Molecular Phylogenetics and Evolution 62 (2012) 581–596

Contents lists available at SciVerse ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

The phylogenetic relationships and generic limits of finches (Fringillidae)

Dario Zuccon [a,*], Robert Prŷs-Jones [b], Pamela C. Rasmussen [c], Per G.P. Ericson [d]

[a] Molecular Systematics Laboratory, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden
[b] Bird Group, Department of Zoology, Natural History Museum, Akeman St., Tring, Herts HP23 6AP, UK
[c] Department of Zoology and MSU Museum, Michigan State University, East Lansing, MI 48824, USA
[d] Department of Vertebrate Zoology, Swedish Museum of Natural History, Box 50007, SE-104 05 Stockholm, Sweden

ARTICLE INFO

Article history:
Received 30 June 2011
Revised 27 September 2011
Accepted 3 October 2011
Available online 17 October 2011

Keywords:
Fringillidae
Drepanidinae
Carpodacus
Chaunoproctus
Phylogeny

ABSTRACT

Phylogenetic relationships among the true finches (Fringillidae) have been confounded by the recurrence of similar plumage patterns and use of similar feeding niches. Using a dense taxon sampling and a combination of nuclear and mitochondrial sequences we reconstructed a well resolved and strongly supported phylogenetic hypothesis for this family. We identified three well supported, subfamily level clades: the Holoarctic genus *Fringilla* (subfamily Fringillinae), the Neotropical *Euphonia* and *Chlorophonia* (subfamily Euphoniinae), and the more widespread subfamily Carduelinae for the remaining taxa. Although usually separated in a different family-group taxon (Drepanidinae), the Hawaiian honeycreepers are deeply nested within the Carduelinae and sister to a group of Asian *Carpodacus*. Other new relationships recovered by this analysis include the placement of the extinct *Chaunoproctus ferreorostris* as sister to some Asian *Carpodacus*, a clade combining greenfinches (*Carduelis chloris* and allies), *Rhodospiza* and *Rhynchostruthus*, and a well-supported clade with the aberrant *Callacanthis* and *Pyrrhoplectes* together with *Carpodacus rubescens*. Although part of the large *Carduelis–Serinus* complex, the poorly known *Serinus estherae* forms a distinct lineage without close relatives. The traditionally delimited genera *Carduelis*, *Serinus*, *Carpodacus*, *Pinicola* and *Euphonia* are polyphyletic or paraphyletic. Based on our results we propose a revised generic classification of finches and describe a new monotypic genus for *Carpodacus rubescens*.

1. Introduction

The true finches (Fringillidae), hereafter finches, are one of several lineages of granivorous passerines. They form the only clade of seedeaters with an almost world-wide distribution, occurring in Africa, Eurasia, and North and South America, although their greatest diversity in terms of number of species and genera is found in Eurasia (Clement et al., 1993; Collar and Newton, 2010). As in several other passerine groups, for a long time finch relationships were confounded by adaptations for sharing feeding niches with the other New World nine-primaried oscines (Sibley and Ahlquist, 1990 and references therein).

The current family composition (Dickinson, 2003) is the result of several anatomical studies by Sushkin (1924, 1925), Beecher (1953), Bock (1960), Ziswiler (1964, 1965) and Zusi (1978). Finches are separated from similar seedeaters by the reduction of the 10th primary and by the presence of grooves at the edge of the horny palate, used to wedge the seeds in the bill and then dehusk them with the tongue (Cramp and Perrins, 1994; Fry and Keith, 2004).

Traditionally the finches have been divided in the subfamilies Fringillinae, including the single genus *Fringilla*, and Carduelinae, for the remaining 130 or so species-level taxa. The segregation of *Fringilla* in a different subfamily was advocated because of their lack of a crop, differences in the bill anatomy, establishment of all-purpose breeding territories and feeding their nestlings only with insects, while the Carduelinae defend only a small area around the nest and feed their nestlings either a mixed diet of insects and seeds or seeds alone (Clement et al., 1993; Cramp and Perrins, 1994; Collar and Newton, 2010). More recently, analyses based on DNA hybridization (Sibley and Ahlquist, 1990) and sequence data (Arnaiz-Villena et al., 2001; Yuri and Mindell, 2002; Van der Meij et al., 2005; Nguembock et al., 2009) have confirmed the position of *Fringilla* as the sister lineage to the Carduelinae.

The phylogenetic relationships among the cardueline finches have now been examined using morphological (van den Elzen and Khoury, 1999; van den Elzen, 2000; Chu, 2002; James, 2004) and molecular data (Arnaiz-Villena et al., 1998, 1999, 2001; van den Elzen et al., 2001; Ryan et al., 2004; Yang et al., 2006; Nguembock et al., 2009; Töpfer et al., 2011). The molecular studies have

* Corresponding author. Present address: UMS 2700, Service de Systématique Moléculaire, Département Systématique et Evolution, Muséum National d'Histoire Naturelle, 57 rue Cuvier CP 26, 75231 Paris Cedex 05, France.

E-mail addresses: dario.zuccon@libero.it (D. Zuccon), r.prys-jones@nhm.ac.uk (R. Prŷs-Jones), rasmus39@gmail.com (P.C. Rasmussen), per.ericson@nrm.se (P.G.P. Ericson).

1055-7903/$ - see front matter © 2011 Elsevier Inc. All rights reserved.
doi:10.1016/j.ympev.2011.10.002

suffered from limited taxon sampling, but nonetheless their results are largely congruent and a common pattern emerges. In particular the three largest carduelinae genera, *Carpodacus*, *Carduelis* and *Serinus*, representing 70% of all species in the subfamily, are polyphyletic, suggesting extensive convergence on similar plumage patterns in distant lineages. With the taxonomically most inclusive dataset so far published, Nguembock et al. (2009) not only revealed the complex relationships between *Carduelis* and *Serinus* but were also able to disclose several cryptic species among the African serins and seedeaters (*Serinus*).

Liang et al. (2008) recently presented a molecular phylogeny of finches and buntings (Emberizidae) based on partial cytochrome oxidase I. Their topology differs in several points from all other published molecular analyses and from our results. An inspection of Liang et al.'s published sequences revealed that only some are putative cytochrome oxidase I, while the majority have unexpected stop codons and/or insertions causing codon frameshift, suggesting the amplification of nuclear copies. All the evidence indicates that Liang et al.'s analysis is deeply biased by the use of non-homologous sequences, and their results therefore will not be discussed further here.

Besides the fringilline and cardueline finches, recent molecular analyses of the New World nine-primaried passerines have identified a third deep finch lineage. Long mistaken for tanagers, the Neotropical *Euphonia* and *Chlorophonia* are actually true finches, although current evidence is conflicted with respect to their exact position (Burns, 1997; Klicka et al., 2000, 2007; Sato et al., 2001; Yuri and Mindell, 2002; Ericson and Johansson, 2003).

A fourth group of birds related to the finches are the drepanids or Hawaiian honeycreepers (Drepanidinae). They represent a classic case of adaptive radiation in an insular environment (Pratt, 2005). Despite their impressive array of bill shapes and plumage patterns that confounded early ornithologists, the monophyly of the drepanids is now well established, being supported by myology (Raikow, 1976), osteology (Zusi, 1978; James, 2004), DNA hybridization (Sibley and Ahlquist, 1982; Bledsoe, 1988) and mitochondrial DNA sequence data (Fleischer et al., 2001). However, relationships of the drepanids to the other finches remain more controversial. They are often treated as a distinct family, with the implicit assumption that their lineage is outside the Fringillidae clade. But several molecular analyses nest the drepanids within the Fringillidae as sister to the Carduelinae (DNA hybridization: Sibley and Ahlquist, 1982; mitochondrial DNA: Fleischer and McIntosh, 2001; Fleischer et al., 2001; Yuri and Mindell, 2002). Osteological data go even further, suggesting that the drepanids represent nothing more than a highly-derived lineage nested within the Carduelinae clade (James, 2004).

In the present work we use a combination of nuclear and mitochondrial sequences to address a number of issues concerning relationships within the Fringillidae. First, we examine the relationships among the main lineages of true finches. Second, we assess the relationships of several poorly known or debated taxa (e.g. *Chaunoproctus*, *Kozlowia*, *Callacanthis*, *Pyrrhoplectes*) and test the monophyly of larger genera. Third, we redefine the generic limits in the family and propose a revised taxonomy.

The finding in this study that *Carpodacus rubescens* does not form a monophyletic clade with other *Carpodacus* rosefinches (see below), but instead is sister to two very distinct taxa, *Callacanthis* and *Propyrrhula*, prompted us to investigate whether a new genus is required for *C. rubescens*. *Carpodacus rubescens* and *C. nipalensis* have sometimes been separated from the other *Carpodacus* and allocated to the genus *Procarduelis* (type species *C. nipalensis* Oates, 1890), on the basis of two shared characteristics: longer, more pointed bill than for other rosefinches; and unstreaked female plumages. The finding herein, based on genetic data, of lack of monophyly of *Procarduelis* as constituted by Oates (1890) suggests that *C. rubescens* requires the erection of a new genus. We therefore examined specimens of nearly all *Carpodacus* and closely related taxa to determine whether morphological characteristics provide additional support for the distinctiveness of *C. rubescens*. We also studied vocalizations of the same group of taxa to determine if the presence of prominent, well-developed song (which is known in relatively few *Carpodacus* species) correlates with phylogeny.

2. Materials and methods

2.1. Taxon sampling strategy

The phylogenetic analysis is based on 93 species of finches, with representatives of all major lineages, genera and species groups previously identified on morphological, biogeographical or molecular evidence. Our sampling is almost complete at the genus level. We were able to include all currently recognized genera except the monotypic genus *Neospiza*, while *Urocynchramus pylzowi*, traditionally classified among the Fringillidae, is not part of the finch clade and will therefore not be discussed further (Groth, 2000; Yang et al., 2006; Gebauer et al., 2006).

