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Phylogeny and classification of the Old World Emberizini (Aves, Passeriformes)

Per Alström [a,b,*,1], Urban Olsson [c,1], Fumin Lei [d], Hai-tao Wang [d,e], Wei Gao [e], Per Sundberg [c]

[a] *Department of Vertebrate Zoology and Molecular Systematics Laboratory, Swedish Museum of Natural History, P.O. Box 50007, SE-104 05 Stockholm, Sweden*
[b] *Department of Systematic Zoology, Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, SE-752 36 Uppsala, Sweden*
[c] *Department of Zoology, Göteborg University, Box 463, SE-405 30 Göteborg, Sweden*
[d] *Institute of Zoology, Chinese Academy of Sciences, Datunlu B5, Changyang District, Beijing 100101, China*
[e] *School of Life Sciences, Northeast Normal University, Changchun 130024, China*

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Abstract

The phylogeny of the avian genus *Emberiza* and the monotypic genera *Latoucheornis*, *Melophus* and *Miliaria* (collectively the Old World Emberizini), as well as representatives for the New World Emberizini, the circumpolar genera *Calcarius* and *Plectrophenax* and the four other generally recognized tribes in the subfamily Emberizinae was estimated based on the mitochondrial cytochrome *b* gene and introns 6–7 of the nuclear ornithine decarboxylase (ODC) gene. Our results support monophyly of the Old World Emberizini, but do not corroborate a sister relationship to the New World Emberizini. *Calcarius* and *Plectrophenax* form a clade separated from the other Emberizini. This agrees with previous studies, and we recommend the use of the name Calcariini. *Latoucheornis*, *Melophus* and *Miliaria* are nested within *Emberiza*, and we therefore propose they be synonymized with *Emberiza*. *Emberiza* is divided into four main clades, whose relative positions are uncertain, although a sister relation between a clade with six African species and one comprising the rest of the species (30, all Palearctic) is most likely. Most clades agree with traditional, morphology-based, classifications. However, four sister relationships within *Emberiza*, three of which involve the previously recognized *Latoucheornis*, *Melophus* and *Miliaria*, are unpredicted, and reveal cases of strong morphological divergence. In contrast, the plumage similarity between adult male *Emberiza* (formerly *Latoucheornis*) *siemsseni* and the nominate subspecies of the New World *Junco hyemalis* is shown to be the result of parallel evolution. A further case of parallel plumage evolution, between African and Eurasian taxa, is pointed out. Two cases of discordance between the mitochondrial and nuclear data with respect to branch lengths and genetic divergences are considered to be the result of introgressive hybridization.

Keywords: Emberizinae; Cardinalini; Icterini; Parulini; Thraupini; Emberizini; *Emberiza*; *Latoucheornis*; *Melophus*; *Miliaria*; Plumage evolution; Introgression

1. Introduction

The avian passerine family Fringillidae comprises the subfamilies Fringillinae and Emberizinae (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990). The latter is divided into five tribes: Cardinalini (cardinals, grosbeaks etc.), Emberizini (buntings, New World sparrows etc.), Icterini (grackles, New World orioles, meadowlarks etc.), Parulini (wood warblers etc.) and Thraupini (tanagers etc.) (Sibley and Ahlquist, 1990; Sibley and Monroe, 1990). Other classifications identify more or less the same groups, but with different taxonomic ranks (e.g. Dickinson, 2003; Paynter and Storer, 1970). In studies based on mitochondrial

* Corresponding author. Present address: Swedish Species Information Centre, Swedish University of Agricultural Sciences, Box 7007, SE-750 07 Uppsala, Sweden.
E-mail address: per.alstrom@artdata.slu.se (P. Alström).
[1] These authors contributed equally to this work.

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DNA, Klicka et al. (2000, 2003, 2007), Lovette and Bermingham (2002) and Yuri and Mindell (2002) found support for the existence of clades roughly corresponding to the five tribes sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990). However, these studies revealed some cases of disagreement between the phylogeny and current classifications; e.g. they suggested that *Calcarius* and *Plectrophenax* are not closely related to *Emberiza*, but instead form a monophyletic group in a sister position to the rest of the Emberizinae.

Most genera in Emberizinae sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990) are restricted to the New World. However, *Emberiza* (buntings) and the monotypic genera *Melophus, Latoucheornis* and *Miliaria* are confined to the Old World. Several studies of Emberizinae based on mitochondrial sequences and with differing taxon sampling have included *Melophus* and/or a few *Emberiza* as representatives of the Old World taxa (Groth, 1998; Klicka et al., 2000, 2003, 2007; Lovette and Bermingham, 2002; Yuri and Mindell, 2002). There is no consensus among these studies regarding the positions of *Emberiza* and *Melophus* in relation to other taxa. Klicka et al. (2000, 2007) and Yuri and Mindell (2002) found support for a sister relationship between *Emberiza* and the New World Emberizini, while Klicka et al. (2003) instead indicated Icterini as sister to *Emberiza*. Groth (1998) also found an association between Old World Emberizini and Icterini, but used *Melophus* instead of *Emberiza*. The study by Lovette and Bermingham (2002) suggested *Zeledonia coronata* and *Icteria virens* as the closest relatives of *Emberiza*, but was uncertain regarding the position of *Emberiza* in relation to the five tribes in Emberizinae. The most comprehensive of these studies with regard to taxon sampling (Klicka et al., 2007) found strong support for a sister relationship between the Old World and New World Emberizini. The only studies based on nuclear markers that involve multiple Emberizinae taxa, including *Emberiza*, are the ones by (Barker et al., 2002, 2004; former RAG-1 and c-*mos*, latter RAG-1 and RAG-2). Both these found support for *Cardinalis* and *Thraupis* as forming the sister clade to *Emberiza*, with *Icterus* and *Parula* forming a sister clade to these three; no representative of the New World Emberizini was included in any of these studies.

The genus *Emberiza* comprises c. 39 currently recognized species, distributed throughout Europe, Asia and Africa (Byers et al., 1995; Dickinson, 2003; Paynter and Storer, 1970). Most of the species show pronounced sexual dimorphism in plumage in the breeding season. Male non-breeding plumage is often more similar to female, which in turn is rather similar to juvenile. Several groups of species share combinations of certain features, such as head patterns, suggesting shared ancestry. *Miliaria calandra* was originally described as *Emberiza calandra*, and is often included in that genus (e.g. Paynter and Storer, 1970; Vaurie, 1959). Voous (1977) placed it in the monotypic genus *Miliaria* based on "size, structure of bill, moult (complete post-juvenal), and behaviour", and Cramp and Perrins (1994) added "marked sexual dimorphism in size (in contrast to most other *Emberiza*, which usually show sexual dimorphism in colour instead)". It has recently been suggested that *Miliaria* be synonymized with *Emberiza* based on analyses of mitochondrial DNA from a small number of European species (Grapputo et al., 2001; Lee et al., 2001). *Melophus lathami* was originally described as *Emberiza lathami*. It differs from all *Emberiza* by its unique plumage pattern and prominent crest. *Latoucheornis siemsseni* is a little-known Chinese endemic, which resembles the nominate subspecies of the North American *Junco hyemalis* in plumage, and was indeed described as *Junco siemssieni*. Bangs (1931) erected the monotypic genus *Latoucheornis*, based on its conspicuously rounded wings, broad and blunt tail feathers, and tiny bill. It is sometimes included in *Emberiza* (e.g. Cheng, 1987; Hartert, 1922; Voous, 1977).

