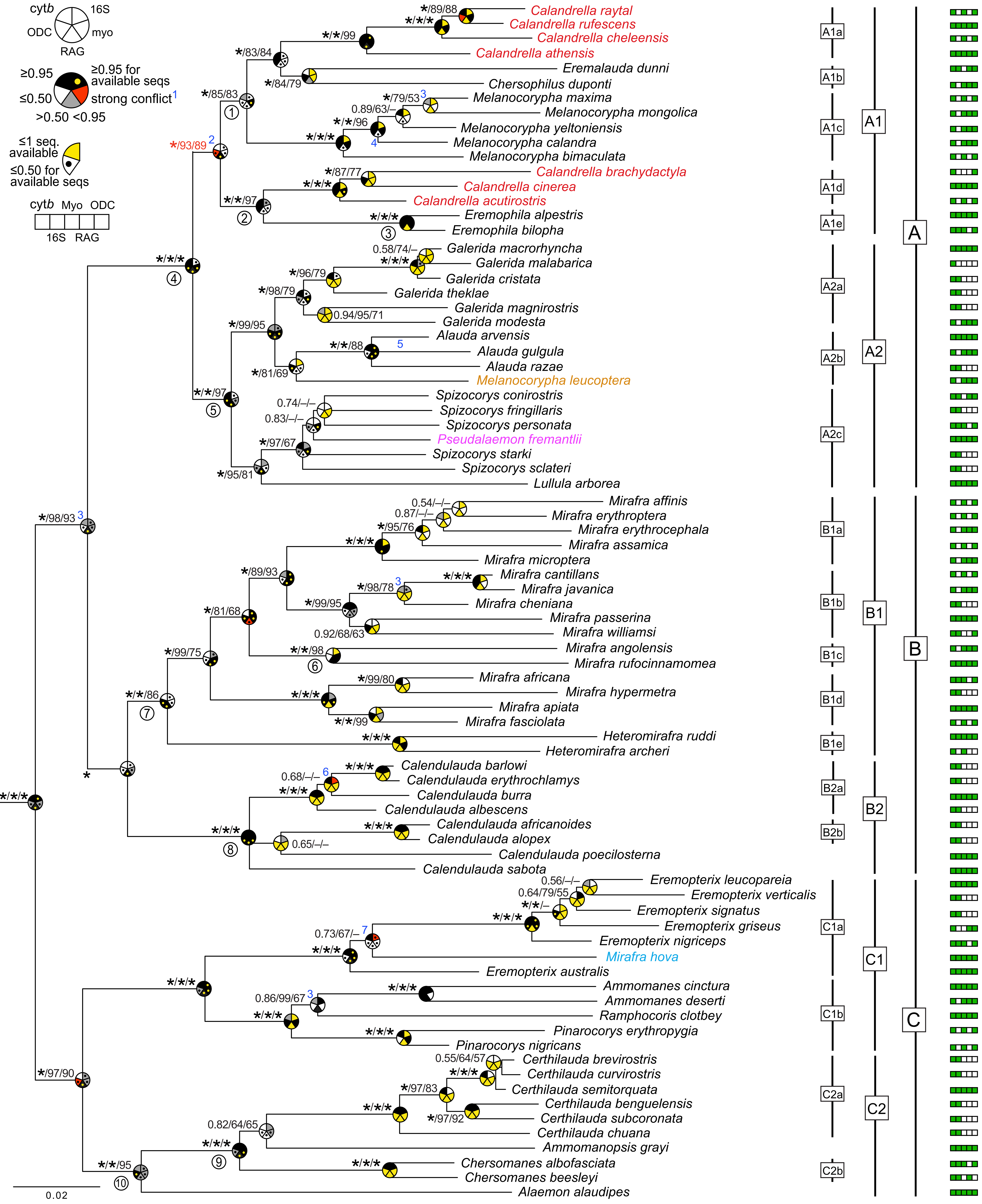
Supplementary Fig. 2. 16S gene tree inferred by Bayesian inference under the mixed+Γ+I model. Values at nodes are posterior probabilities. Only taxa with more than one sequence in the present analysis have identifiers; for others, see Appendix 1.

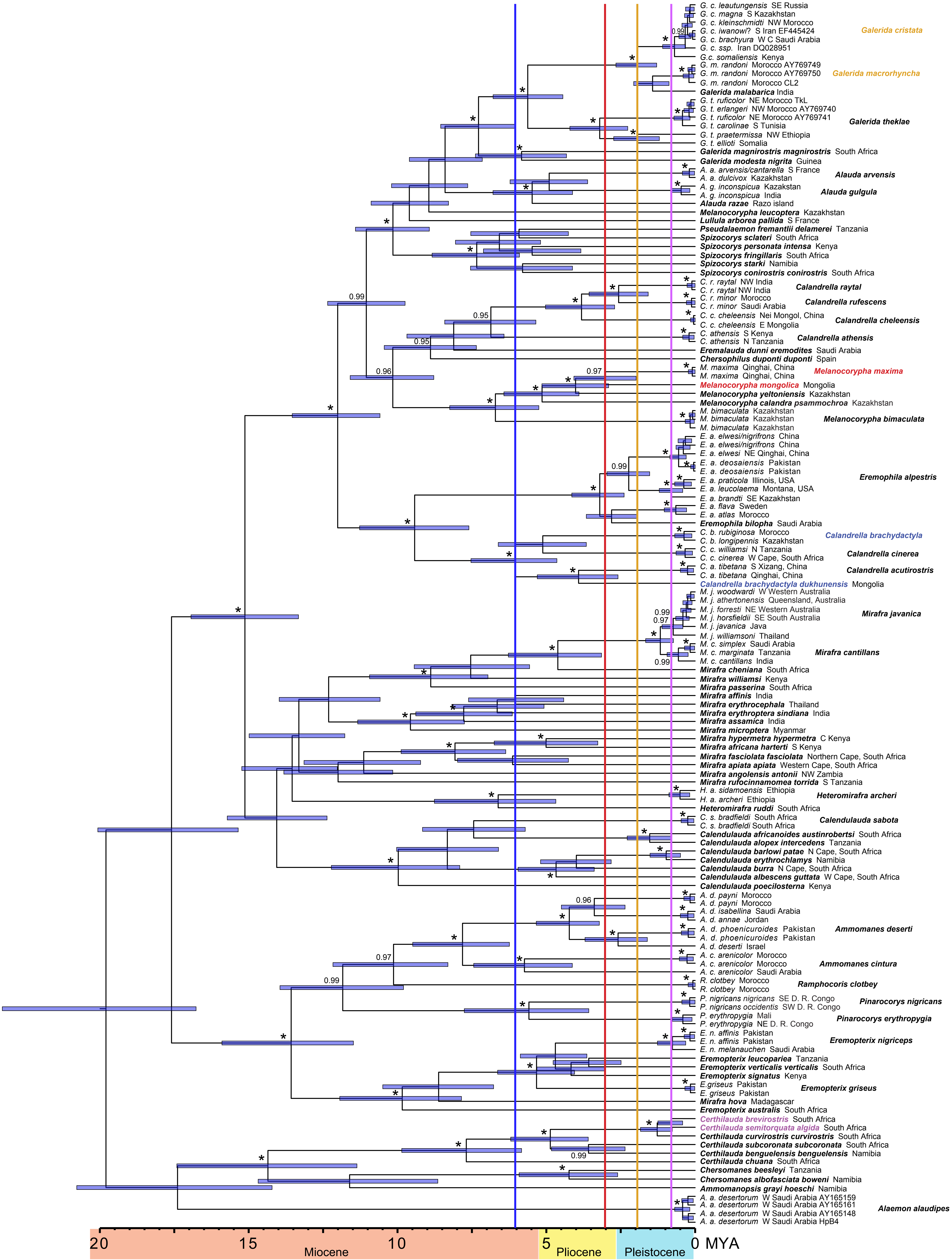
Supplementary Fig. 3. ODC gene tree inferred by Bayesian inference under the mixed+Γ+I model. Values at nodes are posterior probabilities. Only taxa with more than one sequence in the present analysis have identifiers; for others, see Appendix 1.