We included two out of three species of *Fringilla* (subfamily Fringillinae), 10 species out of 32 of the South American euphonias (*Euphonia* and *Chlorophonia*), three representatives of the drepanids (subfamily Drepanidinae), and 78 out of 133 species of subfamily Carduelinae. Overall, we put special emphasis on the Palearctic and Oriental taxa (83% included), where the majority of genera and most species with debated affinities occur. The tree was rooted using 10 species belonging to the Passeridae (*Passer*, *Petronia* and *Montifringilla*), Motacillidae (*Anthus* and *Motacilla*) and other nine-primaried oscines (*Plectrophenax*, *Ammodramus*, *Parula* and *Sturnella*), that are the closest lineages to the true finches (Barker et al., 2004; Fjeldså et al., 2010). Table 1 provides the list of included taxa with sample accession numbers and Genbank accession numbers. The nomenclature follows Dickinson (2003).

2.2. DNA isolation and sequencing

The fresh tissue samples were extracted using the Qiagen DNA Mini Kit, following the manufacturer's protocol. We used the Qiagen DNA Mini Kit for the toe-pad samples with a modified protocol as described in Zuccon (2005) and Irestedt et al. (2006).

We selected two mitochondrial and three nuclear genes that are widely used in bird phylogenetic studies: NADH dehydrogenase II and III genes (ND2 and ND3), intron 2 of the myoglobin gene, introns 6 and 7 of the ornithine decarboxylase (ODC) gene and intron 11 of the glyceraldehyde-3-phosphodehydrogenase (GAPDH). The five loci were amplified and sequenced using standard primers and amplification profiles as described in Zuccon et al. (2006) for ND2, Chesser (1999) for ND3, Irestedt et al. (2002) for myoglobin, Allen and Omland (2003) for ODC and Fjeldså et al. (2003) for GAPDH. The toe-pad samples were amplified in a series of short, overlapping fragments of 200–300 bp, using a large set of internal primers, whose sequences are available from the authors. PCR products were cleaned using QIAquick PCR Purification Kit (Qiagen, Valencia, CA, USA) and run on an ABI Prism 3100 automated DNA sequencer (Perkin-Elmer Applied Biosystems, Waltham, MA, USA).

2.3. Gene characterization and phylogenetic analyses

The five loci were concatenated in a partitioned dataset analyzed under the Bayesian inference and the maximum likelihood criteria.

Table 1
Samples and sequences included in the phylogenetic analysis, with museum accession numbers and collection localities. The taxonomy follows Dickinson (2003). GenBank accession numbers of sequences published previously are followed by their references. Museum acronyms: AJN Ajtte Swedish Mountain and Sami Museum, Jokkmokk; BMNH The Natural History Museum, Tring; IZAS Institute of Zoology, Chinese Academy of Science, Beijing; NHMO Natural History Museum, University of Oslo; NRM Swedish Museum of Natural History, Stockholm; RMNH Naturalis, Leiden. *References*: [1]: Fjeldså et al. (2003); [2]: Ericson and Johansson (2003); [3]: Fjeldså et al. (2010); [4]: Irestedt et al. (2006).

Taxon	Sample	GAPDH	Myoglobin	ODC	ND2	ND3	Origin
Bucanetes githagineus	NRM 20046702#	JN715204	JN715292	JN715384	JN715474	JN715566	Iran
Bucanetes mongolicus	NRM 570783*	JN715205	JN715293	JN715385	JN715475	JN715567	Kyrgyzstan
Callacanthis burtoni	NRM 570789*	JN715135	JN715227	JN715317	JN715409	JN715500	India
Carduelis ambigua	NRM 20026539#	JN715136	JN715228	JN715318	JN715410	JN715501	Captivity
Carduelis atrata	NRM 546071*	JN715137	JN715229	JN715319	JN715411	JN715502	Argentina
Carduelis barbata	NRM 546142*	JN715138	JN715230	JN715320	JN715412	JN715503	Argentina
Carduelis cannabina	NRM 966403*	JN715139	JN715231	JN715321	JN715413	JN715504	Sweden
Carduelis carduelis	NRM 996076*	JN715140	JN715232	JN715322	JN715414	JN715505	Sweden
Carduelis chloris	NRM 986328*	JN715141	JN715233	JN715323	JN715415	JN715506	Sweden
Carduelis citrinella	NRM 553307*	JN715211	JN715299	JN715391	JN715481	JN715573	Liechtenstein
Carduelis cucullata	NRM 20026508#	JN715142	JN715234	JN715324	JN715416	JN715507	Captivity
Carduelis flammea	NRM 20016449	JN715143	JN715235	JN715325	JN715417	JN715508	Sweden
Carduelis flavirostris	NRM 20066634	JN715144	JN715236	JN715326	JN715418	JN715509	Sweden
Carduelis hornemanni	AJN 000043	JN715145	JN715237	JN715327	JN715419	JN715510	Sweden
Carduelis magellanica	NRM 986696	JN715146	JN715238	JN715328	JN715420	JN715511	Paraguay
Carduelis monguilloti	NRM 546196*	JN715147	JN715239	JN715329	JN715421	JN715512	Vietnam
Carduelis pinus	NRM 20016375	JN715148	JN715240	JN715330	JN715422	JN715513	USA
Carduelis psaltria	NRM 20016376	JN715149	JN715241	JN715331	JN715423	JN715514	USA
Carduelis sinica	NRM 20026538#	JN715150	JN715242	JN715332	JN715424	JN715515	Captivity
Carduelis spinoides	NRM 20026503#	JN715151	JN715243	JN715333	JN715425	JN715516	Captivity
Carduelis spinus	NRM 986184	JN715152	JN715244	JN715334	JN715426	JN715517	Sweden
Carduelis tristis	NRM 20016378	JN715153	JN715245	JN715335	JN715427	JN715518	USA
Carpodacus erythrinus	NRM 976373	JN715154	JN715246	JN715336	JN715428	JN715519	Sweden
Carpodacus mexicanus	NRM 20056140	JN715155	JN715247	JN715337	JN715429	JN715520	USA
Carpodacus nipalensis	NRM 570792*	JN715156	JN715248	JN715338	JN715430	JN715521	Vietnam
Carpodacus pulcherrimus	NRM 20026494#	JN715157	JN715249	JN715339	JN715431	JN715522	Captivity
Carpodacus puniceus	NRM 570793*	JN715158	JN715250	JN715340	JN715432	JN715523	India
Carpodacus purpureus	NRM 557743*	JN715159	JN715251	JN715341	JN715433	JN715524	USA
Carpodacus rhodochlamys	NRM 20026491#	JN715160	JN715252	JN715342	JN715434	JN715525	Captivity
Carpodacus rodochroa	NRM 553889*	JN715162	JN715254	JN715344	JN715436	JN715527	India
Carpodacus rodopeplus	RMNH 44517*	JN715163	JN715255	JN715345	JN715437	JN715528	India
Carpodacus roseus	NRM 20026495#	JN715164	JN715256	JN715346	JN715438	JN715529	Captivity
Carpodacus rubescens	NRM 570784*	JN715165	JN715257	JN715347	JN715439	JN715530	China
Carpodacus rubicilla	NRM 20016594#	JN715166	JN715258	JN715348	JN715440	JN715531	Captivity
Carpodacus rubicilloides	NRM 570780*	JN715167	JN715259	JN715349	JN715441	JN715532	China
Carpodacus synoicus	NHMO 26633#	JN715168	JN715260	JN715350	JN715442	JN715533	Israel
Carpodacus thura	NRM 20016581#	JN715169	JN715261	JN715351	JN715443	JN715534	Captivity
Carpodacus vinaceus	NRM 20026493#	JN715170	JN715262	JN715352	JN715444	JN715535	Captivity
Chaunoproctus ferreorostris	BMNH 1855.12.19.71*	–§	–§	–	JN715445	JN715536	Bonin Islands
Chlorophonia cyanea	NRM 20066989#	JN715171	JN715263	JN715353	–	JN715537	Captivity
Coccothraustes coccothraustes	NRM 976374	JN715172	AY228292 [2]	JN715354	JN715446	JN715538	Sweden
Eophona migratoria	NRM 896473*	JN715173	JN715264	JN715355	JN715447	JN715539	Russia
Euphonia cayennensis	NRM 20056062#	JN715174	JN715265	JN715356	–	JN715540	Captivity
Euphonia chlorotica	NRM 956750	JN715175	AY228298 [2]	JN715357	JN715448	JN715541	Paraguay
Euphonia finschi	NRM 20066306#	JN715180	JN715270	JN715362	–	JN715545	Captivity
Euphonia laniirostris	NRM 20066309#	JN715176	JN715266	JN715358	JN715449	–	Captivity
Euphonia minuta	NRM 20066307#	JN715177	JN715267	JN715359	JN715450	JN715542	Captivity
Euphonia musica	NRM 976696	JN715178	JN715268	JN715360	JN715451	JN715543	Paraguay
Euphonia rufiventris	NRM 20066310#	JN715179	JN715269	JN715361	JN715452	JN715544	Captivity
Euphonia violacea	NRM 966943	JN715181	JN715271	JN715363	JN715453	JN715546	Paraguay
Euphonia xanthogaster	NRM 20066305#	JN715182	JN715272	JN715364	JN715454	JN715547	Captivity
Fringilla coelebs	NRM 956301	JN715183	JN715273	JN715365	JN715455	JN715548	Sweden
Fringilla montifringilla	NRM 20046395	JN715184	GU816941 [3]	GU816920 [3]	GU816851 [3]	GU816816 [3]	Sweden
Haematospiza sipahi	NRM 570790*	JN715185	JN715274	JN715366	JN715456	JN715549	India
Hemignathus virens	RCF 2913#	JN715225	JN715313	JN715405	JN715496	JN715588	Hawaii Islands
Hesperiphona vespertina	NRM 570795*	JN715186	JN715275	JN715367	JN715457	JN715550	USA
Kozlowia roborowskii	NRM 570781*	JN715161	JN715253	JN715343	JN715435	JN715526	China
Leucosticte arctoa	NRM 570788*	JN715187	JN715276	JN715368	JN715458	JN715551	Kuril Islands
Leucosticte brandti	NRM 570791*	JN715188	JN715277	JN715369	JN715459	JN715552	India
Leucosticte nemoricola	IZAS uncat#	JN715189	JN715278	JN715370	JN715460	JN715553	China
Leucosticte tephrocotis	NRM 20016579#	JN715190	JN715279	JN715371	JN715461	–	Captivity
Linurgus olivaceus	NRM 20086232#	JN715191	JN715280	JN715372	JN715462	JN715554	Nigeria
Loxia curvirostra	NRM 976546	JN715192	AY228303 [2]	GU816921 [3]	GU816852 [3]	GU816817 [3]	Sweden
Loxia leucoptera	NRM 20026565	JN715193	JN715281	JN715373	JN715463	JN715555	Sweden
Loxia pytyopsittacus	NRM 20046001	JN715194	JN715282	JN715374	JN715464	JN715556	Sweden
Loxioides bailleui	MRSNT 5783*	JN715195	JN715283	JN715375	JN715465	JN715557	Hawaii Islands
Mycerobas carnipes	NRM 570797*	JN715196	JN715284	JN715376	JN715466	JN715558	China
Paroreomyza montana	RCF 1984#	JN715197	JN715285	JN715377	JN715467	JN715559	Hawaii Islands
Pinicola enucleator	NRM 996174	JN715198	JN715286	JN715378	JN715468	JN715560	Sweden
Pinicola subhimachala	NRM 570796*	JN715199	JN715287	JN715379	JN715469	JN715561	India
Pyrrhoplectes epauletta	NRM 570785*	JN715200	JN715288	JN715380	JN715470	JN715562	China