We here present the first comprehensive phylogeny of the Old World taxa allocated to Emberizini sensu Sibley and Ahlquist (1990) and Sibley and Monroe (1990), based on introns 6–7 of the nuclear ornithine decarboxylase gene (ODC) and the mitochondrial cytochrome *b* gene. In order to assess the monophyly of *Emberiza*, shed light on its relation to the remainder of the Emberizini, and evaluate previous phylogenetic studies of Emberizinae, we include a number of New World taxa representing all five generally recognized tribes in Emberizinae. We also discuss plumage evolution and reasons for unexpected branch length discordance between the mitochondrial and nuclear gene trees.

2. Material and methods

2.1. Study group

We analyzed 59 species in Emberizinae, including 33 in the genus *Emberiza,* and one species from each of the following genera, representing all five generally recognized tribes in Emberizinae: *Ammodramus*, *Calcarius*, *Cardinalis*, *Coereba, Dendroica, Emberizoides*, *Helmitheros, Icterus, Junco, Latoucheornis, Sturnella, Melophus, Melospiza, Miliaria, Passerculus, Pheucticus, Pipilo, Piranga, Plectrophenax, Seiurus, Setophaga, Spizella, Thraupis* and *Zonotrichia* (Appendix A). Our selection of *Emberiza* includes all of the species in the world except the Tibetan *E. koslowi*, west Asian *E. cineracea*, Socotran endemic *E. socotrana*, and African *E. affinis* and *E. poliopleura* (Byers et al., 1995). *Carduelis carduelis* and *Passer montanus* were chosen as outgroups, based on the results of Barker et al. (2002), Ericson and Johansson (2003), Klicka et al. (2000), Yuri and Mindell (2002).

2.2. DNA extraction and sequencing

DNA was extracted from blood, feathers, or muscle, 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 two loci: the mitochondrial cytochrome *b* gene and introns 6–7 of the nuclear ornithine decarboxylase gene (ODC). Amplification and sequencing of the cytochrome *b* gene followed the protocols described in Olsson et al. (2005), and of introns 6–7 of the ODC gene Allen and Omland (2003), Friesen et al. (1999), Irestedt et al. (2006). The cytochrome *b* gene was amplified as one fragment to decrease the risk of amplifying nuclear pseudocopies (cf. e.g. Sorensen and Quinn, 1998; Zhang and Hewitt, 1996). The sequences have been deposited in GenBank (Appendix A).

2.3. Phylogenetic analyses

Sequences were aligned using MegAlign 4.03 in the DNASTAR package (DNAstar Inc.); some manual adjustment was necessary for the ODC sequences. Phylogenies were estimated by Bayesian inference (BI) using MrBayes 3.1.1 (Huelsenbeck and Ronquist, 2001; Huelsenbeck, 2005) and by parsimony bootstrapping using PAUP* (Swofford, 2001). In the BI, the mitochondrial and nuclear data were analyzed both separately and combined. In the latter analyses, the data were partitioned such that the non-coding ODC and the protein-coding cytochrome *b* were analyzed separately, using rate multipliers to allow different rates for the different partitions (Nylander et al., 2004; Ronquist and Huelsenbeck, 2003).

The choice of model for the BI was determined based on the Akaike Information Criterion (Akaike, 1973) calculated in MrModeltest 2 (Nylander et al., 2004). For both loci, posterior probabilities were calculated under the general time-reversible (GTR) model (Lanave et al., 1984; Rodríguez et al., 1990; Tavaré, 1986), assuming rate variation across sites according to a discrete gamma distribution with four rate categories (Γ; Yang, 1994) and, for the cytochrome *b* data, also an estimated proportion of invariant sites (I; Gu et al., 1995). Default priors in MrBayes were used. Two simultaneous runs, each with four Metropolis-coupled MCMC chains with incremental heating temperature 0.2 were run for 18,000,000 generations and sampled every 100 generations. The first 5,000,000 generations were discarded after manual inspection of stationarity of chain likelihood values and asymptotic stationarity of standard deviation, to ascertain optimal convergence of the chains (burn-in). The posterior probability was estimated for the remaining 13,000,000 generations.

Maximum likelihood (ML) bootstrapping (1000 replicates) was performed in Treefinder (Jobb et al., 2004; Jobb, 2007) using default settings and the same models as in the BI. Parsimony (MP) bootstrapping was performed in PAUP* (Swofford, 2001): heuristic search strategy, 1000 replicates, starting trees obtained by stepwise addition (random addition sequence, 10 replicates), TBR branch swapping, MulTrees option not in effect (only one tree saved per replicate). Pairwise divergences (uncorrected *p*) between Old World Emberizini species were calculated in PAUP* (Swofford, 2001).

3. Results

3.1. Sequence characteristics and comparison of regions

We obtained a contiguous 530–707 base pair (bp) stretch of the ODC introns for the Old World Emberizini (all except one species $\geqslant$670 bp) and 462–727 bp for the same locus for the rest of the species (all except six $\geqslant$690 bp), and a 1076 bp portion of the cytochrome *b* gene and part of the flanking tRNA-Thr (1041 bp for eight species; one 916 bp; one 881 bp; one 699 bp). No unexpected start or stop codons that could indicate the presence of nuclear copies are present in the cytochrome *b* sequences.

The aligned ODC sequences comprise 813 characters, of which 138 (17%) are parsimony informative, and the aligned cytochrome *b* and tRNA-Thr sequences contain 1076 characters, of which 393 (36.5%) are parsimony informative. The concatenated ODC and cytochrome *b* data set contains 1889 characters, of which 531 (28%) are parsimony informative.

The trees are shown in Figs. 1–3. The resolution is lower in the ODC tree (Fig. 1) than in the cytochrome *b* tree (Fig. 2), although the former is better resolved and supported at deeper nodes than the latter—presumably reflecting the generally different evolutionary rates of nuclear and mitochondrial loci. In the ODC tree, 77% of the nodes are resolved, compared to 82% in the cytochrome *b* tree. In the Old World Emberizini clade, which is the main focus of this paper, 68.5% of the nodes are bifurcating in the ODC tree, compared to 88.5% in the cytochrome *b* tree. There are a number of topological conflicts between the nuclear and mitochondrial trees. However, only two of these receive $\geqslant$0.95 posterior probability in both alternative topologies, namely the positions of *Emberiza yessoensis* (see below) and *Helmitheros vermivorus*/*Seiurus noveboracensis*. The tree based on the concatenated ODC and cytochrome *b* sequences is resolved at 87.5% of the nodes, and at 83% of the nodes in the Old World Emberizini clade. Some clades differ much in support between the BI, ML and MP analyses. The posterior probabilities >0.90 that differ most from the ML/MP bootstrap values are marked with * in Figs. 1–3. A few clades are supported by synapomorphic indels, which are indicated in Figs. 1 and 3. Pairwise divergences (uncorrected *p*) between the Old World Emberizini species are shown in Fig. 4.