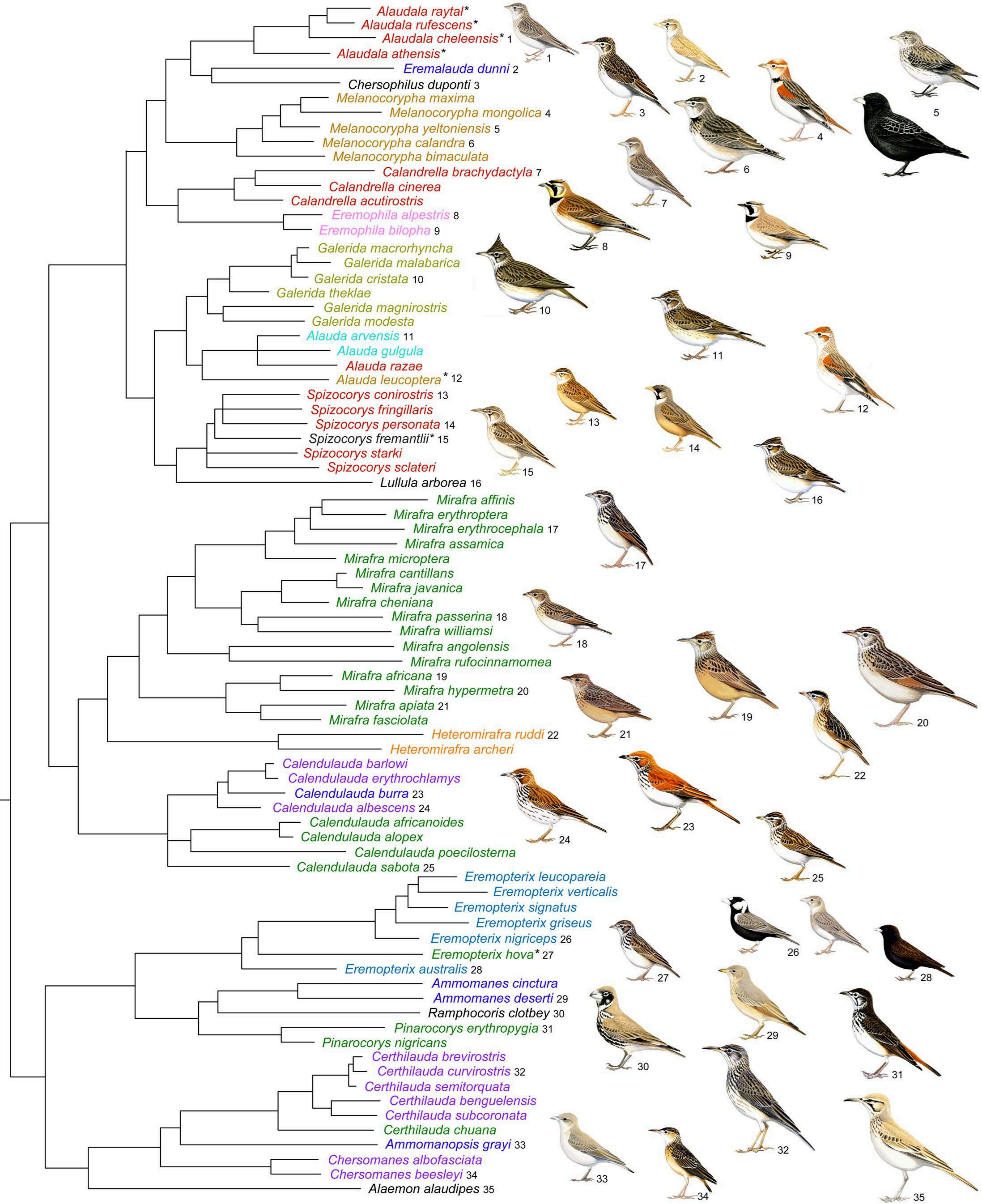
Supplementary Fig. 4. Myoglobin gene tree inferred by Bayesian inference under the mixed+Γ+I model. Values at nodes are posterior probabilities. Only taxa with more than one sequence in the present analysis have identifiers; for others, see Appendix 1.

Supplementary Fig. 5. RAG gene tree inferred by Bayesian inference under the mixed+Γ+I model. Values at nodes are posterior probabilities. Only taxa with more than one sequence in the present analysis have identifiers; for others, see Appendix 1.