(*continued on next page*)

Table 1 (*continued*)

Taxon	Sample	GAPDH	Myoglobin	ODC	ND2	ND3	Origin
Pyrrhula erythaca	NRM 20016568#	JN715201	JN715289	JN715381	JN715471	JN715563	Captivity
Pyrrhula nipalensis	NRM 570787*	JN715202	JN715290	JN715382	JN715472	JN715564	Malaysia
Pyrrhula pyrrhula	NRM 20046541	JN715203	JN715291	JN715383	JN715473	JN715565	Sweden
Rhodopechys sanguineus	NRM 20026504#	JN715207	JN715295	JN715387	JN715477	JN715569	Captivity
Rhodospiza obsoletus	NRM 20046707#	JN715206	JN715294	JN715386	JN715476	JN715568	Iran
Rhynchostruthus socotranus	NRM 570794*	JN715208	JN715296	JN715388	JN715478	JN715570	Yemen
Serinus burtoni	NRM 20086267#	JN715209	JN715297	JN715389	JN715479	JN715571	Nigeria
Serinus canaria	NRM 20026502#	JN715213	JN715301	JN715393	JN715484	JN715576	Captivity
Serinus canicollis	NRM 20076189#	JN715210	JN715298	JN715390	JN715480	JN715572	Captivity
Serinus citrinelloides	NRM 20026501#	JN715212	JN715300	JN715392	JN715482	JN715574	Captivity
Serinus estherae	RMNH 44712*	–	–	–	JN715483	JN715575	Java
Serinus leucopygius	NRM 20106050#	JN715214	JN715302	JN715394	JN715485	JN715577	Nigeria
Serinus mennelli	NRM 20026500#	JN715215	JN715303	JN715395	JN715486	JN715578	Captivity
Serinus mozambicus	NRM 20066026#	JN715216	JN715304	JN715396	JN715487	JN715579	Swaziland
Serinus pusillus	NRM 20046715#	JN715217	JN715305	JN715397	JN715488	JN715580	Iran
Serinus rufobrunneus	NRM 857618*	JN715218	JN715306	JN715398	JN715489	JN715581	Bioko
Serinus serinus	NRM 20046491	JN715219	JN715307	JN715399	JN715490	JN715582	Sweden
Serinus striolatus	NRM 570782*	JN715220	JN715308	JN715400	JN715491	JN715583	DR Congo
Serinus sulphuratus	NRM 20026498#	JN715221	JN715309	JN715401	JN715492	JN715584	Captivity
Serinus syriacus	NRM 570786*	JN715222	JN715310	JN715402	JN715493	JN715585	Israel
Serinus thibetanus	BMNH 1948.34.64*	JN715223	JN715311	JN715403	JN715494	JN715586	Burma
Uragus sibiricus	NRM 20076294#	JN715224	JN715312	JN715404	JN715495	JN715587	Captivity
Outgroup							
Ammodramus humeralis	NRM 966958	JN715126	GU816942 [3]	GU816922 [3]	GU816853 [3]	GU816818 [3]	Paraguay
Anthus trivialis	NRM 976393	JN715127	AY228285 [2]	GU816919 [3]	GU816850 [3]	GU816815 [3]	Sweden
Montifringilla ruficollis	IZAS uncat#	JN715129	AY228306 [2]	GU816915 [3]	GU816848 [3]	GU816813 [3]	China
Motacilla alba	NRM 976193	JN715130	AY228307 [2]	GU816918 [3]	GU816849 [3]	GU816814 [3]	Sweden
Parula pitiayumi	NRM 947170	JN715131	AY228309 [2]	JN715315	JN715407	JN715498	Paraguay
Passer luteus	NRM 20106041#	JN715132	GU816938 [3]	GU816913 [3]	GU816846 [3]	GU816811 [3]	Nigeria
Passer montanus	NRM 976359	AY336586 [1]	AY228311 [2]	DQ785937 [4]	GU816845 [3]	GU816810 [3]	Sweden
Petronia petronia	IZAS uncat#	JN715133	AY228312 [2]	GU816914 [3]	GU816847 [3]	GU816812 [3]	China
Plectrophenax nivalis	NRM 986392	JN715134	AY228315 [2]	JN715316	JN715408	JN715499	Sweden
Sturnella superciliaris	NRM 947221	JN715128	JN715226	JN715314	JN715406	JN715497	Paraguay

* Toe-pad sample.
\# Tissue sample only without voucher.
§ Sequence too short for submission to Genbank, see Appendix A.

The Bayesian inference was carried out using MrBayes 3.1.2 (Ronquist and Huelsenbeck, 2003), implemented on the freely available Bioportal (www.bioportal.uio.no). A mixed model approach was implemented to account for the potential differences in evolutionary model parameters between the data partitions corresponding to the five genes. The models best fitting the data were obtained with MrModelTest (Nylander, 2004), using the AIC criterion, in conjunction with PAUP* (Swofford, 2003). MrModelTest output suggested as the best fit the GTR + Γ model for the introns and the GTR + Γ + I model for the mitochondrial genes. We assumed uniform interval priors for the parameters, except for base frequencies, which were assigned a Dirichlet prior (Huelsenbeck and Ronquist, 2001). Two independent runs of four incrementally heated Metropolis-coupled MCMC chains for 10 million generations were run, with sampling every 1000 generations, yielding 20,000 trees. We used the online version of AWTY (Nylander et al., 2008) to assess the convergence of the MCMC chains and to estimate the number of generations to discard as "burn-in" (2000 trees).

Maximum likelihood searches of the partitioned dataset were conducted with RAxML v. 7.0.3 (Stamatakis, 2006) using a GTR + Γ + I model and random starting tree, with α-shape parameters, GTR-rates, and empirical base frequencies estimated and optimized for each partition. Nodal support was estimated using 100 bootstrap replicates.

Additionally, we compared the phylogenetic signal in the nuclear and mitochondrial genomes by analyzing concatenated mtDNA and nucDNA data sets independently using the same conditions indicated above for the Bayesian inference.

We compared alternative phylogenetic hypotheses using the Shimodaira-Hasegawa test (SH-test, Shimodaira and Hasegawa, 1999), as implemented in RAxML v. 7.0.3 (Stamatakis, 2006). The tested topologies were obtained enforcing the monophyly of selected taxa (see Table 3) in the maximum likelihood searches in RAxML.

2.4. Morphological and acoustic analysis of Carpodacus rubescens and related taxa

Five study skin specimens of *Carpodacus rubescens* were compared by a single researcher (PCR) with a large collection of study skins of nearly all related taxa (of those included in the phylogeny, only *Chaunoproctus* and *Koslowia* were unavailable for study) at the Field Museum of Natural History, Chicago. External morphological characteristics qualitatively examined included: bill shape, structure of narial capsule, plumage pattern, wing shape, wing formula, tail shape, tarsal scutellation and hindclaw curvature. The following 12 measurements were taken for each *C. rubescens*, a sample of 18 *C. nipalensis*, and a pair of each of the remaining *Carpodacus* taxa (except for *C. trifasciatus*, for which only a single male was available), as well as *Rhodopechys*, *Bucanetes*, *Callacanthis*, *Pyrrhoplectes*, and Asian *Leucosticte*: bill length from base of skull; bill height at distal edge of nares; wing length (flattened); length of primary projection beyond longest tertial; proximal point of emargination of primaries 8 and 7 (numbered from the innermost primary) to tip of each feather; tarsus length; length of hindclaw from distal edge of terminal scute; tail length (from point of insertion between central rectrices); distance between tips of longest uppertail covert and tail tip, and longest undertail covert to tail tip; and width of outer rectrix.

Vocalizations of *C. rubescens* were compared with those of the same grouping of species. Species were categorized by whether

an apparent territorial song is known, and whether the vocalizations are well-known enough to draw conclusions. The data on vocalizations are summarized from Rasmussen and Anderton (2005), and from recordings used in that book, as well as from other online sources (xeno-canto.com, avocet.zoology.msu.edu, macaulaylibrary.org, ibc.lynxeds.com).

3. Results

3.1. Phylogenetic analysis

We obtained an almost complete dataset (see Table 1). For *Serinus estherae* we were not able to sequence the three nuclear genes, while for *Chaunoproctus ferreorostris* we obtained only the mitochondrial genes and short portions of the GAPDH and myoglobin introns. The sequence alignment was straightforward, thanks to the limited number of indels in the three introns. However, inspection of the ODC gene alignment revealed the presence of two long insertions in three outgroup species: an autapomorphic insertion of 109 bp in *Sturnella superciliaris* and a synapomorphic insertion of 630 bp in *Motacilla alba* and *Anthus trivialis*. In order to reduce the computational time we exclude these two insertions from the combined dataset. The five genes were concatenated in a single dataset of 3134 bp. Table 2 presents a summary of the molecular properties of each partition.