3.2. The Emberizinae clade

In the tree based on the combined mitochondrial and nuclear data (Fig. 3) the taxa in Emberizinae sensu Sibley and Ahlquist (1990), Sibley and Monroe (1990) fall into major clades representing Sibley and Ahlquist's (1990), Sibley and Monroe's (1990) Old World Emberizini, New World Emberizini, Icterini, Cardinalini, Thraupini and Parulini, as well as a clade comprising *Calcarius* and *Plectrophenax*. All these receive >0.90 posterior probability. However, Icterini, Cardinalini and Thraupini have low

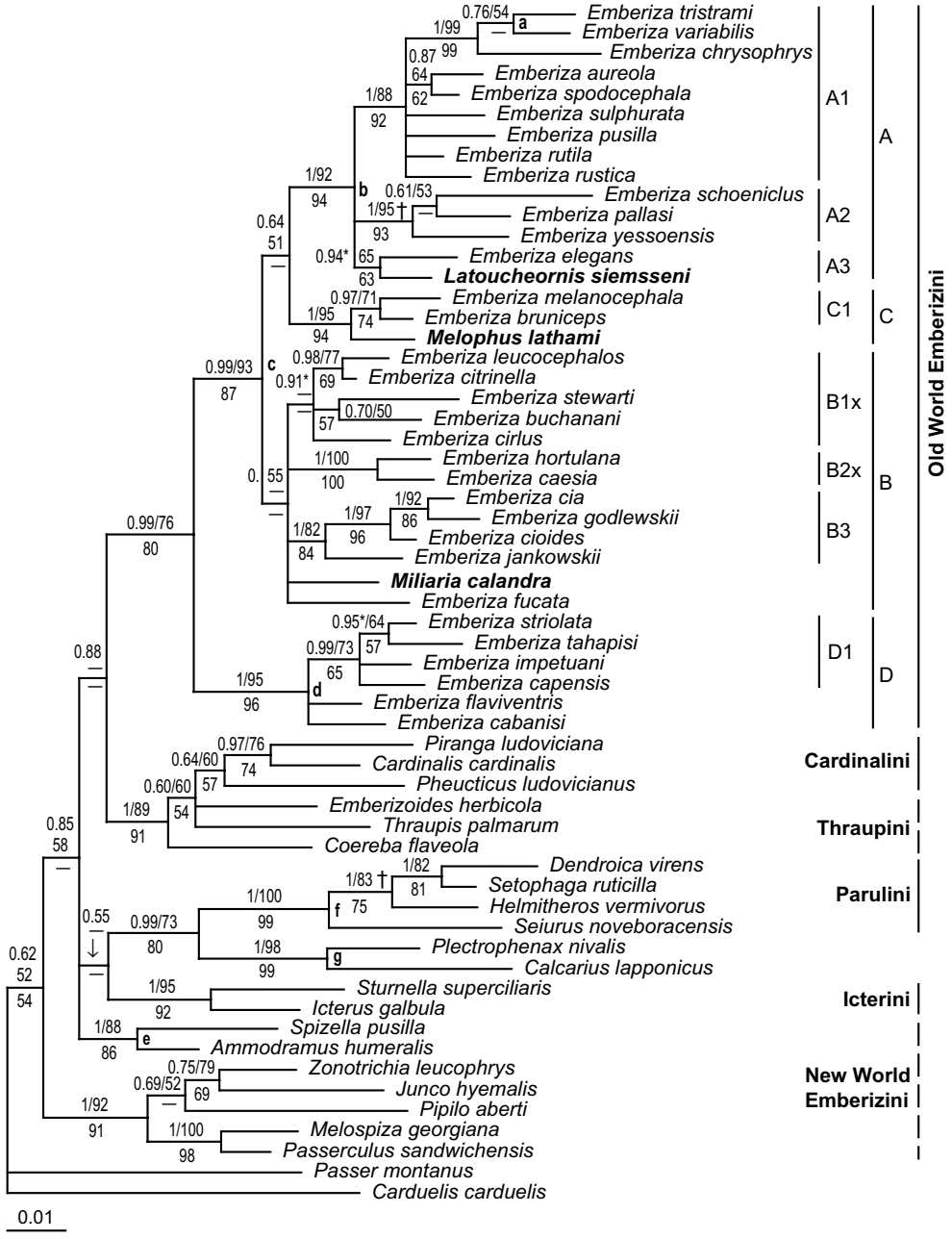

Fig. 1. Relationships of the Old World Emberizini and representatives of the other tribes recognized by Sibley and Ahlquist (1990) and Sibley and Monroe (1990). Estimated by Bayesian analysis of introns 6–7 of the nuclear ODC gene, analyzed under the GTR+Γ model. Posterior probabilities (⩾0.50; 360,000 trees) and maximum likelihood bootstrap values (⩾50%; 1000 replicates) are indicated above the nodes (posterior probabilities top or left) and parsimony bootstrap values (⩾50%; 1000 replicates) below the nodes. The clades with the greatest differences between the posterior probability values, when >0.90, and maximum likelihood/parsimony bootstrap values are marked with ∗. Apparently synapomorphic indels are indicated by letters adjacent to the nodes: a—1-bp insertion; b—4-bp deletion; c—6-bp deletion; d—18-bp deletion; e—8-bp deletion; f—1-bp insertion; g—14-bp deletion. Relationships that are incongruent with Fig. 2 and having ⩾0.95 posterior probability in both trees are marked by †. Clade B1x and B2x differ slightly from the corresponding clades in Fig. 3. Tribes indicated by dashed bars are not monophyletic in this analysis. In the maximum likelihood bootstrap, *E. flaviventris* and *E. cabanisi* are sisters with 79% support.

support in the ML and MP bootstrap analyses, reflecting conflicts between the mitochondrial and nuclear data (see below). The relationships among these major clades are best considered as unresolved; only the sister relationship between Cardinalini and Thraupini receives >0.95 posterior probability and >80% ML bootstrap support (but no parsimony bootstrap support). The monophyly of Emberizini sensu Sibley and Ahlquist (1990), Sibley and Monroe (1990), comprising Old World and New World Emberizini, *Calcarius* and *Plectrophenax*, is not supported, although our data do not strongly reject the possibility that they could form a clade.