Supplementary Table 1. Primers used for amplification and sequencing of *Pinarocorys* samples.


cytb
16S
ODC
myo
RAG
≥0.95
≥0.95 for available seqs
≤0.50
strong conflict1
>0.50 <0.95
≤1 seq. available
≤0.50 for available seqs
cytb Myo ODC
16S RAG
*/89/88
Calandrella raytal
//*
Calandrella rufescens
//99
Calandrella cheleensis
*/83/84
Calandrella athensis
Eremalauda dunni
*/84/79
Chersophilus duponti
*/85/83
*/79/53 3
Melanocorypha maxima
0.89/63/–
Melanocorypha mongolica
//96
Melanocorypha yeltoniensis
//*
4
Melanocorypha calandra
①
Melanocorypha bimaculata
*/93/89 2
*/87/77
Calandrella brachydactyla
//*
Calandrella cinerea
//97
Calandrella acutirostris
②
//*
Eremophila alpestris
③
Eremophila bilopha
//*
④
0.58/74/–
Galerida macrorhyncha
//*
Galerida malabarica
*/96/79
Galerida cristata
*/98/79
Galerida theklae
Galerida magnirostris
0.94/95/71
Galerida modesta
*/99/95
Alauda arvensis
//88 5
Alauda gulgula
*/81/69
Alauda razae
Melanocorypha leucoptera
//97
⑤
Spizocorys conirostris
0.74/–/–
Spizocorys fringillaris
0.83/–/–
Spizocorys personata
Pseudalaemon fremantlii
*/97/67
Spizocorys starki
*/95/81
Spizocorys sclateri
Lullula arborea
A1a
A1b
A1c
A1d
A1e
A1
A2a
A2b
A2c
A2
A
*/98/93 3
0.54/–/–
Mirafra affinis
0.87/–/–
Mirafra erythroptera
*/95/76
Mirafra erythrocephala
//*
Mirafra assamica
Mirafra microptera
*/89/93
//*
Mirafra cantillans
*/98/78 3
Mirafra javanica
*/99/95
Mirafra cheniana
*/81/68
Mirafra passerina
0.92/68/63
Mirafra williamsi
//98
Mirafra angolensis
⑥
Mirafra rufocinnamomea
*/99/75
*/99/80
Mirafra africana
//*
Mirafra hypermetra
//86
Mirafra apiata
⑦
//99
Mirafra fasciolata
//*
Heteromirafra ruddi
Heteromirafra archeri
//*
*
//*
Calendulauda barlowi
0.68/–/– 6
Calendulauda erythrochlamys
//*
Calendulauda burra
Calendulauda albescens
//*
//*
Calendulauda africanoides
⑧
Calendulauda alopex
0.65/–/–
Calendulauda poecilosterna
Calendulauda sabota
B1a
B1b
B1c
B1d
B1e
B1
B2a
B2b
B2
B
0.56/–/–
Eremopterix leucopareia
0.64/79/55
Eremopterix verticalis
//–
Eremopterix signatus
//*
Eremopterix griseus
0.73/67/– 7
Eremopterix nigriceps
//*
Mirafra hova
//*
Eremopterix australis
//*
Ammomanes cinctura
0.86/99/67 3
Ammomanes deserti
//*
Ramphocoris clotbey
//*
Pinarocorys erythropygia
Pinarocorys nigricans
*/97/90
0.55/64/57
Certhilauda brevirostris
//*
Certhilauda curvirostris
*/97/83
Certhilauda semitorquata
//*
Certhilauda benguelensis
*/97/92
Certhilauda subcoronata
0.82/64/65
Certhilauda chuana
//*
Ammomanopsis grayi
⑨
//*
Chersomanes albofasciata
//95
Chersomanes beesleyi
⑩
Alaemon alaudipes
C1a
C1b
C1
C2a
C2b
C2
C
0.02