The Bayesian inference and the maximum likelihood analysis recovered almost identical well-resolved topologies from the concatenated dataset, and the large majority of nodes received high support values in both analyses (Fig. 1). The two *Fringilla* (clade 1), the euphonias (*Euphonia* and *Chlorophonia*, clade 2) and the remaining taxa form the three major clades in the finch radiation, with the *Fringilla* lineage basal to the other two. The four grosbeak genera (*Coccothraustes*, *Eophona*, *Hesperiphona*, *Mycerobas*, clade 3) cluster together. In the Bayesian tree the first three taxa form an unresolved trichotomy, while in the maximum likelihood analysis *Coccothraustes* and *Hesperiphona* are sister taxa, with *Eophona* basal to them. The drepanid lineage (*Hemignathus*, *Loxioides* and *Paroreomyza*, clade 4) is sister to a large clade of several Palearctic taxa (clade 5), including the majority of *Carpodacus* rosefinches plus *Pinicola subhimachala* and the monotypic genera *Uragus*, *Kozlowia*, *Haematospiza* and *Chaunoproctus*. Two other Palearctic species of *Carpodacus* are part of a lineage including morphologically diverse taxa (clade 6). *Pinicola enuclator* and *Pyrrhula* form the most basal branch, followed by the *Rhodopechys-Bucanetes* lineage; the monotypic *Callacanthis* and *Pyrrhoplectes* cluster together with *Carpodacus rubescens*, while *Carpodacus nipalensis* is sister to *Leucosticte*. The two North American *Carpodacus* belong to a distinct lineage (clade 7), with the two species separated by a remarkably high genetic distance (uncorrected ND2 *p*-distance 13.7%).

The genera *Carduelis* and *Serinus* are highly polyphyletic, intermixing in a large, complex clade that includes also the genus *Loxia* and the monotypic *Rhodospiza*, *Rhynchostrutus* and *Linurgus*. The taxa cluster in a number of more homogenous lineages: the greenfinches together with *Rhodospiza* and *Rhynchostruthus* (clade 8), the African serins with *Linurgus* (clade 9), a mostly Holarctic group made up by linnets (clade 10), redpolls and crossbills (clade 11), the distinctive *Serinus estherae* (clade 12), the Eurasian goldfinch *Carduelis carduelis* and the citril finch *C. citrinella* (clade 13), the "Eurasian" serins (clade 14) and the siskins and the American goldfinches (clade 15).

The analyses of the nuclear and mitochondrial partitions support similar topologies, although minor differences exist (Fig. 2). The 15 clades identified in the combined analysis are all recovered also from the mitochondrial partition. In the analysis of the nuclear partition only two clades were not recovered, the American rosefinches (clade 7 in Fig. 1) and the "Eurasian" serins (clade 14), but in both cases their most basal nodes were simply collapsed, resulting in unresolved polytomies. Polytomies occur elsewhere in the two trees, resulting in clade arrangements that are in most cases topologically not different from the topology obtained from the combined analysis.

The mitochondrial and nuclear topologies differ mostly in the arrangement of the clades in the *Serinus–Carduelis* complex (clades 8–15). It is worth noting that the basal branches in the complex are all very short and also that in the combined analysis these nodes receives generally low support values. The mitochondrial topology agrees better with the combined analysis than the nuclear tree, but this is not surprising. In the *Serinus–Carduelis* complex the mitochondrial informative characters outnumber the nuclear characters almost five to one.

We compared the topology obtained from the combined dataset to 11 alternative phylogenetic hypotheses, obtained by enforcing selected groups of taxa, but in all cases the SH-test rejected the alternative topologies as significantly less likely that our combined topology (Table 3).

3.2. Morphological comparisons of Carpodacus rubescens and related taxa

Examination of 12 structural characteristics of the members of Clade 5 (Fig. 1A; minus *Chaunoproctus* and *Kozlowia*) and Clade 6 (Fig. 1B; minus *Pinicola* and *Pyrrhula*) showed that all members of these groups are similar in qualitative characters. However, *C. rubescens* differs from all other *Carpodacus* species in several quantitative characteristics, as follows.

First, the plumage of *C. rubescens* in both sexes is totally unstreaked; all other rosefinches except *C. nipalensis* have strongly streaked females and usually males, and even in *C. nipalensis* females have vague streaking on the back. Second, the bill of *C. rubescens* is much longer and thinner, more rounded and less conical than in other *Carpodacus* species except *C. nipalensis*, but in *C. rubescens* it is more swollen, deeper, and with a more pronounced tomial angle on the lower mandible than in *C. nipalensis*, and a much more distinct narrowing of the upper mandible toward the

Table 2
Sequence characteristics of the five loci analyzed. The numbers of variable and parsimony informative bases are calculated for the ingroup only. The synapomorphic insertions in ODC have been excluded from the computation, see text.

Gene region	GAPDH	Myoglobin	ODC	ND2	ND3
Alignment length	321	727	694*	1041	351
Number of variable bases (%)	157 (49%)	252 (35%)	243 (35%)	559 (54%)	186 (53%)
Number of parsimony informative bases (%)	80 (25%)	130 (18%)	130 (19%)	507 (49%)	171 (49%)
% A nucleotides (range)	22.2 (20.9–28.4)	28.4 (27.4–30.1)	27.2 (25.9–29.3)	30.7 (28.5–33.0)	28.5 (25.9–31.9)
% C (range)	21.5 (17.8–24.2)	22.4 (21.2–26.0)	17.2 (16.5–18.1)	34.2 (30.6–36.4)	32.9 (27.9–36.2)
% G (range)	32.3 (29.6–34.4)	23.3 (21.9–28.8)	20.2 (19.3–21.1)	10.3 (8.9–12.5)	12.4 (10.5–15.7)
% T (range)	24.0 (20.9–25.7)	26.0 (17.8–27.2)	35.4 (33.9–36.2)	24.8 (22.1–26.9)	26.2 (24.2–29.3)
Selected substitution model	GTR + Γ	GTR + Γ	GTR + Γ	GTR + Γ + I	GTR + Γ + I

* Length of the ODC alignment excluding the insertions; with the insertions the total length is 1427 bp.

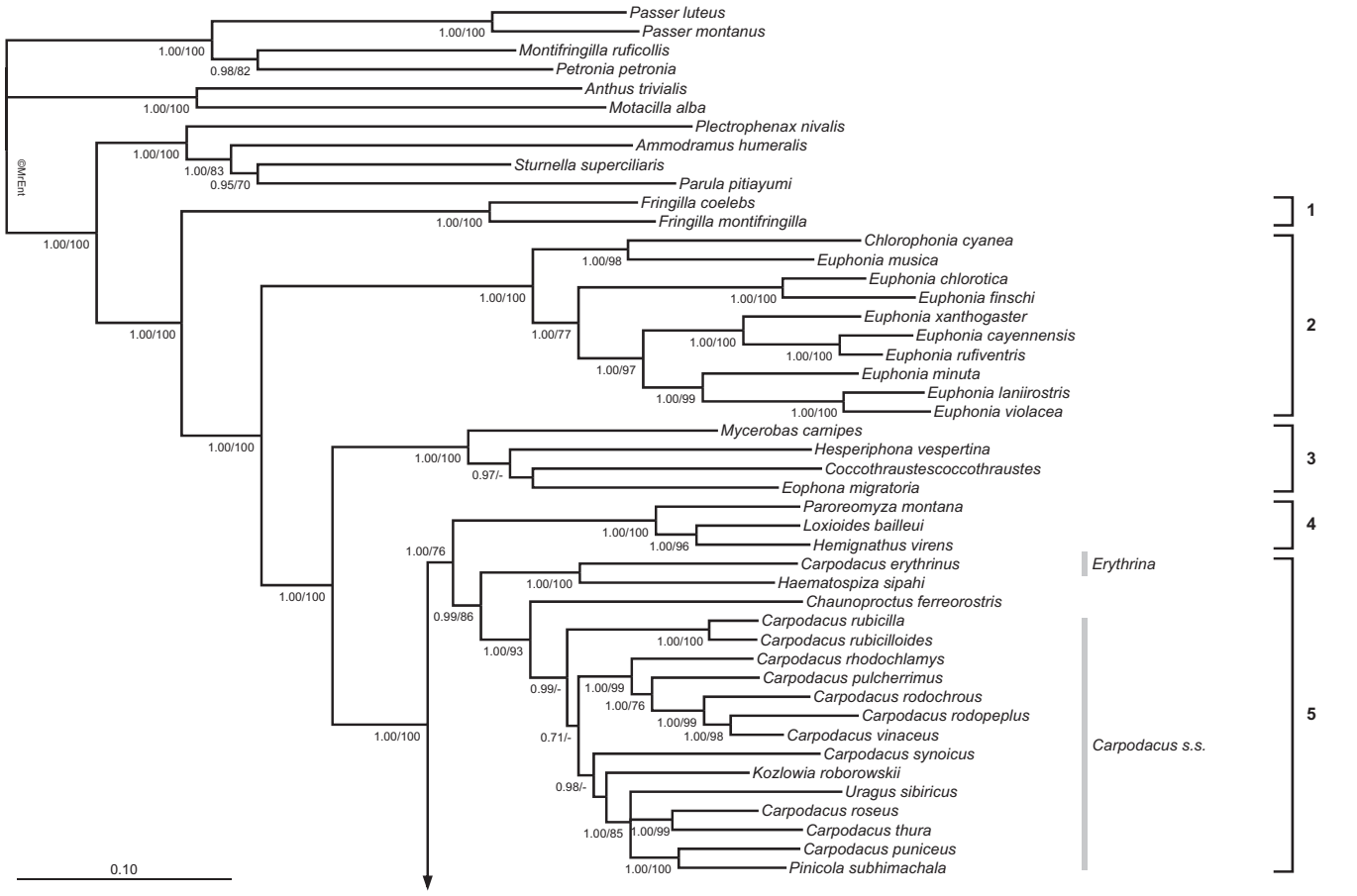

Fig. 1. The majority rule consensus tree obtained from the mixed-model Bayesian analysis of the concatenated dataset. The support values indicated at the node are the posterior probability (threshold 0.70) and the bootstrap support (threshold 70%) obtained from the maximum likelihood analysis, respectively. Brackets and numbers on the right refer to the clades discussed in the text. The grey bars identify those clades for which we propose changes of generic name and/or generic limits. The tree was edited in MrEnt v.2.2 (Zuccon and Zuccon, 2010).

tip. Thus, even in the two characters that have been used to group *C. rubescens* with *C. nipalensis* in *Procarduelis*, there are differences.