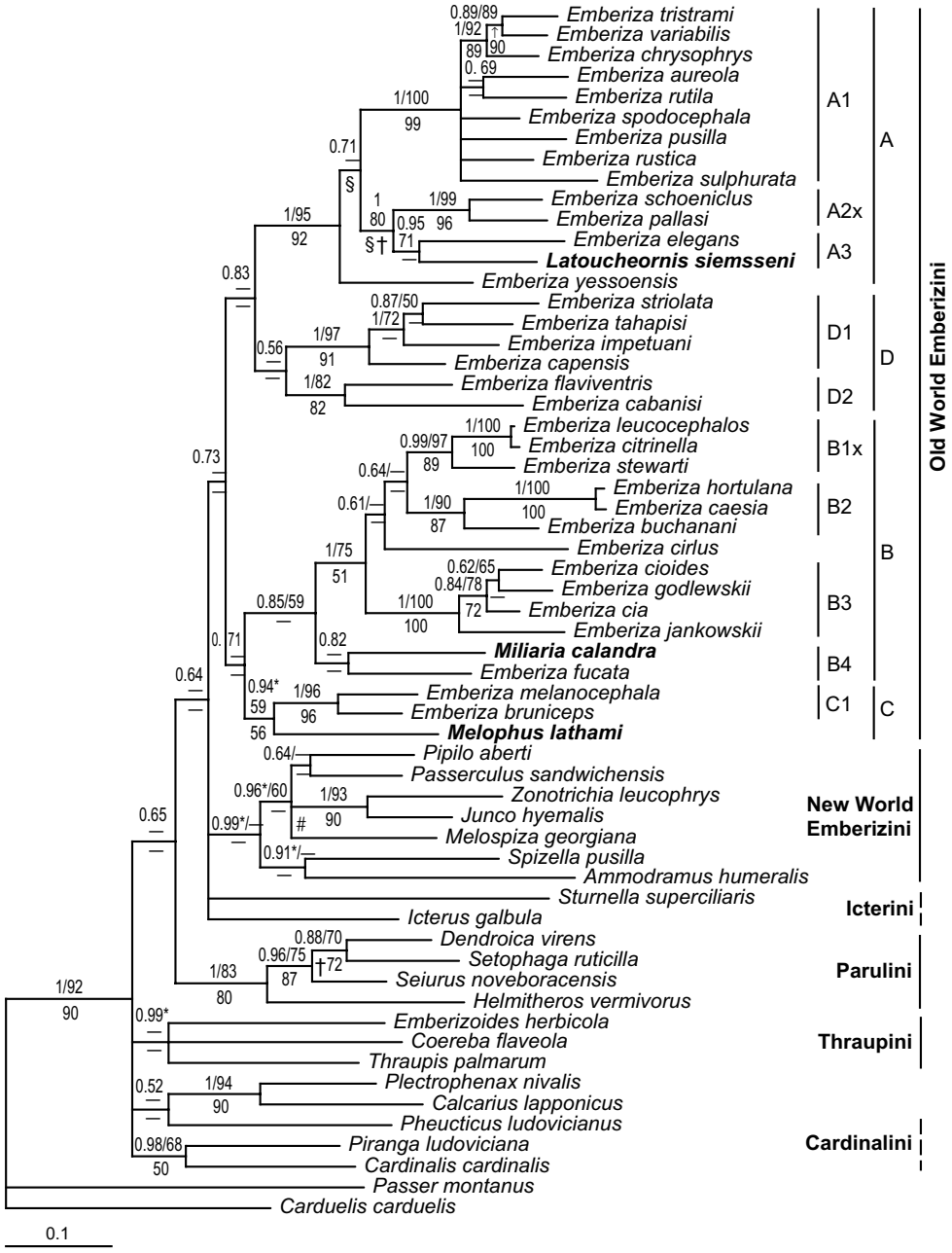

Fig. 2. Relationships of the same taxa as in Fig. 1, estimated by Bayesian analysis of the mitochondrial cytochrome *b* gene, analyzed under the GTR+Γ+I model. Posterior probabilities (⩾0.50; 360,000 trees) and maximum likelihood bootstrap values (⩾50%; 1000 replicates) are indicated above the nodes (posterior probabilities top or left) and parsimony bootstrap values (⩾50%; 1000 replicates) below the nodes. The clades with the greatest differences between the posterior probability values, when >0.90, and maximum likelihood/parsimony bootstrap values are marked with ∗. Relationships that are incongruent with Fig. 1 and having ⩾0.95 posterior probability in both trees are marked by †. § refers to a clade comprising *E. schoeniclus*, *E. pallasi*, *E. yessoensis*, *E. elegans* and *L. siemsseni*, which was recovered in 55% of the trees in the parsimony bootstrap. # refers to a clade with *Passerculus* and *Melospiza*, which receives 70% in the parsimony bootstrap. Clades A2x and B1x differ from the corresponding clades in Fig. 3. Tribes indicated by dashed bars are not monophyletic in this analysis.

All of the major clades, corresponding to established taxonomic units, are found in the ODC tree (Fig. 1), except that the New World Emberizini are divided into two, non-sister, clades; the support for their non-sister relationship is, however, poor. Cardinalini and Thraupini form a more strongly supported clade than in the combined analysis, although within this clade only the *Piranga–Cardinalis* sister relationship is well supported. Unlike in the combined analysis, the monophyly of Icterini is strongly supported. *Calcarius*/*Plectrophenax* and Parulini form a clade that is reasonably well supported in all analyses. The relationships among the main clades are uncertain.

The cytochrome *b* tree (Fig. 2) recovers the Old World Emberizini, New World Emberizini, Thraupini, Parulini

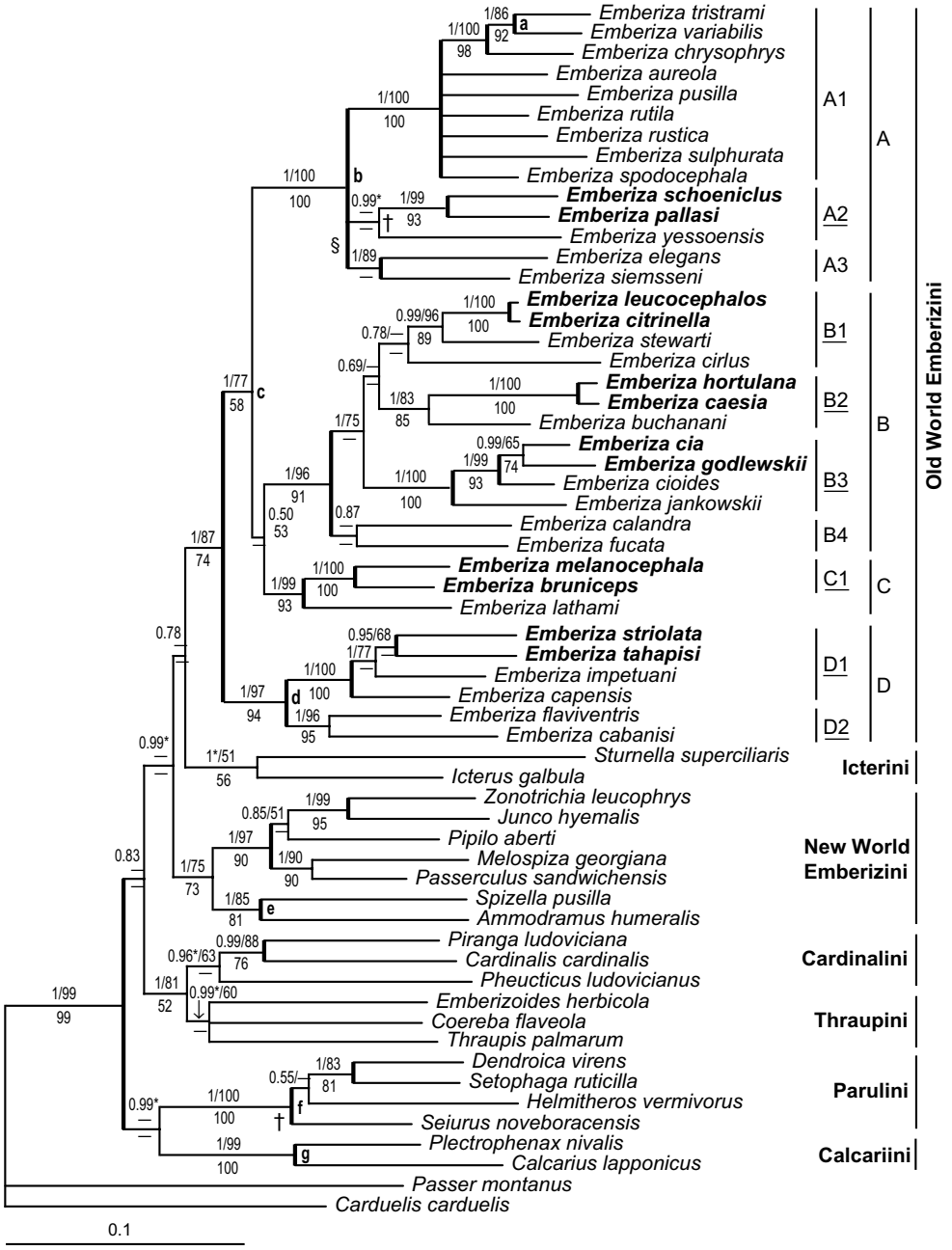

Fig. 3. Relationships of the same taxa as in Figs. 1 and 2, with the taxonomic changes proposed here applied. Estimated by Bayesian analysis of concatenated ODC and cytochrome *b* sequences, divided into two partitions analyzed under the same models as in Figs. 1 and 2. Posterior probabilities ($\geqslant$0.50; 360,000 trees) and maximum likelihood bootstrap values ($\geqslant$50%; 1000 replicates) are indicated above the nodes (posterior probabilities top or left) and parsimony bootstrap values ($\geqslant$50%; 1000 replicates) below the nodes. The clades with the greatest differences between the posterior probability values, when >0.90, and maximum likelihood/parsimony bootstrap values are marked with $*$. Apparently synapomorphic indels in the ODC alignment are indicated by letters adjacent to the nodes (see Fig. 1). Clades that agree between the ODC and cytochrome *b* trees have bold highlights, while strongly supported incongruent relationships are marked by † ($\geqslant$0.95 posterior probability in both trees). One of these has 82% parsimony bootstrap support for *Seiurus* being sister to *Dendroica* and *Setophaga*. § refers to a clade combining clades A2 and A3, which receives 63% maximum likelihood bootstrap and 70% parsimony bootstrap support. The Old World Emberizini clades that are generally recognized by traditional classifications are underlined (e.g. A2), and the sister species that have been identified by traditional taxonomy are in bold.