G. c. leautungensis SE Russia
G. c. magna S Kazakhstan
G. c. kleinschmidti NW Morocco
G. c. iwanowi? S Iran EF445424
G. c. brachyura W C Saudi Arabia
G. c. ssp. Iran DQ028951
G.c. somaliensis Kenya
Galerida cristata
G. m. randoni Morocco AY769749
G. m. randoni Morocco AY769750
G. m. randoni Morocco CL2
Galerida macrorhyncha
Galerida malabarica India
G. t. ruficolor NE Morocco TkL
G. t. erlangeri NW Morocco AY769740
G. t. ruficolor NE Morocco AY769741
G. t. carolinae S Tunisia
G. t. praetermissa NW Ethiopia
G. t. ellioti Somalia
Galerida theklae
Galerida magnirostris magnirostris South Africa
Galerida modesta nigrita Guinea
A. a. arvensis/cantarella S France
A. a. dulcivox Kazakhstan
Alauda arvensis
A. g. inconspicua Kazakstan
A. g. inconspicua India
Alauda gulgula
Alauda razae Razo island
Melanocorypha leucoptera Kazakhstan
Lullula arborea pallida S France
Pseudalaemon fremantlii delamerei Tanzania
Spizocorys sclateri South Africa
Spizocorys personata intensa Kenya
Spizocorys fringillaris South Africa
Spizocorys starki Namibia
Spizocorys conirostris conirostris South Africa
C. r. raytal NW India
C. r. raytal NW India
Calandrella raytal
C. r. minor Morocco
C. r. minor Saudi Arabia
Calandrella rufescens
C. c. cheleensis Nei Mongol, China
C. c. cheleensis E Mongolia
Calandrella cheleensis
C. athensis S Kenya
C. athensis N Tanzania
Calandrella athensis
Eremalauda dunni eremodites Saudi Arabia
Chersophilus duponti duponti Spain
M. maxima Qinghai, China
M. maxima Qinghai, China
Melanocorypha maxima
Melanocorypha mongolica Mongolia
Melanocorypha yeltoniensis Kazakhstan
Melanocorypha calandra psammochroa Kazakhstan
M. bimaculata Kazakhstan
M. bimaculata Kazakhstan
M. bimaculata Kazakhstan
Melanocorypha bimaculata
E. a. elwesi/nigrifrons China
E. a. elwesi/nigrifrons China
E. a. elwesi NE Qinghai, China
E. a. deosaiensis Pakistan
E. a. deosaiensis Pakistan
E. a. praticola Illinois, USA
E. a. leucolaema Montana, USA
Eremophila alpestris
E. a. brandti SE Kazakhstan
E. a. flava Sweden
E. a. atlas Morocco
Eremophila bilopha Saudi Arabia
C. b. rubiginosa Morocco
C. b. longipennis Kazakhstan
Calandrella brachydactyla
C. c. williamsi N Tanzania
C. c. cinerea W Cape, South Africa
Calandrella cinerea
C. a. tibetana S Xizang, China
C. a. tibetana Qinghai, China
Calandrella acutirostris
Calandrella brachydactyla dukhunensis Mongolia
M. j. woodwardi W Western Australia
M. j. athertonensis Queensland, Australia
M. j. forresti NE Western Australia
M. j. horsfieldii SE South Australia
M. j. javanica Java
Mirafra javanica
M. j. williamsoni Thailand
M. c. simplex Saudi Arabia
M. c. marginata Tanzania
M. c. cantillans India
Mirafra cantillans
Mirafra cheniana South Africa
Mirafra williamsi Kenya
Mirafra passerina South Africa
Mirafra affinis India
Mirafra erythrocephala Thailand
Mirafra erythroptera sindiana India
Mirafra assamica India
Mirafra microptera Myanmar
Mirafra hypermetra hypermetra C Kenya
Mirafra africana harterti S Kenya
Mirafra fasciolata fasciolata Northern Cape, South Africa
Mirafra apiata apiata Western Cape, South Africa
Mirafra angolensis antonii NW Zambia
Mirafra rufocinnamomea torrida S Tanzania
H. a. sidamoensis Ethiopia
H. a. archeri Ethiopia
Heteromirafra archeri
Heteromirafra ruddi South Africa
C. s. bradfieldi South Africa
C. s. bradfieldi South Africa
Calendulauda sabota
Calendulauda africanoides austinrobertsi South Africa
Calendulauda alopex intercedens Tanzania
Calendulauda barlowi patae N Cape, South Africa
Calendulauda erythrochlamys Namibia
Calendulauda burra N Cape, South Africa
Calendulauda albescens guttata W Cape, South Africa
Calendulauda poecilosterna Kenya
A. d. payni Morocco
A. d. payni Morocco
A. d. isabellina Saudi Arabia
A. d. annae Jordan
A. d. phoenicuroides Pakistan
A. d. phoenicuroides Pakistan
A. d. deserti Israel
Ammomanes deserti
A. c. arenicolor Morocco
A. c. arenicolor Morocco
A. c. arenicolor Saudi Arabia
Ammomanes cintura
R. clotbey Morocco
R. clotbey Morocco
Ramphocoris clotbey
P. nigricans nigricans SE D. R. Congo
P. nigricans occidentis SW D. R. Congo
Pinarocorys nigricans
P. erythropygia Mali
P. erythropygia NE D. R. Congo
Pinarocorys erythropygia
E. n. affinis Pakistan
E. n. affinis Pakistan
E. n. melanauchen Saudi Arabia
Eremopterix nigriceps
Eremopterix leucopareia Tanzania
Eremopterix verticalis verticalis South Africa
Eremopterix signatus Kenya
E.griseus Pakistan
E. griseus Pakistan
Eremopterix griseus
Mirafra hova Madagascar
Eremopterix australis South Africa
Certhilauda brevirostris South Africa
Certhilauda semitorquata algida South Africa
Certhilauda curvirostris curvirostris South Africa
Certhilauda subcoronata subcoronata South Africa
Certhilauda benguelensis benguelensis Namibia
Certhilauda chuana South Africa
Chersomanes beesleyi Tanzania
Chersomanes albofasciata boweni Namibia
Ammomanopsis grayi hoeschi Namibia
A. a. desertorum W Saudi Arabia AY165159
A. a. desertorum W Saudi Arabia AY165161
A. a. desertorum W Saudi Arabia AY165148
A. a. desertorum W Saudi Arabia HpB4
Alaemon alaudipes
0.99
0.99
0.95
0.95
0.96
0.97
0.99
0.99
0.97
0.99
0.96
0.97
0.99
0.99
20
15
10
5
0 MYA
Miocene
Pliocene
Pleistocene


Alaudala raytal*
Alaudala rufescens*
Alaudala cheleensis* 1
Alaudala athensis*
Eremalauda dunni 2
Chersophilus duponti 3
Melanocorypha maxima
Melanocorypha mongolica 4
Melanocorypha yeltoniensis 5
Melanocorypha calandra 6
Melanocorypha bimaculata
Calandrella brachydactyla 7
Calandrella cinerea
Calandrella acutirostris
Eremophila alpestris 8
Eremophila bilopha 9
Galerida macrorhyncha
Galerida malabarica
Galerida cristata 10
Galerida theklae
Galerida magnirostris
Galerida modesta
Alauda arvensis 11
Alauda gulgula
Alauda razae
Alauda leucoptera* 12
Spizocorys conirostris 13
Spizocorys fringillaris
Spizocorys personata 14
Spizocorys fremantlii* 15
Spizocorys starki
Spizocorys sclateri
Lullula arborea 16
Mirafra affinis
Mirafra erythroptera
Mirafra erythrocephala 17
Mirafra assamica
Mirafra microptera
Mirafra cantillans
Mirafra javanica
Mirafra cheniana
Mirafra passerina 18
Mirafra williamsi
Mirafra angolensis
Mirafra rufocinnamomea
Mirafra africana 19
Mirafra hypermetra 20
Mirafra apiata 21
Mirafra fasciolata
Heteromirafra ruddi 22
Heteromirafra archeri
Calendulauda barlowi
Calendulauda erythrochlamys
Calendulauda burra 23
Calendulauda albescens 24
Calendulauda africanoides
Calendulauda alopex
Calendulauda poecilosterna
Calendulauda sabota 25
Eremopterix leucopareia
Eremopterix verticalis
Eremopterix signatus
Eremopterix griseus
Eremopterix nigriceps 26
Eremopterix hova* 27
Eremopterix australis 28
Ammomanes cinctura
Ammomanes deserti 29
Ramphocoris clotbey 30
Pinarocorys erythropygia 31
Pinarocorys nigricans
Certhilauda brevirostris
Certhilauda curvirostris 32
Certhilauda semitorquata
Certhilauda benguelensis
Certhilauda subcoronata
Certhilauda chuana
Ammomanopsis grayi 33
Chersomanes albofasciata
Chersomanes beesleyi 34
Alaemon alaudipes 35
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35

Appendix 1. List of samples (in alphabetical order), with GenBank accession numbers. New sequences are in bold. Taxonomy follows Gill & Donsker (2012). ANWC – Australian National Wildlife Collection, Australia; BZU – Institute of Pure & Applied Biology, Bahauddin Zakariya University, Multan, Pakistan; CEFE – CEFE, Montpellier, France; DZUG – Department of Zoology, University of Gothenburg, Göteborg, Sweden; FMNH – Field Museum of Natural History, Chicago, USA; MNHN – Muséum National d'Histoire Naturelle, Paris; NMK – National Museums of Kenya, Kenya; NHMO – National Centre for Biosystematics, Natural History Museum, Oslo, Norway; NRM – Swedish Museum of Natural History, Stockholm, Sweden; PFP – Percy FitzPatrick Institute of African Ornithology, University of Cape Town, South Africa; RMCA – Royal Museum for Central Africa, Tervuren, Belgium; UWBM – University of Washington Burke Museum, Seattle, USA; VH – Vogelwarte Hiddensee, Zoological Institute and Museum, Ernst Moritz Arndt University of Greifswald, Greifswald, Germany. Sequences used in the multilocus analyses are in italics. Samples without voucher specimens or photos have an * after the specimen number; samples with only photo documentation have *P* after the specimen number (in Appendix 2).