No other external characters were noted that can be used to justify the placement of *C. rubescens* together with *C. nipalensis* in *Procarduelis*, and in several characters *C. rubescens* and *C. nipalensis* differ distinctly, as follows: *C. rubescens* has a relatively short wing but long primary extension, and a short tail with very long uppertail and undertail coverts, all of which differ strikingly from *C. nipalensis*. The plumage of *C. rubescens* is fuller than for *C. nipalensis*, especially on the belly and flanks, and its thighs are much more thickly feathered, with the thigh feathers extending farther distally onto the anterior edge of the tarsus. The emarginations for primaries 6–8 (from inside) are much closer to the feather tips in *C. rubescens* than for *C. nipalensis*. The tips of the inner primaries of *C. rubescens* examined appear more rounded (vs. more angled in *nipalensis*) and the tips of the outer secondaries appear squarer (vs. more rounded in *nipalensis*). In the five *C. rubescens* examined, tarsal scutellation was slightly to distinctly more prominent than in *C. nipalensis*. The hindclaw of *C. rubescens* typically appears distinctly shorter and more curved than in *C. nipalensis*, though there is some overlap in the former character at least.

Principal components analysis confirms the proportional distinctiveness of these two species: in a PCA of seven external measurements (Fig. 3), the two taxa are fairly well-separated on a general size axis (PC-1, on which primary projection and bill length are uncorrelated to the other characters; Table 4) and on a shape axis (PC-2, which contrasts primary projection and bill length against tarsus length and undertail covert length).

Of the above characters that distinguish *C. rubescens* from *C. nipalensis*, two also distinguish the former from *Carpodacus sensu stricto* (as recovered in our phylogeny), notably the short but very pointed wing and the short tail with very long coverts. In addition, unlike all other species, the male of *C. rubescens* lacks areas of contrastingly bright red or pink color, the forehead and rump being only slightly brighter than surrounding areas. It is also the only *Carpodacus* species that has the red color restricted to a narrow tip on an otherwise grey feather (much as in *Pinicola enucleator*); the others have much of the feather pink, overlying white (except *C. puniceus*, which has drab, streaked brown bases), and it is the only species that has a distinctly grey belly, owing to the lack of red feather tips in that area. *C. rubescens* also has more pronounced tarsal scutellation than the majority of *Carpodacus sensu stricto* species, but this character is often difficult to discern in specimens and requires further study. *C. rubescens* is similar to several *Carpodacus* species in its relatively curved hindclaw.

The male of *C. rubescens* is extremely similar in plumage to the much larger, much longer-tailed male *Pinicola enucleator*, including in the distribution of red pigment on the body and on feathers, and in its white-edged grey-brown undertail coverts, but *rubescens* lacks white wingbars, has the red less blotchy and including the sides and flanks, and the bill is much less curved than for *P. enucleator*. Female plumages are very different.

In comparison to the superficially very distinct *Callacanthis burtoni*, males of this species and *C. rubescens* share the pattern of red on underparts just forming tips of duller feathers, but in *C. rubescens* the feathers concerned are principally grey while in *C. burtoni*

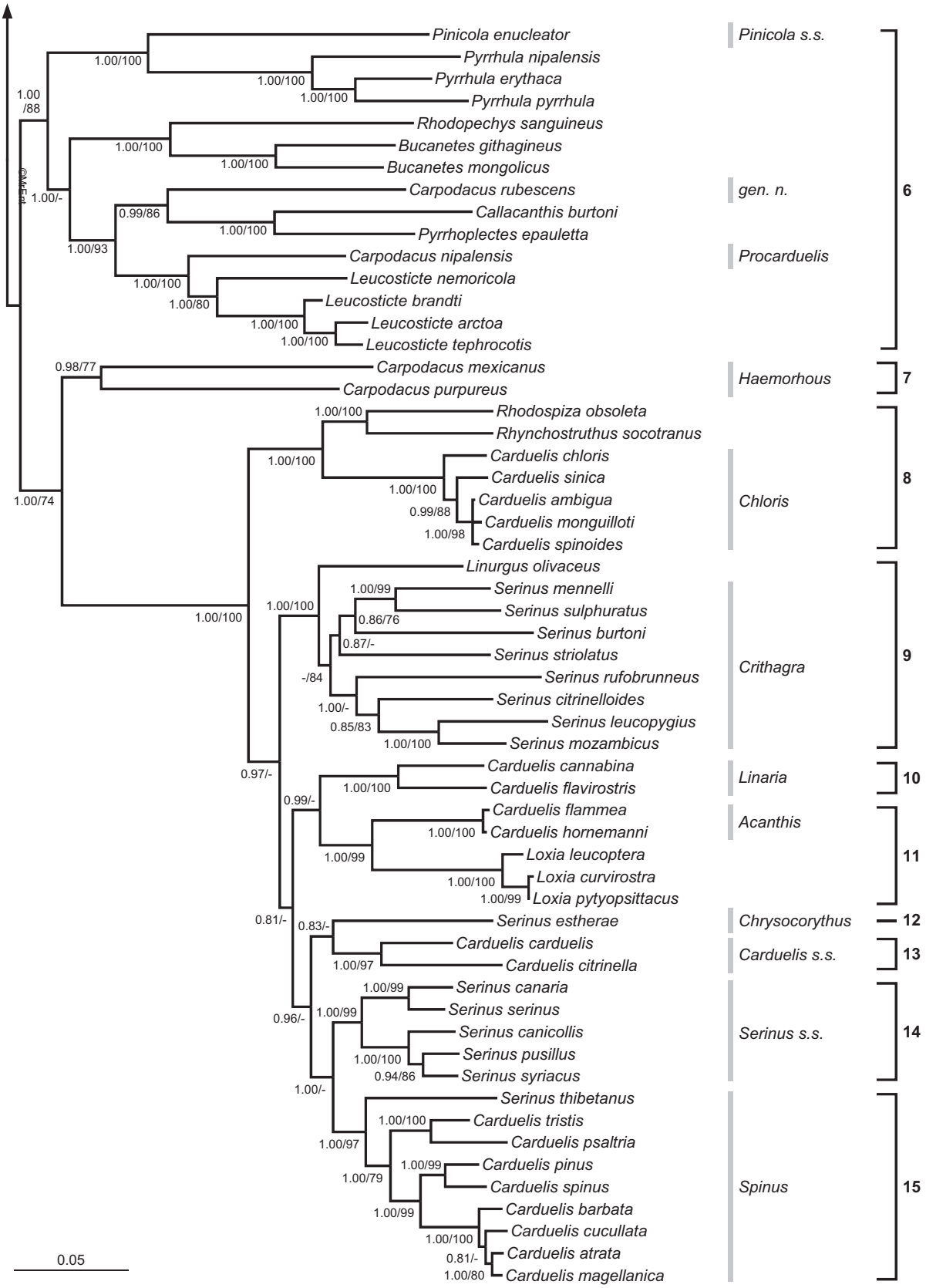

Fig. 1 (*continued*)

they are warm brown, except on the throat where they are blackish. No such similarities exist in upperparts pattern, in which the male of *Callacanthis* has a black head with red spectacles (the red feathers white-based and contrasting very strongly with the head), while *C. rubescens* has dull red feathers on a dark grey background; the upperparts of *Callacanthis* are brown and very vaguely

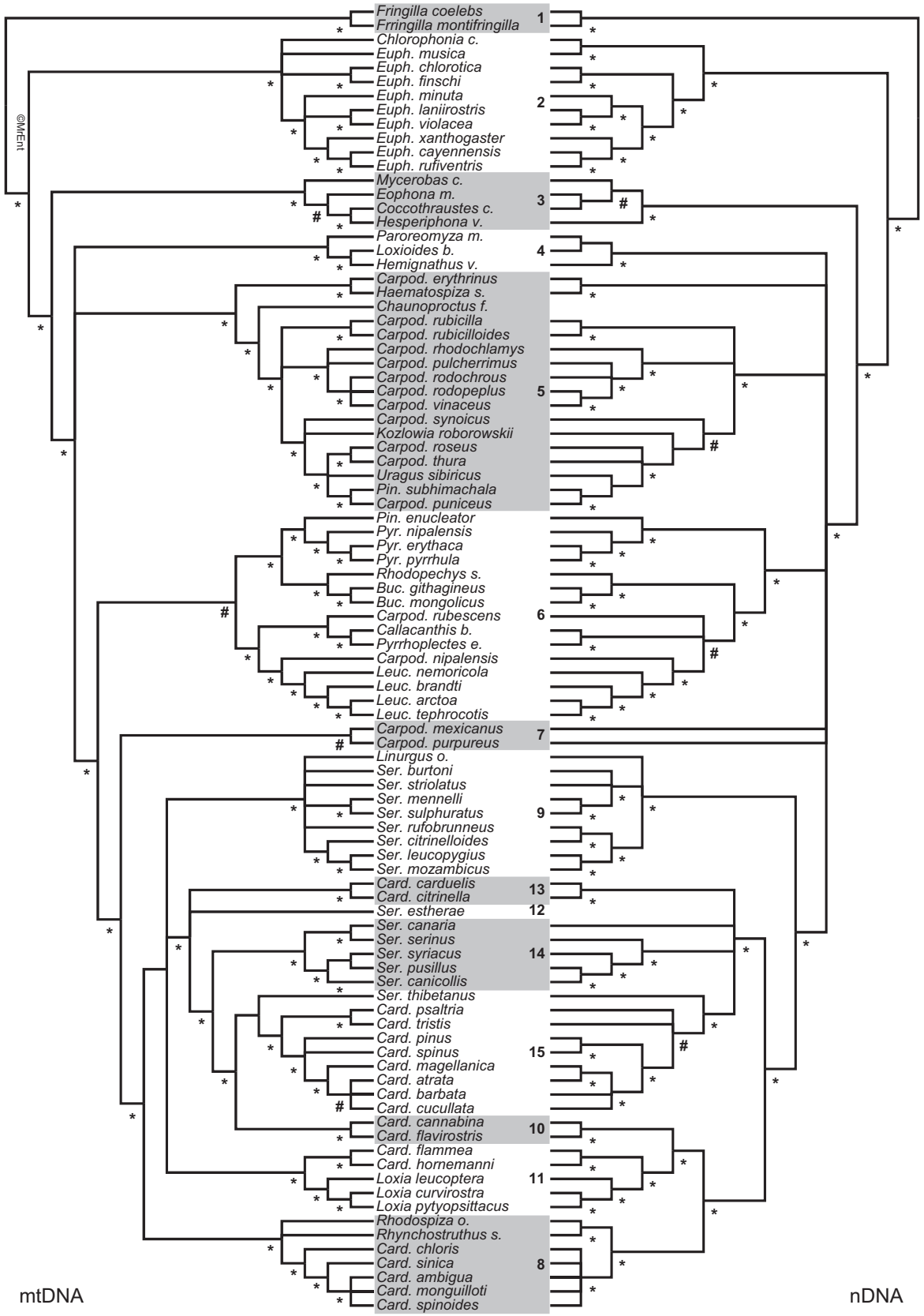

Fig. 2. Comparison of the topologies obtained from the mixed-model Bayesian analysis of the concatenated mitochondrial (mtDNA) and nuclear (nDNA) genes. ∗: nodes with posterior probability equal to or higher than 0.95. #: nodes with posterior probability equal to or higher than 0.90. Nodes with posterior probability below 0.80 have been collapsed. Taxon shading delimits the same groups identified in the combined analysis of all genes and indicated in Fig. 1.