and *Calcarius*/*Plectrophenax*, although only the two latter clades are unanimously well supported in all analyses. Icterini and Cardinalini are not recovered as monophyletic, although there is no support for their non-monophyly either. The relationships among the main clades are uncertain.

3.3. The Old World Emberizini clade

The Old World Emberizini clade (Figs. 1–3) comprises the genus *Emberiza* and the three monotypic genera *Melophus, Miliaria* and *Latoucheornis*. In all analyses, this clade is divided into four main clades (A, B, C and D).

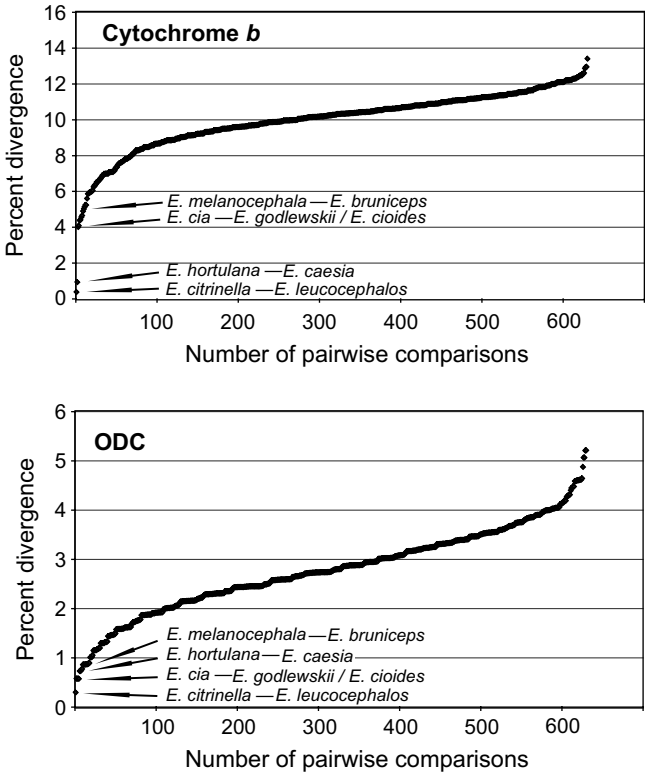

Fig. 4. Plot of pairwise cytochrome *b* and ODC divergences (uncorrected *p* values) in the Old World Emberizini species. Four of the pairs with the smallest divergences are marked.

However, the support for clade B is insignificant in the single-locus analyses, and in the cytochrome *b* tree clade C is only supported in the BI analyses and clade D is practically unsupported. The relative positions of these four clades vary among the trees, and are generally poorly supported by the data. The sister relationship between clade D and the others is strongly supported in the ODC tree, while the alternative topology in the cytochrome *b* tree is weakly supported; in the combined data tree, the former topology has a posterior probability of 1, while the ML and MP bootstrap support values are moderate or low, respectively, probably due to conflict between the nuclear and mitochondrial data. One unique 6-bp deletion in the ODC alignment is shared by clades A, B and C (Figs. 1 and 3).

Clade A can be divided into three subclades (A1–A3; Figs. 1–3) forming a trichotomy in the ODC and combined trees, while in the cytochrome *b* tree clade A2 is less inclusive than in the other trees (see below). Clade A1 is mainly polytomous in all analyses. The clade with *E. chrysophrys* as sister to *E. tristrami* and *E. variabilis* is the only part of clade A1 that receives consistently high support. The sister relationship between *E. tristrami* and *E. variabilis* is also corroborated by a unique 1-bp insertion in the ODC alignment. *E. aureola* has different sisters in the ODC and cytochrome *b* trees, in both cases with negligible support. In the ODC and combined trees, clade A2 comprises *E. schoeniclus* as sister to *E. pallasi*, and *E. yessoensis* as sister to these two. Also the cytochrome *b* tree supports the sister relation between *E. schoeniclus* and *E. pallasi*, but in contrast excludes *E. yessoensis* from clade A2 with high posterior probability and reasonably high (80%) ML bootstrap support. However, there is weak MP bootstrap support (55%) for the inclusion of *E. yessoensis* in a clade with *E. schoeniclus*, *E. pallasi*, *E. elegans* and *L. siemsseni*. The sister relationship between *Latoucheornis siemsseni* and *E. elegans* (clade A3) has high posterior probability in all trees, although the ML and MP support is generally low or lacking. Clade A is further supported by a unique 4-bp deletion in the ODC alignment (Figs. 2 and 3).

Clade B comprises four subclades (B1–B4) which, however, are not unanimously well supported, and which vary somewhat in inclusiveness among the trees. In the combined tree, clade B1 includes *E. citrinella*, which is the type species of the genus *Emberiza*, as well as *E. leucocephalos*, *E. stewarti* and *E. cirlus*, although the support for the inclusion of *E. cirlus* is insignificant in the BI analysis and nonexistent in the ML and MP bootstrap analyses. In the ODC tree, *E. buchanani* is added to this clade, with near-significant posterior probability (0.91), but <50% ML and MP bootstrap, and in the cytochrome *b* tree the position of *E. cirlus* in relation to clades B1, B2 and B3 is best considered as unresolved. In the combined and cytochrome *b* trees, *E. buchanani* is firmly placed in clade B2 as sister to *E. hortulana* and *E. caesia*. Clade B3 receives strong support in all trees, but in the cytochrome *b* tree support for the relative positions of *E. cia*, *E. godlewski* and *E. cioides* is low. In the cytochrome *b* and combined trees, clade B4 comprises *Miliaria calandra* and *E. fucata*, albeit with insufficient support; in the ODC tree, their relationships are uncertain.

Clade C, which is strongly supported in all analyses, consists of *E. melanocephala* and *E. bruniceps* as sister species (C1) and *Melophus lathami* as sister to these two. In the cytochrome *b* tree, the inclusion of *M. lathami* is only well supported by the BI.

Clade D is well supported in the combined and ODC trees, and is further corroborated by two unique adjacent deletions ($\sum$18 bp) in the ODC alignment (Figs. 2 and 3). It is divided into two strongly supported subclades (D1 and D2) in the combined and cytochrome *b* trees; in the ODC tree, clade D1 is found, while clade D2 is unresolved. Within clade D1, *E. striolata* and *E. tahapisi* are sisters in all trees, while the support for this relationship is not unanimously strong in all analyses. *E. impetuani* is sister to these two in the combined and cytochrome *b* trees, with posterior probability 1 and ML bootstrap support >70%, but with <50% MP bootstrap support.

The cytochrome *b* sequences are considerably more similar in the two sister pairs *E. leucocephalos–E. citrinella* and *E. hortulana–E. caesia* than in other sister species (Figs. 2 and 4).