[1] Incorrectly labelled *Ammomanes phoenicurus* in GenBank. [2] Incorrectly stated to refer to sample from Saudi Arabia in Fregin et al. (2012). [3] See comments on subspecies in Shirihai (1996). [3] Described in Khan (1999).

Taxon	**Locality**	**Sample No. / Specimen No. / Reference**	**Locus**				
			Cytochrome *b*	**16S**	**ODC**	**Myoglobin**	**RAG**
Alaemon alaudipes desertorum	W Saudi Arabia	Tieleman et al. (2003)	AY165148	–	–	–	–
Alaemon alaudipes desertorum	W Saudi Arabia	Tieleman et al. (2003)	AY165159	–	–	–	–
Alaemon alaudipes desertorum	W Saudi Arabia	Tieleman et al. (2003)	AY165161	–	–	–	–
Alaemon alaudipes desertorum	W Saudi Arabia	PFP HpB4 *	***KF060400***	***KF060343***	**–**	**–**	**–**
Alaemon alaudipes alaudipes	S Morocco	MNHN 2003-2729	**–**	**–**	***KF060550***	***KF060498***	***KF060609***

Alauda arvensis arvensis	Sweden	Johansson et al. (2007) (ODC); Ericson and Johansson (2003) (myo)	–	–	*EF625336*	*AY228284*	–
Alauda arvensis arvensis	Netherlands	PFP SkyL2 *	–	–	–	–	***KF060610***
Alauda arvensis arvensis/cantarella	Nimes, France	Tieleman et al. (2003) / PFP SkyL1 *	*AY165156*	***KF060362***	–	–	–
Alauda arvensis dulcivox	SE Kazakhstan	DZUG U581 (*P*)	**KF060401**	–	–	–	–
Alauda gulgula inconspicua	SE Kazakhstan	NRM 20066712	***KF060402***	–	***KF060551***	***KF060499***	***KF060611***
Alauda gulgula inconspicua	Haryana, India	DZUG U3267 (*P*)	**KF060403**	–	–	–	–
Alauda razae	Raso Island, Cape Verde Islands	PFP Raz *	***KF060404***	***KF060361***	–	–	–
Ammomanes cinctura arenicolor	Morocco	PFP BrTdLk1 (*P*)	**KF060405**	***KF060353***	–	–	–
Ammomanes cinctura arenicolor	S Morocco	MNHN 2003-2735	***KF060406***	–	***KF060552***	***KF060500***	***KF060612***
Ammomanes cinctura arenicolor	W Saudi Arabia	Tieleman et al. (2003) / PFP BTL *	AY165150	**KF060352**	–	–	–
Ammomanes deserti annae	Azraq, Jordan	Fregin et al. (2012) / VH A1592 (B0703)	JX236373	–	JX236460[2]	JX236343	JX236414
Ammomanes deserti isabellina	W Saudi Arabia	Tieleman et al. (2003)	AY165152[1]	–	–	–	–
Ammomanes deserti deserti[3]	Arava valley, Israel	DZUG U770 *	**KF060411**	–	**–**	**–**	–

Ammomanes deserti payni	Morocco	PFP DLS6 (*P*)	**KF060410**	**KF060351**	**–**	–	**–**
Ammomanes deserti payni	S Morocco	MNHN 2013-66	**KF060409**	–	**KF060553**	**KF060501**	**KF060613**
Ammomanes deserti phoenicuroides	Dera Ghazi Khan district, Punjab, Pakistan	BZU 200A/11	***KF060407***	–	***KF060554***	***KF060502***	***KF060615***
Ammomanes deserti phoenicuroides	Mari Indus, Mianwali, Pakistan	BZU 15/11	**KF060408**	–			**KF060614**
Ammomanopsis grayi hoeschi	Van Zyl's Pass, NW Namibia	Tieleman et al. (2003) / PFP P94 *	*AY165168*	***KF060374***	***KF060556***	***KF060503***	***KF060617***
Calandrella acutirostris tibetana	NE Qinghai, China	DZUG U577 *	***KF060412***	–	***KF060557***	***KF060504***	–
Calandrella acutirostris tibetana	S Xizang, China	NHMO 17039 *	**KF060413**	–	–	–	–
Calandrella athensis	S Kenya	PFP AST1 *	***KF060414***	–	***KF060558***	***KF060505***	***KF060618***
Calandrella athensis	N Tanzania	Tieleman et al. (2003) / PFP AST2 *	AY165166	***KF152963***	–	–	–
Calandrella brachydactyla dukhunensis	E Mongolia	UWBM 59838 / CSW5805	**KF060417**	–	–	–	–
Calandrella brachydactyla longipennis	SE Kazakhstan	DZUG U582 (*P*)	**KF060416**	–	–	–	–
Calandrella brachydactyla rubiginosa	C Morocco	CEFE Cbra1 *	***KF060415***	–	***KF060559***	–	–
Calandrella cheleensis cheleensis	NE Nei Mongol, China	DZUG U2202 *	***KF060418***	–	***KF060560***	***KF060506***	–
Calandrella cheleensis cheleensis	E Mongolia	UWBM 59820 / CSW5787	**KF060419**	–	**–**	**–**	–