streaked, with a brighter cinnamon rump with a very slight reddish wash; *C. rubescens* has plain tertials with indistinctly paler brown outer parts of outer webs, while *Callacanthis* has black wings and tail with white tips forming distinct spots. *Callacanthis* is much

Table 3
Comparison of alternative phylogenetic hypotheses using the Shimodaira–Hasegawa test performed with RAxML. $\Delta - \ln L$: difference in tree likelihood compared to the best tree. Significant: significantly worse than the best topology, $p < 0.05$.

Topology tested	Tree likelihood	$\Delta - \ln L$	SH-test
Best tree	−47017.332486		Best
Monophyly of Carduelinae	−47080.277898	−62.945412	Significant
Monophyly of *Carduelis*	−47241.615873	−224.283386	Significant
Monophyly of the American *Carduelis*	−47064.130419	−46.797933	Significant
Monophyly of *Carpodacus*	−47450.638460	−433.305974	Significant
Monophyly of the Eurasian *Carpodacus*	−47418.796659	−401.464172	Significant
Monophyly of *Carpodacus nipalensis* + *C. rubescens*	−47265.499724	−248.167237	Significant
Monophyly of *Rhodopechys* + *Bucanetes* + *Rhodospiza*	−47265.487752	−248.155266	Significant
Monophyly of *Pinicola*	−47217.945979	−200.613493	Significant
Monophyly of *Chaunoproctus* + *Coccothraustes* + *Mycerobas* + *Eophona* + *Hesperiphona*	−47055.614978	−38.282492	Significant
Monophyly of *Serinus*	−47163.935897	−146.603410	Significant
Monophyly of the Afrotropical *Serinus*	−47202.340370	−185.007883	Significant

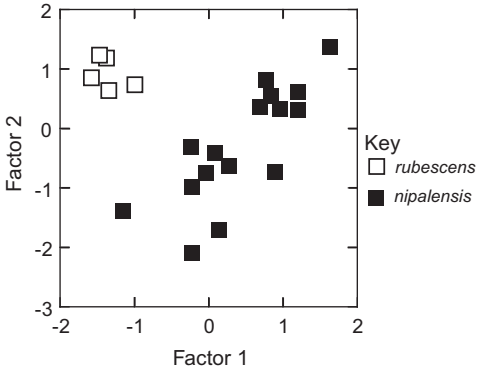

Fig. 3. Factor scores for individual specimens of *Carpodacus rubescens* and *C. nipalensis* using seven external morphological characters.

Table 4
Summary statistics for a principal components analysis of seven external morphological characters between *Carpodacus nipalensis* and *C. rubescens*.

Loadings	Factor 1	Factor 2
Bill length	0.08	0.78
Wing length	0.94	0.15
Primary projection	0.35	0.71
Tarsus length	0.70	−0.53
Hindclaw length	0.67	0.17
Tail length	0.92	0.16
Undertail coverts length	0.83	−0.41
Variance explained by components	3.50	1.63
% total variance explained	49.9	23.30

longer-winged than *rubescens*, with only slightly longer primary projection. *Callacanthis* however has P9 distinctly shorter than P8, while the two feathers are of similar length in *C. rubescens*. *Callacanthis* is much longer-tailed than *C. rubescens*, with tail coverts not especially long, and it has prominent white outer tail feathers. The undertail coverts of male *Callacanthis* are warm buffy, the centers of feathers vaguely darker, while the undertail coverts of *rubescens* are mostly dark grey-brown with fairly distinct, rather narrow whitish edges. Female *Callacanthis* has a similar but much duller pattern to that of the male. *Callacanthis* is not as thickly or lax-feathered as *C. rubescens*. The bill of *Callacanthis* is similar in overall shape to *C. rubescens* but larger and more swollen, with the tip narrowing much as in *C. rubescens* but slightly less distinctly. The tarsal scutellation of *Callacanthis* is similar to *C. rubescens* in being fairly obvious anteriorly, and the degree of hindclaw curvature is similar.

Males of *Pyrrhoplectes epauletta* and *C. rubescens* show no obvious shared plumage characters. Male *Pyrrhoplectes* is all velvety black with gold hindcrown and nape, white on inner webs of tertials and wing lining, and rusty-gold pectoral tufts and center of belly. The plumage of the underparts of *Pyrrhoplectes* is less full and lax than in *rubescens*, but much more so on the hindcrown and nape color patch. The undertail and uppertail coverts of *Pyrrhoplectes* are not notably long, and the tail is of average length for the broader clade. The wing of *Pyrrhoplectes* is slightly shorter, with the primary projection being notably shorter. The wing of *Pyrrhoplectes* is much more rounded, with P9–8 much shorter than P7. *Pyrrhoplectes* has P8–5 strongly emarginated. The tarsal scutellation of *Pyrrhoplectes* is moderately prominent, as in most *C. rubescens*. The bill shape of *Pyrrhoplectes* is similar to *C. rubescens* overall but deeper, broader, more swollen, and much shorter (lacking the long narrow tip, just the very tip narrowed strongly). In plumage, female *Pyrrhoplectes* is similar to *C. rubescens* in being unstreaked, but it has the male's white wing patches, and has much warmer brown overall plumage, especially below; plain warm brown undertail coverts, rich warm brown uppertail coverts, mantle color only slightly brighter, forecrown similar but hindcrown and nape strongly washed greenish.

The main external characters shared between *C. rubescens*, *Pyrrhoplectes*, and *Callacanthis* are the general bill shape (differing in relative size and proportions), the fairly strongly scutellated tarsus, and the nearly or totally unstreaked females. Overall, given the extremely striking differences between all three taxa, and the deep branch separating *C. rubescens* from *Callacanthis* and *Pyrrhoplectes*, we consider three genera to be warranted for this clade.

3.3. *Vocalizations of* Carpodacus rubescens *and related taxa*

While *Carpodacus rubescens* has a well-developed, loud, musical territorial song, in addition to its very different loud and distinctive call notes (P. I. Holt recordings, described in Rasmussen and Anderton, 2005), *C. nipalensis* appears to lack a distinct territorial song that differs noticeably from its call notes (although it is possible that it sings infrequently or inconspicuously on its breeding grounds). For most of the *Carpodacus sensu stricto* (as defined herein), no true song is known. As with *C. nipalensis*, many of them vocalize frequently but the vocalizations appear to be best classified as calls, although further contextual study and larger samples are needed. The known exceptions include *Carpodacus thura*, *C. dubius*, *C. severtzovi*, *C. punicea*, *Pinicola subhimachala*, and *Carpodacus erythrinus*, the latter in this analysis being sister to other rosefinches. The apparent lack of true song falls, for species represented in this phylogeny, within the *rhodochlamys–pulcherrimus–rodochrous–vinaceus–rodopeplus* clade (Fig. 1A). Of the other taxa in Clade 6 (Fig. 1B), *Pinicola* is a frequent singer, and *Pyrrhula* species give varied vocalizations that often blur the distinction between songs and calls. *Rhodopechys sanguineus* has a territorial song, as well as a variety of calls, some of which appear to be song fragments,

and both *Bucanetes* species have distinct songs and calls. For the clade in which *rubescens* falls in this analysis, *Callacanthis* has distinct songs and calls, while *Pyrrhoplectes* has fairly simple but melodious vocalizations that could fit either category. The clade to which *Procarduelis nipalensis* is sister, *Leucosticte*, also appears to lack true song.

In summary, there is good evidence that, at least in clades 5 and 6 in the present study, presence of a distinct song is related to phylogenetic history, as its absence appears to be restricted to several species in two lineages.

4. Discussion

4.1. Major finch lineages

With a denser taxon sampling and more genetic markers than previous studies, we obtained a well-resolved topology that significantly improves understanding of relationships within the Fringillidae. The true finch radiation comprises three major branches: the genus *Fringilla*, the euphonias (*Euphonia* and *Chlorophonia*) and a large clade for the Carduelinae and the drepanids.

The separation of *Fringilla* into its own subfamily is generally not questioned (e.g. Sushkin, 1924, 1925; Paynter, 1968; Cramp and Perrins, 1994; Dickinson, 2003; Collar and Newton, 2010). Our finding is in line with all published molecular analyses, either based on DNA hybridization (Sibley and Ahlquist, 1990) or sequence data (Arnaiz-Villena et al., 2001; Van der Meij et al., 2005; Yang et al., 2006; Nguembock et al., 2009), with some morphological and behavioral characters, e.g. cranial osteology (Zusi, 1978), presence/absence of a crop, territorial behavior and food choices (Cramp and Perrins, 1994), and with the cladistic osteological analysis of James (2004).