4. Discussion

4.1. The Emberizinae clade

The clades corresponding to Old and New World Emberizini, Icterini, Cardinalini, Thraupini and Parulini are recovered in our analyses, although the support for these clades is not unanimously strong, and their relative positions are best considered as unresolved (as in previous studies based on mitochondrial markers: Groth, 1998; Klicka et al., 2000, 2003, 2007; Lovette and Bermingham, 2002; Yuri and Mindell, 2002). None of our analyses recovers the Old and New World Emberizini as monophyletic, although support for the non-monophyly is weak and the topology varies among the trees. The separation of the Old and New World emberizines was also suggested by Harrison (1967) based on the presence of a "double-scratching" foraging behaviour, which is widespread in New World species, but absent in *Emberiza*, *Melophus*, *Calcarius* and *Plectrophenax* (see also Greenlaw, 1977, and references therein). Clark (1972) came to the same conclusion based on the scutellation at the base of the upperside of the two outer toes. All of the New World Emberizini in the present study have what Clark described as "a single scute at the base of the two outer toes", unlike *Emberiza*, *Melophus*, *Calcarius*, *Plectrophenax* and most other passerine families studied, which have "divided scutes at the base of the two outer toes". He remarked that "all emberizine species known to double-scratch have a single scute condition".

If the non-monophyly of Emberizini suggested here is corroborated by further studies, this name is applicable to the Old World clade rather than to the New World group. The former, which is synonymous with the genus *Emberiza* as circumscribed here (see below), includes *E. citrinella*, which is the type of *Emberiza*, and by extension also of Emberizini (and Emberizinae). The New World Emberizini clade then requires a new name. However, we consider it premature to propose a name for this clade.

In the ODC tree, the Old World Emberizini is sister to a clade combining Cardinalini and Thraupini. This is in conflict with our cytochrome *b* and combined trees, as well as all previously published mitochondrial analyses (Groth, 1998; Klicka et al., 2000, 2003, 2007; Lovette and Bermingham, 2002; Yuri and Mindell, 2002), but in agreement with the only previous studies based on nuclear markers that include a representative of Emberizini other than *Plectrophenax* and *Calcarius* (Barker et al., 2002, 2004). In the two latter, *Cardinalis* and *Thraupis* were placed as sisters to *Emberiza*, with *Icterus* and *Parula* forming the sister clade to these. The support for the Cardinalini/Thraupini–Old World Emberizini sister relationship is not strong in the present study or in Barker et al. (2002): 0.88 posterior probability and <50% ML and MP bootstrap in our ODC tree, and 72% MP bootstrap support for RAG-1 and 62% for c-*mos* in the Barker et al. (2002) analyses. In contrast, in the Barker et al. (2004) analysis of RAG-1 and RAG-2, this relationship receives 1.0 posterior probability, 70% ML bootstrap, and <50% MP bootstrap. Despite the low support in most individual analyses, the fact that three independent data sets (ODC, c-*mos* and RAG-1/RAG-2) recover the same topology makes this a more likely hypothesis than the tree found based on cytochrome *b* and other, previously published, mitochondrial data. Moreover, the more slowly evolving nuclear loci can be expected to be better at recovering these deep divergences than faster-evolving mitochondrial genes. Further exploration is required.

Our analyses are congruent with previous results showing that *Calcarius* and *Plectrophenax* are sisters, and that they are not closely related to *Emberiza* (Grapputo et al., 2001; Klicka et al., 2000, 2003, 2007; Lovette and Bermingham, 2002; Yuri and Mindell, 2002). The exact position of this clade in relation to others is unclear, both in our study and in previous analyses (above, and Ericson and Johansson, 2003). However, the distinctness of this group and the long branch leading up to it suggest that it would be appropriate to use a name for this clade. The family-group name Calcariini is available (Ridgway, 1901; Bock, 1994).

4.2. The Old World Emberizini clade

The monophyly of the Old World Emberizini is well corroborated by our data. The support for inclusion of *Miliaria, Melophus* and *Latoucheornis* is overwhelming, and we propose that they be synonymized with *Emberiza*, resulting in the species names *Emberiza calandra, Emberiza lathami* and *Emberiza siemsseni*, respectively. *Miliaria* has recently been suggested to be synonymized with *Emberiza* based on two studies of mitochondrial DNA of five and three, respectively, European species (Grapputo et al., 2001; Lee et al., 2001). Klicka et al. (2007) also found *Melophus* and *Miliaria* to be nested among *Emberiza*, although they did not comment on that (and the latter was treated as *Emberiza calandra*).

The four main *Emberiza* clades (A–D) are well corroborated in the combined analysis, although their relative positions are uncertain. However, the sister relationship between clade D and the others is reasonably well supported in the ODC and combined data trees, and is further corroborated by clades A, B and C sharing a unique 6-bp deletion in the ODC alignment. It is of interest to note that clade D comprises African taxa (*E. striolata* ranging into western Asia), while the other species are Palearctic.

Seven out of the 10 clades in the combined analysis comprise species which have previously been considered to be closely related based on morphological and vocal similarity (e.g. Byers et al., 1995; Cramp and Perrins, 1994). The sister relationships between *E. leucocephalos* and *E. citrinella*; *E. melanocephala* and *E. bruniceps*; *E. schoeniclus* and *E. pallasi*; *E. hortulana* and *E. caesia*; *E. striolata* and *E. tahapisi*; and *E. cia* and *E. godlewskii*, respectively, are uncontroversial, since they have long been regarded to be each other's nearest relatives in traditional taxonomic

treatments (e.g. Byers et al., 1995; Cramp and Perrins, 1994). Except for *E. cia–E. godlewskii*, these sister pairs are strongly corroborated by our data, being found in all trees and with generally strong support. In the cytochrome *b* tree, the interrelationships among *E. cia*, *E. godlewskii* and *E. cioides* are best considered to be unresolved. The pairs *E. leucocephalos–E. citrinella* and *E. melanocephala–E. bruniceps* are known to hybridize where their ranges overlap, and both these and *E. cia–E. godlewskii* are sometimes treated as conspecific (cf. Byers et al., 1995; Cramp and Perrins, 1994). However, the sister relations between *E. tristrami* and *E. variabilis*; *E. lathami* and *E. melanocephala*/*E. bruniceps*; *E. elegans* and *E. siemsseni*; and *E. calandra* and *E. fucata*, respectively, are totally unexpected (see below). The first three pairs are recovered in all three trees, and receive strong support in the combined analysis. However, in the ODC tree the sister relationship between *E. elegans* and *E. siemsseni* differs much in support between the BI and ML/MP analyses. This may suggest the possibility that the BI has assigned spuriously high support to an arbitrary resolution of a hard or near-hard polytomy (e.g. Lewis et al., 2005). However, the fact that this relationship is recovered by both the mitochondrial and nuclear data is evidence that it indeed represents the species phylogeny. The fourth sister pair is poorly supported in the combined and cytochrome *b* trees, and not recovered at all in the ODC tree, and is therefore considered unreliable.

The inclusion of *E. yessoensis* in clade A2 receives contradictory support in different trees. However, because of its morphological and ecological similarity with *E. schoeniclus* and *E. pallasi* (Byers et al., 1995), we strongly believe that the ODC and combined trees rather than the cytochrome *b* tree reflect the species phylogeny.

With respect to clades B1 and B2, we favour the topology of the combined analysis over any of the others. The taxa in each of these clades are united by morphological and vocal characteristics (Byers et al., 1995; Martens, 1996).