Calandrella cinerea cinerea	St Helena Bay, Western Cape, South Africa	PFP CcinP119 *	**KF060421**	**KF060358**	–	–	–
Calandrella cinerea williamsi	near Nairobi, Kenya	PFP RC2 *	**–**	–	***KF060561***	***KF060507***	***KF060619***
Calandrella cinerea williamsi	Oldonyo sambu, Tanzania	PFP RCL13 *	***KF060420***	***KF060357***	–	–	–
Calandrella raytal raytal	Haryana, India	DZUG 2200 (*P*)	***KF060422***	–	–	***KF060508***	–
Calandrella raytal raytal	Haryana, India	DZUG 2201 (*P*)	**KF060423**	–	***KF060562***	–	–
Calandrella rufescens minor	Mahazat, Saudi Arabia	Tieleman et al. (2003) / PFP LST1 *	*AY165154*	***KF060355***	***KF060563***	***KF060509***	***KF060620***
Calandrella rufescens minor	Morocco	PFP LST ad *	**KF060424**	**KF060354**	–	–	–
Calendulauda africanoides austinrobertsi	Groblershoop, Northern Cape, South Africa	PFP P175 *	***KF060425***	***KF060370***	–	–	–
Calendulauda albescens guttata	Prince Albert, Western Cape, South Africa	PFP Pi3 *	***KF060426***	***KF060365***	–	–	–
Calendulauda alopex intercedens	Oldonyo sambu, Tanzania	PFP FCL15 *	***KF060427***	***KF060369***	–	–	–
Calendulauda barlowi patae	Alexander Bay, Northern Cape, South Africa	PFP Pi4 *	***KF060428***	***KF060367***	–	–	–
Calendulauda burra	Kleinputz, Northern Cape, South Africa	PFP P119 *	***KF060429***	***KF060364***	***KF060564***	***KF060510***	***KF060621***
Calendulauda erythrochlamys	Walvis Bay, Namibia	Tieleman et al. (2003) / PFP P-	*AY165167*	***KF060366***	–	–	–

		Dune					
Calendulauda poecilosterna	Chyulu Hills, S Kenya	NMK PBR4 *	***KF060430***	***KF060368***	***KF060598***	***KF060541***	***KF060643***
Calendulauda sabota bradfieldi	Prieska, Northern Cape, South Africa	Tieleman et al. (2003) / PFP P181 *	*AY165172*	***KF060363***	***KF060600***	***KF060543***	***KF060645***
Calendulauda sabota bradfieldi	Dwaalhoek Farm, Northern Cape, South Africa	DZUG U2344 (*P*)	**KF060432**	**–**	**KF060601**	**KF060544**	**–**
Certhilauda benguelensis benguelensis	Uniab River, Namibia	PFP P204/L *	***KF060433***	***KF060376***	–	–	–
Certhilauda brevirostris	Bredasdorp, Western Cape, South Africa	PFP P215/L2 *	***KF060434***	***KF060377***	–	–	–
Certhilauda chuana	Pietersburg, KwaZulu-Natal, South Africa	PFP P96 *	***KF060435***	***KF060375***	–	–	–
Certhilauda curvirostris curvirostris	Pater Noster, Western Cape, South Africa	PFP P220/L7 *	***KF060436***	***KF060379***	–	–	–
Certhilauda semitorquata algida	Stutterheim, Eastern Cape, South Africa	PFP P214/L1 *	***KF060437***	***KF060378***	***KF060565***	***KF060511***	***KF060622***
Certhilauda subcoronata subcoronata	near Brandvlei, Northern Cape, South Africa	PFP P219/L6 *	***KF060438***	***KF060380***	–	–	–
Chersomanes albofasciata boweni	Van Zyl's Pass, Namibia	Tieleman et al. (2003) / PFP P203 *	*AY165165*	***KF060373***	–	–	–
Chersomanes albofasciata ssp.	?	Johansson et al.	–	–	*EU680716*	*EU680604*	–

		(2007)					
Chersomanes beesleyi	Oldonyo sambu, Tanzania	PFP ShTz *	***KF060440***	***KF060372***	–	–	***KF060623***
Chersophilus duponti duponti	Spain	DZUG U2255 *	***KF060441***	–	***KF060566***	***KF060512***	***KF060624***
Eremalauda dunni eremodites	Saudi Arabia	Tieleman et al. (2003) / PFP DNL1 *	*AY165153*	*AY165128*	***KF060555***	–	***KF060616***
Eremophila alpestris atlas	Morocco	MNHN 2003-2730	**KF060443**	–	–	–	–
Eremophila alpestris brandti	SE Kazakhstan	DZUG U2491 (*P*)	**KF060444**	–	–	–	–
Eremophila alpestris deosaiensis[4]	Deosai, Baltistan, Pakistan	BZU 20120608-D32	**KF060447**	–	–	–	–
Eremophila alpestris deosaiensis[4]	Deosai, Baltistan, Pakistan	BZU 20120608-D35	**KF060448**	–	–	–	–
Eremophila alpestris elwesi	NE Qinghai, China	DZUG U576 (*P*)	**KF060445**	–	**KF060567**	–	–
Eremophila alpestris elwesi	NE Qinghai, China	DZUG U154 *	**–**	–	–	***KF060513***	–
Eremophila alpestris elwesi	Qinghai or Xizang, China	Qu et al. (2000)	FJ952456				
Eremophila alpestris elwesi	Qinghai or Xizang, China	Qu et al. (2000)	FJ952457	–	–	–	–
Eremophila alpestris flava	Sweden	NRM 20046759	**KF060442**	–	–	–	–
Eremophila alpestris leucolaema	Montana, USA	Klicka et al. (2000)	AF290137	**–**	**–**	–	**–**
Eremophila alpestris praticola	Illinois, USA	FMNH 351146	***KF060446***	***KF060359***	***KF060568***	–	***KF060625***

Eremophila bilopha	Saudi Arabia	Tieleman et al. (2003) / PFP THL *	*AY165157*	***KF060360***	***KF060569***	–	–
Eremophila bilopha	Morocco	MNHN 2003-2732	–	–	–	***KF060514***	–
Eremopterix australis	Droëgrond, Northern Cape, South Africa	PFP P176 *	***KF060449***	***KF060348***	***KF060570***	***KF060515***	–
Eremopterix australis	South Africa	Barker et al. (unpublished)	–	–	–	–	*AY319982*
Eremopterix griseus	Sind, Pakistan	DZUG 2257 *	***KF060450***	–	***KF060571***	–	***KF060627***
Eremopterix griseus	Sind, Pakistan	DZUG 2258 *	**KF060451**	–	–	–	–
Eremopterix leucopareia	Arusha, Tanzania	PFP FFL6 *	***KF060452***	***KF060346***	***KF060572***	***KF060516***	***KF060628***
Eremopterix nigriceps affinis	Saudi Arabia	Tieleman et al. (2003) / PFP BCL *	AY165149	***KF060344***	–	–	–
Eremopterix nigriceps melanauchen	Sind, Pakistan	DZUG U2259 *	***KF060453***	–	***KF060573***	***KF060517***	–
Eremopterix nigriceps melanauchen	Sind, Pakistan	DZUG U2260 *	**KF060454**	–	–	–	–
Eremopterix signatus	Shaba Game Reserve, C Kenya	NMK CHSL *	***KF060455***	***KF060347***	–	–	–
Eremopterix verticalis verticalis	Western Cape, South Africa	Tieleman et al. (2003) / PFP P99	*AY165164*	***KF060345***	–	–	–
Galerida cristata brachyura	Taif, Saudi Arabia	Tieleman et al. (2003) / PFP CL	*AY165151*	***KF060399***			
Galerida cristata (*iwanowi*?)	S Iran	Guillaumet et al. (2008)	EF445424	–	–	–	–
Galerida cristata ssp.	Iran	Guillaumet et al.	DQ028951	–	–	–	–