However, in a combined cladistic analysis of 148 osteological and 77 integumentary characters, Chu (2002) obtained alternative topologies depending on the dataset analyzed. None of these topologies recovered a sister relationship *Fringilla*-Carduelinae. The disagreement of Chu's analysis with the majority of other studies might not be unexpected. When mapping Chu's characters onto our topology, 63 characters were constant within the Fringillidae, 38 parsimony uninformative and only 124 (55%) parsimony informative (data not shown). The mapping of the parsimony informative characters revealed that only 26 (21%) of them have a homoplasy index below 0.33. Similarly, Raikow (1978) failed to recover *Fringilla* as sister to the Carduelinae using hindlimb myology. In a different bird family, the woodcreepers Dendrocolaptidae, Irestedt et al. (2004) observed poor agreement between molecular and morphological phylogeny, the latter based mostly on hindlimb myology and bill structure. They concluded that structures involved in locomotion and feeding are under strong selective pressure in response to lifestyle or ecological niche and are not suitable for inferring phylogenetic relationships. Presumably therefore, the lack of agreement of Raikow's (1978) and Chu's (2002) studies with other analyses is due to a suboptimal choice of possibly adaptive characters.

Previous molecular studies identified the euphonias as belonging to the Fringillidae, but were rather inconclusive on their more detailed relationships. It was suggested that they were sister either to *Fringilla* (Yuri and Mindell, 2002) or to the Carduelinae (Klicka et al., 2007), or even nested within the Carduelinae (Ericson and Johansson, 2003), although in all cases without statistical support. With a larger dataset we are able confidently to place the euphonia clade as sister to the Carduelinae. The current taxonomic division of euphonias into two genera is not supported. The genus *Euphonia* is paraphyletic, with *Chlorophonia* nested in it, but a taxonomic reassessment will require a denser sampling.

The euphonias differ strongly in a number of traits from the other finches (Isler and Isler, 1987; Ridgely and Tudor, 1989). Their plumage patterns are at odds with those of other finches, but somewhat reminiscent of the tanagers (Thraupidae), with which group the euphonias were usually included (e.g. Paynter and Storer, 1970). In *Chlorophonia* the plumage is predominantly green, while males of *Euphonia* typically have a yellow to rufous ventral side and dark iridescent blue upper parts. Glossy plumage is almost unknown in finches, except for a weak gloss in limited areas in *Coccothraustes* and *Pyrrhula*. Equally divergent are the feeding habits and reproduction of euphonias. Euphonias are frugivorous and feed their nestlings with regurgitated fruits, while finches are typically granivorous, though supplementing their summer diet to varying degrees with insects. The typical finch open cup nest, built by the female alone, is replaced in the euphonias by a domed nest with a side entrance, built by both parents. The majority of finches occur in the Old World and only few *Carduelis* have reached the South American continent in what seems to have been a quite recent radiation (van den Elzen et al., 2001). The presence of an entirely South American clade deeply nested within the Fringillidae suggests that the early family history saw significant intercontinental dispersals, with the euphonias representing a distinct radiation that adapted to a different ecological niche in the Neotropics.

The drepanids form a clade (clade 4) nested well within the large and heterogeneous Carduelinae radiation, contradicting all previous molecular analyses that recovered the drepanids as sister to the Carduelinae (Sibley and Ahlquist, 1982; Fleischer et al., 2001; Yuri and Mindell, 2002). However, in all previous attempts to investigate the phylogenetic relationships of the drepanids with other finches, the number of finch species sampled was rather scanty, suggesting that at least in part those findings were spurious due to inadequate sampling.

4.2. Relationships within the Carduelinae

Within the Carduelinae the hawfinch and grosbeaks (*Coccothraustes*, *Mycerobas*, *Hesperiphona*, *Eophona*) form a well defined clade, sister to the remaining taxa (clade 3). It comprises a small group of fairly large and stocky finches, with massive bills used for breaking hard seeds and kernels. In the prevailing taxonomic treatment they are divided into four genera (e.g. Vaurie, 1959; Voous, 1977; Clement et al., 1993; Dickinson, 2003), but a few authors (Paynter, 1968; Howard and Moore, 1980; Ripley, 1982) recognize an enlarged *Coccothraustes* encompassing all species. Despite disagreement concerning generic subdivision, the close relationship of the four grosbeak genera has never been questioned and the molecular evidence supports the traditional view. Compatible topologies were recovered by Arnaiz-Villena et al. (2001) and Yang et al. (2006) from cytochrome *b* data and confirmed by Van der Meij et al. (2005) and Nguembock et al. (2009) using multi-locus datasets. Very large bills occur in some other finch species (*Chaunoproctus*, *Rhynchostruthus*, *Neospiza*) and were sometimes used to group these species with the grosbeaks (e.g. Sharpe, 1909), but our results clearly indicate that these similarities in bill morphology are convergence, presumably to similar feeding niches.

Under the current generic limits the three most speciose Carduelinae genera, *Carpodacus*, *Carduelis* and *Serinus*, were already known to be polyphyletic (Arnaiz-Villena et al., 2001; Van der Meij et al., 2005; Yang et al., 2006; Nguembock et al., 2009), and it is therefore not surprising that the taxonomic history of these genera has been especially complex. With our larger dataset the degree of polyphyly can be seen to be even more widespread than previously understood. The SH-test rejected as significantly less likely the topologies obtained through constraining the monophyly of selected groups, lending further support to our findings.

The *Carpodacus* rosefinches are a group of Holarctic species with maximum diversity in the Himalayan region. Sexually dimorphic, the males' plumage is marked by a variable amount of red, pink or vinous, while the females are brown and more or less streaked. Since the revision by Vaurie (1959), prevailing opinion has largely accepted a broad *Carpodacus* genus for all taxa (Ripley, 1961, 1982; Paynter, 1968; Cheng, 1976; Voous, 1977; Clement et al., 1993; Eck, 1996; Dickinson, 2003; Collar and Newton, 2010). Disagreements were limited to three species. *Carpodacus nipalensis* and *C. rubescens* were sometimes removed to the genus *Procarduelis*, because of a thinner and more pointed bill (e.g. Hartert, 1910; Stuart Baker, 1930), while *C. puniceus* has been separated in the monotypic genus *Pyrrhospiza* on the grounds of differences in bill shape and wing and tail proportions (e.g. Dementiev and Gladkov, 1954; Rasmussen and Anderton, 2005; Collar and Newton, 2010). The classification of *Kozlowia roborowskii* has been more controversial, with it either being retained in a monotypic genus for its long wing, short tail and slender bill (Hartert, 1910; Vaurie, 1959; Cheng, 1976; Voous, 1977; Dickinson, 2003; Collar and Newton, 2010) or, dismissing these characters as adaptations to the high altitude, merged in *Carpodacus* (Paynter, 1968; Clement et al., 1993; Eck, 1996). The molecular results indicate that morphological characters are inadequate to understand relationships in the rosefinches. Although most species form a core rosefinch clade (clade 5), a few are closer to other taxa. Our results are compatible with the topologies of Arnaiz-Villena et al. (2001) and Yang et al. (2006), identifying a core rosefinch clade that includes most but not all Eurasian species plus *Kozlowia*, thereby supporting the derived nature of the latter's unique morphology. The same core rosefinch clade also includes *Uragus sibiricus* and *Pinicola subhimachala*. However, *Carpodacus erythrinus* belongs to a more basal branch, sister to the monotypic *Haematospiza sipahi*, another Himalayan large-billed form that was sometimes considered for this reason to be related to the grosbeaks (e.g. Clement et al., 1993).

Within the core *Carpodacus* clade is also the extinct *Chaunoproctus ferreorostris*, a large species with a massive bill that occurred in the Bonin Islands, a volcanic archipelago located about 1000 km south of Japan. It was discovered in 1827 during Beechey's voyage in HMS Blossom, when two individuals were collected, and it was observed again in 1828 during the voyage of the Senjawin, when Kittlitz collected a small series of about 10 individuals (BirdLife International, 2000). Subsequent expeditions did not find the species and it is believed to have become extinct soon after its discovery, following the colonization of the Bonin Islands by whalers and the introduction of predatory mammals (Fuller, 2001). Hartert (1910) and Morioka (1992) have already suggested that *Chaunoproctus* is likely to be linked to the *Carpodacus* rosefinches, being dimorphic, with males with red head and throat and females brown, while Taka-Tsukasa and Hachisuka (1907) noted plumage similarities with *Pinicola subhimachalus*, which according to our tree is nested within the *Carpodacus* clade. The flocking behavior common in many finches, and the long range migration of some species, unquestionably make them good potential colonizers (Bock, 1960). It is nonetheless remarkable that the two lineages that colonized remote Pacific oceanic islands, *Chaunoproctus* and the drepanids, are both closely related to the Asian rosefinches.

Of the remaining rosefinches, the North American species belong to a distinct lineage (clade 7), sister to the large *Serinus–Carduelis* radiation, while *Carpodacus nipalensis* and *C. rubescens* are nested within a clade mostly comprising Palearctic species of other genera (clade 6). The two latter *Carpodacus* taxa are not sister species, rejecting the hypothesis of close relationship based on a thinner bill and their separation in the genus *Procarduelis* (e.g. Hartert, 1910). The relationships recovered from all datasets are further supported by the rejection of a constrained topology enforcing *Carpodacus nipalensis* and *C. rubescens* as sister species. *C. nipalensis* stands apart from the other *Carpodacus*, being the only species laying white eggs with brown speckling, while the other species in the genus lay blue or greenish eggs (Ottaviani, 2008). The peculiar egg colour in *C. nipalensis* is shared only with *Leucosticte*, further supporting their placement as sister lineage.

Clade 6 is a rather heterogeneous assemblage, including species differing in morphology and plumage patterns, habitats and life histories. Together with *Pinicola*, a Holarctic coniferous forest specialist, and *Pyrrhula*, another woodland and forest genus, it also includes two open habitat groups, *Leucosticte* and *Rhodopechys* + *Bucanetes*, and the monotypic *Callacanthis* and *Pyrrhoplectes*. Most species belonging to this clade develop gular pouches during the breeding season and use them to store seeds with which they feed the nestlings. Gular pouches have been observed in *Pinicola* (French, 1954), *Pyrrhula* (Nicolai, 1956), *Leucosticte* (Miller, 1941), *Rhopopechys* (Niethammer, 1966) and *Bucanetes* (Cramp and Perrins, 1994). Although no information is available on the remaining taxa (*Callacanthis*, *Pyrrhoplectes*, *Carpodacus nipalensis* and *C. rubescens*), gular pouches have never been recorded in any other finch outside those belonging to clade 6 and we suggest that they might represent a synapomorphy restricted to this lineage.