Clade A1 is mainly polytomous in all analyses. Although the addition of data might resolve the relationships among the taxa in this clade, the polytomy seems more likely to be the result of a rapid, "simultaneous" radiation. The uncorrected cytochrome *b* divergence among the species in unresolved positions in clade A1 are 5.1–8.3%, which would seem to be sufficient to resolve the relationships unless there has been a rapid, "simultaneous" radiation.

4.3. Morphological evolution

In the genus *Emberiza*, the sexual dimorphism in plumage is generally pronounced in the breeding season, with males being more brightly and contrastingly coloured than females. Females and juveniles are basically rather similar to each other. Adult males in non-breeding plumage are often similar to females. Most adult breeding males are easily distinguishable, while females and juveniles are generally more difficult to identify to species. Plumage differences among closely related species are generally more pronounced than structural differences (cf. Byers et al., 1995). These facts indicate that sexual selection has played a role in the evolution of plumage traits (Andersson, 1994; Panhuis et al., 2001).

Most clades contain predominantly morphologically rather similar species, although there are several examples where aberrant plumages have evolved. In clade A1, all except two species are markedly different in adult male breeding plumage, while other plumages are more similar. The most deviant species, *E. variabilis*, does not resemble any other *Emberiza* in adult male plumage, and all plumages differ from most other species of *Emberiza* (including all of those in clade A) in lacking prominent white patterns on the outer tail feathers. Another example of aberrant plumage is shown by *E. siemsseni*, which in all plumages is strikingly different from all other *Emberiza*, which is the main reason why it is usually placed in the monotypic genus *Latoucheornis*. The close resemblance of the adult male to adult male of the nominate subspecies of the North American *Junco hyemalis* is a remarkable case of convergent evolution. The three species in clade C are markedly different from each other (albeit only in adult male plumage in *E. bruniceps* and *E. melanocephala*). This is particularly true for *E. lathami*, which is so divergent from all other *Emberiza*, both in plumage and in having a prominent crest on the crown, that until now it has been placed in the monotypic genus *Melophus*. A different example of divergent plumage is presented by *E. calandra*, which is unique in lacking sexual dimorphism in plumage, all plumages being "female-like". Its position in the tree indicates a loss of the male plumage.

Emberiza cia and *E. godlewskii* resemble *E. capensis*, *E. striolata* and *E. tahapisi*, especially the subspecies *goslingi* of the latter, and these have all been suggested to be closely related (Hall and Moreau, 1970). However, our results suggest that the similarity between *E. cia* and *E. godlewskii*, on the one hand, and *E. capensis*, *E. striolata* and *E. tahapisi*, on the other hand, is the result of parallel evolution.

4.4. Conflicting branch lengths: recent divergence or introgressive hybridization?

The morphologically distinct sister species *E. leucocephalos–E. citrinella* and *E. hortulana–E. caesia* are separated by unexpectedly small cytochrome *b* divergences (0.4% and 0.9% uncorrected, respectively) and associated very short branch lengths in the cytochrome *b* tree. The pairwise cytochrome *b* divergence between the species in the first pair is comparable to that within populations of the same species in other passerine birds (e.g. Aleixo, 2006; Baker et al., 2003; Dietzen et al., 2007; Olsson et al., 2005; Päckert et al., 2006; Questiau et al., 1998). In a larger, unpublished, data set we have found shared haplotypes even between very distant locations, such as southern Sweden (*E. citrinella*) and easternmost Russia (*E. leucocephalos*). These obser-

vations could indicate recent separations from their respective common ancestors. This is indeed supported by the ODC data. However, surprisingly, in both species pairs, the more slowly evolving ODC locus shows relatively greater divergence than the faster-evolving cytochrome *b*. This might be the result of amplification of nuclear pseudogenes instead of mitochondrial DNA (e.g. Sorensen and Quinn, 1998; Zhang and Hewitt, 1996). However, the sequences show no evidence of being of nuclear origin (although pseudogenes can be hard to detect; cf. Klitgaard Nielsen and Arctander, 2001). Introgression of mitochondrial DNA seems to be a more likely explanation for the discordant patterns. *E. leucocephalos* and *E. citrinella* have extensively overlapping distributions (Byers et al., 1995; Cramp and Perrins, 1994). In some parts of the overlap zone, hybridization is frequent, while in other parts both species occur side by side without interbreeding (Byers et al., 1995; Cramp and Perrins, 1994; Panov et al., 2003). *E. hortulana* and *E. caesia* are not known to hybridize, but their present-day distributions hardly overlap (Byers et al., 1995; Cramp and Perrins, 1994; Roselaar, 1995). Past hybridization leading to introgression is nevertheless a possibility. Weckstein et al. (2001) argued that introgressive hybridization is the cause of discordant patterns of mitochondrial and allozyme data in the North American sparrows *Zonotrichia leucophrys* and *Z. atricapilla*. Also in other groups of birds, introgression has been considered the most likely explanation for conflicting patterns between different data sets (e.g. Helbig et al., 2001; Peters et al., 2007; Tegelström and Gelter, 1990). In contrast, *E. melanocephala* and *E. bruniceps*, which hybridize frequently where their ranges meet in a narrow zone (Byers et al., 1995; Cramp and Perrins, 1994; Haffer, 1977; Schütz, 1959), show relatively large genetic divergences in both loci, indicating long-standing reproductive isolation.

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Appendix A

List of samples (in alphabetical order), with geographic origin, museum reference number, GenBank accession number and type of documentation

Taxon	Locality	Museum No.	Regions	GenBank No.	Documentation
Ammodramus humeralis xanthornus	Paraguay	NRM 976701	cyt *b* ODC	EU325784 EU325842	Complete skeleton, photo
Calcarius lapponicus lapponicus	Sweden	NRM 20076332	cyt *b* ODC	EU325769 EU325827	–
	Sweden	NRM 976540*	cyt *b*	EU571278	Skin
Cardinalis cardinalis cardinalis	New York state, USA	NRM 20036311	cyt *b* ODC	EU325777 EU325835	Skin, partial skeleton
Carduelis carduelis carduelis	Sweden	NRM 20076333	cyt *b* ODC	EU325788 EU325846	–
	Sweden	NRM 20006471*	cyt *b*	EU571279	Skin
Coereba flaveola barbadensis	Barbados	NRM 20076334	cyt *b* ODC	EU325780 EU325838	Photo
Dendroica virens	El Salvador	NRM 20066318	cyt *b* ODC	EU325770 EU325828	Photo

(*continued on next page*)

Appendix A (*continued*)