		(2006)					
Galerida cristata kleinschmidti	NW Morocco	Guillaumet et al. (2005)	AY769746	–	–	–	–
Galerida cristata leautungensis	SE Russia	Guillaumet et al. (2008)	EF445427	–	–	–	–
Galerida cristata magna	S Kazakhstan	Guillaumet et al. (2008)	EF445425	–	–	–	–
Galerida cristata somaliensis	Kenya	Guillaumet et al. (2008)	EF445429	–	–	–	–
Galerida macrorhyncha randoni	Errachidia, Morocco	PFP CL2a (*P*)	***KF060456***	***KF060398***	***KF060574***	***KF060518***	***KF060629***
Galerida macrorhyncha randoni	E C Morocco	Guillaumet et al. (2005)	AY769749	–	–	–	–
Galerida macrorhyncha randoni	E C Morocco	Guillaumet et al. (2005)	AY769750	–	–	–	–
Galerida magnirostris	St Helena Bay, Western Cape, South Africa	Tieleman et al. (2003) / PFP TL *	*AY165169*	***KF060396***	–	–	–
Galerida malabarica	India	Guillaumet et al. (2008)	EF445430	–	–	–	–
Galerida modesta nigrita	Guinea	VH A1428 *	***KF060457***	–	***KF060575***	***KF060519***	***KF060630***
Galerida theklae carolinae	S Tunisia	Guillaumet et al. (2008)	EF445418	–	–	–	–
Galerida theklae ellioti	Somalia	Guillaumet et al. (2008)	EF445423	–	–	–	–
Galerida theklae erlangeri	NW Morocco	Guillaumet et al. (2005)	AY769740	–	–	–	–

Galerida theklae praetermissa	NW Ethiopia	Guillaumet et al. (2008)	EF445421	–	–	–	–
Galerida theklae ruficolor	NE Morocco	Guillaumet et al. (2005)	AY769741				
Galerida theklae ruficolor	Errachidia, Morocco	PFP TkL (*P*)	***KF060458***	***KF060397***	–	–	–
Heteromirafra archeri sidamoensis	Liben Plain, SE Ethiopia	Spottiswoode et al. (2013) / DZUG U2810 (*P*)	*KC512763*	–	–	***KF060521***	–
Heteromirafra archeri archeri	Jijiga, SE Ethiopia	Spottiswoode et al. (2013) / DZUG 2805 (*P*)	KC512760	–	–	**–**	–
Heteromirafra ruddi	Wakkerstroom, South Africa	PFP L8 *	*KC869742*	***KF060371***	***KF060576***	***KF060520***	***KF060631***
Lullula arborea pallida	Nimes, France	Tieleman et al. (2003) / PFP WL *	*AY165158*	***KF060356***	***KF060577***	***KF060522***	***KF060632***
Melanocorypha bimaculata	SE Kazakhstan	DZUG U2281 (*P*)	**KF060459**	–	–	–	–
Melanocorypha bimaculata	SE Kazakhstan	DZUG U2282 (*P*)	***KF060460***	–	–	***KF060523***	–
Melanocorypha bimaculata	SE Kazakhstan	DZUG U2283 (*P*)	**KF060461**	–	***KF060578***	–	–
Melanocorypha calandra calandra	NE Morocco	MNHN 2003-2733	**–**	–	***KF060579***	***KF060524***	***KF060633***
Melanocorypha calandra psammochroa	SE Kazakhstan	DZUG U583 (*P*)	***KF060462***	–	–	–	–
Melanocorypha leucoptera	SE Kazakhstan	DZUG U579 (*P*)	***KF060463***	–	***KF060580***	***KF060525***	***KF060634***
Melanocorypha maxima	Qinghai, China	DZUG U578 (*P*)	**KF060464**	–	**KF060581**	**–**	–
Melanocorypha maxima	Qinghai, China	DZUG U588 (*P*)	***KF060465***	–	***KF060582***	***KF060526***	–

Melanocorypha mongolica	Mongolia	UWBM 59839 / CSW5806	***KF060466***	–	***KF060583***	***KF060527***	***KF060635***
Melanocorypha yeltoniensis	SE Kazakhstan	DZUG U575 (*P*)	***KF060467***	–	***KF060584***	***KF060528***	***KF060636***
Mirafra affinis	Andhra Pradesh, India	DZUG U3268 (*P*)	***KF060468***	–	***KF060585***	***KF060529***	–
Mirafra africana harterti	Chyulu Hills, S Kenya	NMK RN1 *	***KF060469***	***KF060389***	–	–	–
Mirafra africana harterti	S Kenya	NMK RN2 *	–	–	***KF060586***	***KF060530***	–
Mirafra angolensis antonii	Hillwood Farm, NW Zambia	PFP MA1 *	***KF060470***	–	***KF060587***	***KF060531***	***KF060637***
Mirafra apiata apiata	Silwerstroomstrand, Western Cape, South Africa	PFP P174 *	*KC869741*	***KF060388***	***KF060588***	***KF060532***	***KF060638***
Mirafra assamica	Punjab, India	DZUG U3269 (*P*)	***KF060471***	–	***KF060589***	***KF060533***	–
Mirafra cantillans cantillans	Punjab, India	DZUG U3273 (*P*)	***KF060472***	–	***KF060590***	***KF060534***	–
Mirafra cantillans marginata	Sanya Juu, Tanzania	PFP SBL *	**KF060473**	**KF060386**	**–**	–	–
Mirafra cantillans simplex	Mahazat, Saudi Arabia	Tieleman et al. (2003) / PFP SBL1 *	AY165155	***KF060385***	–	–	–
Mirafra cheniana	Boskop, Free State, South Africa	PFP P192 *	***KF060474***	***KF060384***	–	–	–
Mirafra erythrocephala	Thailand	DZUG U3270 *	***KF060475***	–	***KF060591***	***KF060535***	–
Mirafra erythroptera sindiana	Haryana, India	DZUG U3271 (*P*)	***KF060476***	–	***KF060592***	***KF060536***	***KF060639***
Mirafra fasciolata fasciolata	Northern Cape, South Africa	DZUG U2345 (*P*)	***KF060477***	–	***KF060593***	***KF060537***	–