Taxon	Locality	Museum No.	Regions	GenBank No.	Documentation
Emberiza aureola ornata	E Siberia, Russia (m)	NRM 20076335	cyt *b* ODC	EU325735 EU325793	Photo
Emberiza bruniceps	Kazakhstan (m)	NRM 20076336	cyt *b* ODC	EU325749 EU325807	Photo
Emberiza buchanani neobscura	Kazakhstan (m)	NRM 20076337	cyt *b* ODC	EU325757 EU325815	–
Emberiza cabanisi cabanisi	Cameroon	VH, uncatalogued	cyt *b* ODC	EU325767 EU325825	–
Emberiza caesia	Lesbos, Greece (b)	NRM 20076338	cyt *b* ODC	EU325756 EU325814	Photo
Emberiza calandra parroti	Sardinia, Italy (b)	NRM 20076363	cyt *b* ODC	EU325746 EU325804	–
Emberiza capensis capensis	Cape prov., South Africa	PFI, uncatalogued	cyt *b* ODC	EU325765 EU325823	–
Emberiza chrysophrys	Hebei, China (m)	NRM 20076339	cyt *b* ODC	EU325733 EU325791	–
Emberiza cia cia	Spain (b)	NRM 20076340	cyt *b* ODC	EU325758 EU325816	Wing
Emberiza cioides weigoldi	Hebei, China (b)	NRM 20076341	cyt *b* ODC	EU325759 EU325817	–
Emberiza cirlus cirlus	Bulgaria (b)	NRM 20076342	cyt *b* ODC	EU325752 EU325810	–
Emberiza citrinella citrinella	Sweden (b)	NRM 20076343	cyt *b* ODC	EU325753 EU325811	–
	Sweden (b)	NRM 996158*	cyt *b*	EU571277	Skin
Emberiza elegans elegans	Heilongjiang, China (b)	NRM 20076344	cyt *b* ODC	EU325744 EU325802	Photo
Emberiza flaviventris ssp.	Captive	UMMZ 233274	cyt *b* ODC	EU325766 EU325824	Wing, skeleton
Emberiza fucata fucata	Hebei, China (m)	NRM 20076345	cyt *b* ODC	EU325747 EU325805	–
Emberiza godlewskii omissa	Hebei, China (b)	NRM 20076346	cyt *b* ODC	EU325760 EU325818	Photo, sound recording
Emberiza hortulana	Kazakhstan (m)	NRM 20076347	cyt *b* ODC	EU325755 EU325813	Photo
Emberiza impetuani sloggetti	Orange Free State, South Africa	NMB GA85845	cyt *b* ODC	EU325764 EU325822	–
Emberiza jankowskii	Jilin, China (b)	IZB 4547	cyt *b* ODC	EU325761 EU325819	–
Emberiza lathami ssp.	Captive	ZMUC 118549	cyt *b* ODC	EU325750 EU325808	–
Emberiza leucocephalos leucocephalos	Kazakhstan (m)	NRM 20076348	cyt *b* ODC	EU325751 EU325809	–
Emberiza melanocephala	Turkey (b)	NRM 20076349	cyt *b* ODC	EU325748 EU325806	Photo
Emberiza pallasi polaris	Japan (w)	NRM 20076350	cyt *b* ODC	EU325742 EU325800	–
	Anadyr, Russia (b)	NRM 20066065*	cyt *b*	EU571276	Skin
Emberiza pusilla	Hebei, China (m)	NRM 20076351	cyt *b* ODC	EU325740 EU325798	–
	Anadyr, Russia (b)	NRM 20066110*	cyt *b*	EU571275	Skin

Appendix A (*continued*)

Taxon	Locality	Museum No.	Regions	GenBank No.	Documentation
Emberiza rustica rustica	Sweden (m)	NRM 20076352	cyt *b*	EU325738	Photo
			ODC	EU325796	
Emberiza rutila	Heilongjiang, China (b)	NRM 20076353	cyt *b*	EU325739	Photo
			ODC	EU325797	
Emberiza schoeniclus schoeniclus	Sweden (b)	NRM 20076354	cyt *b*	EU325741	–
			ODC	EU325799	
	Sweden (b)	NRM 20056559*	cyt *b*	EU571273	Skin
Emberiza siemsseni	Shaanxi, China (b)	IZB 2447	cyt *b*	EU325745	Photo
			ODC	EU325803	
Emberiza spodocephala spodocephala	Hebei, China (m)	NRM 20076355	cyt *b*	EU325736	–
			ODC	EU325794	
Emberiza stewarti	Kazakhstan (m)	NRM 20076356	cyt *b*	EU325754	Photo
			ODC	EU325812	
Emberiza striolata striolata	Israel (b)	NRM 20076357	cyt *b*	EU325762	Photo
			ODC	EU325820	
Emberiza sulphurata	Japan (b)	NRM 20076358	cyt *b*	EU325737	–
			ODC	EU325795	
Emberiza tahapisi tahapisi	Malawi	NRM 20076359	cyt *b*	EU325763	Photo
			ODC	EU325821	
Emberiza tristrami	Hebei, China (m)	NRM 20076360	cyt *b*	EU325732	–
			ODC	EU325790	
Emberiza variabilis	Japan (b)	NRM 20076361	cyt *b*	EU325734	–
			ODC	EU325792	
Emberiza yessoensis yessoensis	Japan (b)	NRM 20076362	cyt *b*	EU325743	–
			ODC	EU325801	
Emberizoides herbicola herbicola	Paraguay	NRM 986731	cyt *b*	EU325778	Complete skeleton,
			ODC	EU325836	photo
Helmitheros vermivorus	El Salvador	NRM 20066522	cyt *b*	EU325771	Photo
			ODC	EU325829	
Icterus galbula galbula	USA	BMNH 42547	cyt *b*	AF099290	?
Icterus galbula galbula	Kansas, USA	UKNHM 90711	ODC	AF491985	Skin
Junco hyemalis ssp.	California, USA	NRM 20016363	cyt *b*	EU325787	Skin, partial
			ODC	EU325845	skeleton
Sturnella superciliaris	Paraguay	NRM 996695	cyt *b*	EU325781	Complete skeleton.
			ODC	EU325839	photo
Melospiza georgiana georgiana	New York, USA	NRM 20036312	cyt *b*	EU325783	Skin, partial
			ODC	EU325841	skeleton
Passer montanus montanus	Sweden	NRM 20076364	cyt *b*	EU325789	–
			ODC	EU325847	
Passerculus sandwichensis athinus	Prince Albert Sound, Canada	NRM 20036550	cyt *b*	EU325786	Skin, partial
			ODC	EU325844	skeleton
Pheucticus ludovicianus	New York state, USA	NRM 20036252	cyt *b*	EU325774	Skin, partial
			ODC	EU325832	skeleton
Pipilo aberti aberti	California, USA	NRM 20016355	cyt *b*	EU325776	Skin, partial
			ODC	EU325834	skeleton
Piranga ludoviciana	California, USA	NRM 20016353	cyt *b*	EU325775	Complete skeleton
			ODC	EU325833	
Plectrophenax nivalis nivalis	Norway	NRM 20076365	cyt *b*	EU325768	–
			ODC	EU325826	

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Appendix A (*continued*)

Taxon	Locality	Museum No.	Regions	GenBank No.	Documentation
Seiurus noveboracensis	El Salvador	NRM 20066376	cyt *b* ODC	EU325772 EU325830	Photo
Setophaga ruticilla	El Salvador	NRM 20066387	cyt *b* ODC	EU325773 EU325831	Photo
Spizella pusilla pusilla	Michigan, USA	NRM 20036262	cyt *b* ODC	EU325782 EU325840	Skin, partial skeleton
Thraupis palmarum melanoptera	Tobago	NRM 20076366	cyt *b* ODC	EU325779 EU325837	–
Zonotrichia leucophrys leucophrys	New York state, USA	NRM 20036310	cyt *b* ODC	EU325785 EU325843	Skin, partial skeleton

BMNH: Bell Museum of Natural History, University of Minnesota; IZB: Institute of Zoology, Beijing, China; NMB: Nasionale Museum, Bloemfontein, South Africa; NRM: Swedish Museum of Natural History, Stockholm, Sweden; PFI: Percy FitzPatrick Institute of African Ornithology, Cape Town, South Africa; ZMUC: Zoological Museum of the University of Copenhagen, Copenhagen, Denmark; KUNHM: University of Kansas Natural History Museum, Lawrence, Kansas, USA; UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Michigan, USA; VH: Vogelwarte Hiddensee, Germany. m=migrant, w=winter visitor.

* refers to sequence not used in analyses (very similar or identical to analysed sequence); b means breeding area, m migrant and w winter area.

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