Mirafra hova	Madagascar	FMNH 352844	***KF060478***	***KF060349***	***KF060594***	***KF060538***	***KF060640***
Mirafra hypermetra hypermetra	Shaba Game Reserve, C Kenya	NMK RWBL *	***KF060479***	***KF060387***	–	–	–
Mirafra javanica athertonensis	Queensland, Australia	ANWC B31226	**KF060484**	–	–	–	–
Mirafra javanica forresti	NE Western Australia	ANWC B55078	**KF060482**	–	–	–	–
Mirafra javanica javanica	Java, indonesia	DZUG U3272 *	**KF060480**	–	**KF060595**	–	–
Mirafra javanica woodwardi	W Western Australia	ANWC B33326	**KF060481**	–	–	–	–
Mirafra javanica horsfieldii	SE South Australia	ANWC B45130	**KF060483**	–	–	–	–
Mirafra javanica williamsoni	Thailand	Alström et al. (2006) (cytb, myo); Alström et al. (2011) (ODC); Fregin et al. (2012) (RAG)	*DQ008520*	–	*HQ333089*	*DQ008571*	*JX236441*
Mirafra microptera	Myanmar	DZUG U3275 (*P*)	***KF060485***	–	***KF060596***	–	***KF060641***
Mirafra microptera	Myanmar	DZUG U3276 (*P*)	**–**	–	**–**	***KF060539***	**–**
Mirafra passerina	Rooipoort, Northern Cape, South Africa	Tieleman et al. (2003) / PFP P186 *	*AY165163*	***KF060383***	***KF060597***	***KF060540***	***KF060642***
Mirafra rufocinnamomea torrida	Iringa, S Tanzania	PFP FLTz *	***KF060486***	***KF060381***	***KF060599***	***KF060542***	***KF060644***
Mirafra williamsi	C Kenya	NMK WL1 *	***KF060487***	***KF060382***	–	–	–
Mirafra williamsi	C Kenya	PFP WillLk4 *	**–**	**–**	***KF060602***	–	**–**

Pinarocorys erythropygia	Mali	RMCA 105748	***KF060488***	–	–	***KF060545***	–
Pinarocorys erythropygia	NE D. R. Congo	RMCA 101081	**KF060489**	–	***KF060603***	–	–
Pinarocorys nigricans nigricans	SE D. R. Congo	RMCA 106597	***KF060490***	–	–	–	–
Pinarocorys nigricans occidentis	SW D. R. Congo	RMCA 101105	**KF060491**	–	***KF060604***	***KF060546***	–
Pseudalaemon fremantlii delamerei	Oldonyo Sambo, N Tazania	PFP STL9 *	***KF060492***	***KF060390***	***KF060605***	***KF060547***	***KF060646***
Ramphocoris clotbey	Morocco	PFP CLOT1 *	**KF060493**	***KF060350***	–	–	–
Ramphocoris clotbey	Morocco	CEFE Rhcl1 *	***KF060494***	–	***KF060606***	***KF060548***	***KF060647***
Spizocorys conirostris conirostris	Volksrust, KwaZulu-Natal, South Africa	PFP P177 *	***KF060495***	***KF060395***	***KF060607***	–	***KF060648***
Spizocorys fringillaris	Vaalpoort, Mpumalanga, South Africa	PFP P179 *	***KF060496***	***KF060394***	–	–	–
Spizocorys personata intensa	Shaba Game Reserve, C Kenya	NMK ML1 *	***KF060497***	***KF060393***	**–**	**–**	–
Spizocorys personata intensa	C Kenya	PFP MSKLk6 *	**–**	**–**	***KF060608***	***KF060549***	
Spizocorys sclateri	near Brandvlei, Northern Cape, South Africa	Tieleman et al. (2003) / PFP P191 *	*AY165170*	***KF060391***	–	–	–
Spizocorys starki	Grunau, S Namibia	Tieleman et al. (2003) / PFP P178 *	*AY165162*	***KF060392***	–	–	–
Outgroup							
Acrocephalus arundinaceus		A.J. Vastermark (unpublished)	–	AB492871	–	–	–

Aegithalos concinnus		Päckert et al. (2010)	–	GU433980	–	–	–
Panurus biarmicus		Barker et al. (unpublished) (RAG); Ericson and Johansson (2003) (myo); Fregin et al. (2012) (cyt*b*); Johansson et al. (2008) (ODC)	*JX236397*	**–**	*EU680747*	*AY228308*	*AY319993*
Prinia bairdii		Barker (2004) (cyt*b*); Barker et al. (unpublished) (RAG); Cibois et al. (1999) (16S); Fregin et al. (2012) (ODC, myo)	*AY352536*	*AF094647*	*JX236470*	*JX236364*	*AY319998*
Cisticola brachyptera		Cibois et al. (1999)	–	AF094670	–	–	–

References not in reference list of paper:

Alström, P., Fjeldså, J., Fregin, S., Olsson, U., 2011. Gross morphology betrays phylogeny: the Scrub Warbler *Scotocerca inquieta* is not a cisticolid. Ibis 153, 87–97.

Cibois, A., Pasquet, E., Schulenberg, T.S., 1999. Molecular systematics of the Malagasy babblers (Passeriformes: Timaliidae) and warblers (Passeriformes: Sylviidae), based on cytochrome b and 16S rRNA sequences. Mol. Phylogenet. Evol. 13, 581–595.

Khan, A.A., 1999. A new Horned Lark *Eremophila alpestrs deosaiensis*, (subsp. Nov.) from Deosai, Baltistan Pakistan. Pak. J. Ornithol. 3, 27–33.

Klicka, J., Johnson, K.P., Lanyon, S.M., 2000. New world nine-primaried oscine relationships: constructing a mitochondrial DNA framework. Auk 117, 321–336.

Päckert, M., Martens, J., Sun, Y.-H. 2010. Phylogeny of long-tailed tits and allies inferred from mitochondrial and nuclear markers (Aves: Passeriformes, Aegithalidae). *Mol. Phylogenet. Evol.* 55, 952–967.

Qu, Y., Lei, F., Zhang, R., Lu, X., 2000. Comparative phylogeography of five avian species: implications for Pleistocene evolutionary history in the Qinghai-Tibetan plateau. Mol. Ecol. 19, 338–351.

Shirihai, H. 1996. The birds of Israel. London.