Our topology of clade 6 is not fully congruent with previous molecular analyses. Although a clade for *Pinicola* and *Pyrrhula* was identified by both Arnaiz-Villena et al. (2001) and Yang et al. (2006), they disagree on the position of *Carpodacus nipalensis*, recovered as either sister to *C. mexicanus* or to *Leucosticte tephrocotis*, respectively. Both studies, however, relied only on cytochrome *b*, and the use of a single mitochondrial marker might not be suitable for resolving older divergences. Recently Töpfer et al. (2011) clarified the relationships in the *Pinicola–Pyrrhula* clade using cytochrome *b* only and a combined mitochondrial-nuclear dataset. Both datasets suggested the same branching pattern in the *Pinicola–Pyrrhula* clade, which is fully congruent with our results. However, differences exist in the relative placement of *Pinicola–Pyrrhula* and the other lineages recovered in our clade 6. In Töpfer et al.'s cytochrome *b* topology a *Leucosticte-Pyrrhoplectes* clade and *Bucanetes githagineus* are placed basally in the tree, far away from *Pinicola-Pyrrhula*. In this case the disagreements might be the result of a rooting problem caused by a suboptimal choice of a too-distant outgroup. In fact the pruning of *Fringilla* and *Turdus* from Töpfer et al.'s cytochrome *b* tree generates a topology that is congruent with our clade 6. But in the combined mitochondrial-nuclear dataset *Bucanetes*, *Pinicola* and *Pyrrhula* form a clade sister to *Carpodacus*, and more distantly related to *Leucosticte–Pyrrhoplectes*.

Although in our analyses we always recovered clade 6 and its main lineages, the relationships among the main lineages are nevertheless not fully congruent across the dataset analyzed. Thus *Pinicola–Pyrrhula* is recovered as sister to the other species in the combined and nuclear datasets, but it shifts to a position as sister to the *Rhodopechys–Bucanetes* lineage in the mitochondrial dataset. However, in the mitochondrial topology the nodes receive lower support values compared to the other two trees, and the topology recovered by the combined and nuclear dataset is further supported by two synapomorphic deletions of 17 and 2 bp in the ODC gene in *Leucosticte*, *Rhodopechys*, *Bucanetes*, *Callacanthis*, *Pyrrhoplectes*, *Carpodacus nipalensis* and *C. rubescens*.

The genus *Leucosticte* comprises a number of taxa adapted to cold climates, occurring either in the Himalayas above the tree line or in the Siberian and North American tundra. Our topology agrees with the phylogeographic analysis of Drovetski et al. (2009), which supports a single species, *Leucosticte tephrocotis*, for the North American taxa , sister to the Asiatic *L. arctoa*. *Leucosticte* shows a remarkable plumage similarity to the unrelated *Montifringilla* snowfinches, which belong to the Passeridae and occur in similar mountain habitats above the tree line across Eurasia. Due to their morphological similarity, the *Leucosticte* mountain finches have

in the past been merged into *Montifringilla* (e.g. Sharpe, 1909; Hartert, 1910). However, the prevailing brown and/or grey plumage in *Leucosticte* and *Montifringilla* is usually interpreted as a convergent adaptation to their treeless habitat in the tundra or high mountains (Clement et al., 1993).

A pale plumage as an adaptation to desert and arid habitats is shown also in four species occurring from Central Asia to North Africa that are usually allocated to the genera *Rhodopechys*, *Bucanetes* (two species) and *Rhodospiza*, but sometimes are all merged in an enlarged *Rhodopechys* (e.g. Vaurie, 1959; Paynter, 1968; Clement et al., 1993). According to the molecular data *Rhodopechys* and *Bucanetes* form a single lineage, but *Rhodospiza* belongs to a different clade, indicating another case of plumage convergence in finches. Our findings do not support the recognition of a distinct genus, *Eremopsaltria*, for *Bucanetes mongolicus*, as proposed by Kirwan and Gregory (2005) on grounds of differences in plumage, morphometry and caryotype from *B. githagineus*. Although the two *Bucanetes* species clearly differ in plumage colour, they share the same plumage patterns, have an almost parapatric distribution and are better considered congeneric.

Finally, clade 6 also contains two poorly known Himalayan species. *Pyrrhoplectes epauletta* has a male plumage unique among finches, mostly black with an orange crown and white tertial edges. Its affinities were unknown, but it has been regarded as possibly related to the grosbeaks or not even related to finches at all (Paynter, 1968; Desfayes, 1971). Nguembock et al. (2009) recovered *Pyrrhoplectes* as sister to *Pyrrhula*, the only other species of our clade 6 that they included in their study. *Callacanthis burtoni* has a peculiar bright red or yellow eye patch, in males and females respectively, but the rest of the plumage is reminiscent of some *Carpodacus* rosefinches, to which it has been considered related (Clement et al., 1993), although it has also been regarded as close to or congeneric with *Rhodopechys* (Paynter, 1968; Desfayes, 1969) or close to *Carduelis* (Voous, 1977). Our results do not support previous placements and reinforce the idea that these two species have aberrant plumages.

Several molecular studies have indicated that the genera *Serinus* and *Carduelis* are polyphyletic (Arnaiz-Villena et al., 1998, 1999, 2001; van den Elzen et al., 2001; Ryan et al., 2004; Van der Meij et al., 2005; Yang et al., 2006; Nguembock et al., 2009), forming a complex world-wide radiation together with the genera *Loxia* and *Linurgus*. Our findings confirm the complex relationships in the radiation, which also comprises the monotypic genera *Rhodospiza* and *Rhynchostruthus*. The molecular data identify, with high support, a number of clades grouping more homogeneous taxa. The relationships among these clades are not fully resolved, with conflicting evidence provided by the nuclear and mitochondrial genomes (Fig. 2). Incongruent signals from different genes were observed also by Nguembock et al. (2009), but even using the same gene, cytochrome *b*, changes in taxa included in the analysis resulted in quite different topologies (Arnaiz-Villena et al., 1998, 1999, 2001; van den Elzen et al., 2001; Ryan et al., 2004; Yang et al., 2006).

Despite these differences, some common patterns emerge. The *Carduelis* species collectively known as greenfinches (*Carduelis chloris*, *C. sinica*, *C. ambigua*, *C. spinoides* and *C. monguilloti*) cluster separately from congeneric species and, together with the monotypic *Rhodospiza* and *Rhynchostruthus*, form a distinct lineage (clade 8) of comparatively large-billed forms in the *Serinus–Carduelis* complex. This lineage is recovered as sister to the rest of the complex in the mitochondrial and combined dataset, as already found by Yang et al. (2006) and Nguembock et al. (2009). However, the nuclear genes shift the clade to a nested position in the *Serinus–Carduelis* complex (Fig. 2). The basal internodes in the complex are comparatively short and the differences in topology might be the result of incomplete lineage sorting. The affinity of *Rhynchostruthus* with the greenfinches was already suggested by Paynter (1968), dismissing Ripley and Bond's hypothesis (1966) of relationships with *Pinicola* and *Hesperiphona*, who further suggested that the large bill of *Rhynchostruthus* might represent an adaptation to dealing with the thick hulls of desert seeds. However, it should be noted that the species in clade 8 have quite strong bills, suggesting that the large bill is equally likely to represent a lineage symplesiomorphy. By contrast, the plumage of *Rhodospiza*, reminiscent of *Rhodopechys* and *Bucanetes*, the other finches of arid habitats with which it was often merged (e.g. Vaurie, 1959; Paynter, 1968; Clement et al., 1993), is a likely adaptation to desert habitat. *Rhodospiza* differs from *Rhodopechys* and *Bucanetes* in song, choice of breeding site and wing beat pattern during flight (Cramp and Perrins, 1994).

Most African *Serinus* serins and seedeaters fall within a large radiation (clade 9 and Arnaiz-Villena et al., 1999; Ryan et al., 2004; Nguembock et al., 2009). With a fairly well-sampled dataset of African *Serinus*, Nguembock et al. (2009) identified three lineages that match rather well the groups defined by van den Elzen and Khoury (1999) using morphological and behavioral characters. The apparent congruence of molecular and morphological evidence prompted Nguembock et al. (2009) to propose a revised taxonomy for the African serins, applying generic names to the three major lineages. Unfortunately the molecules-morphology congruence is not universally supported, as is evident from examining Ryan et al.'s (2004) results and our topology. In our tree, the species belonging to the purported *Poliospiza* group (*sensu* van den Elzen and Khoury, 1999), i.e. *Serinus mennelli*, *S. burtoni*, *S. striolatus* and *S. rufobrunneus*, are paraphyletic, making Nguembock et als' taxonomy untenable. The *Poliospiza* group is equally paraphyletic in Ryan et als' tree, where there is also evidence for paraphyly in the *Dendrospiza* group (*sensu* van den Elzen and Khoury, 1999). Thus we consider it more appropriate to retain all species in this clade in a single genus.

Recently Melo (2007) and Melo and Jones (in press) showed that another species belongs to the African serins' clade. The São Tomé grosbeak *Neospiza concolor* appears to be sister to *Serinus rufobrunneus*, a seedeater endemic to São Tomé and the nearby island of Príncipe in the Gulf of Guinea. *Neospiza* may provide a case of body size increase and bill hypertrophy in island birds (Grant, 1968; Clegg and Owens, 2002) that parallels the *Chaunoproctus–Carpodacus* case mentioned above, although competitive interactions with its sister species may have also been involved (Grant, 1998).

Another African species, *Linurgus olivaceus*, is recovered together with the African serins' clade in all analyses. It is a stocky species with black head, yellow-greenish body and strong bill, which differs in body structure, plumage and call from the serins and has long been considered either related to the grosbeaks, and in particular to the North American *Hesperiphona* (Desfayes, 1971), or a rather isolated lineage (Fry and Keith, 2004). The placement of *Linurgus* and the African *Serinus* in a single lineage was consistently recovered in all analyses, but Nguembock et al. (2009) found a sister relationships of *Linurgus* with the *Carduelis* goldfinches' clade (corresponding to our clade 8 in Fig. 1). Although our results seem to be strongly supported, they should therefore be confirmed with independent data.

Despite a remarkable plumage similarity, the Western Palearctic serins (*Serinus serinus*, *S. canaria*, *S. syriacus* and *S. pusillus*) are not the sister clade to the main African radiation and form a distinct lineage (clade 14) that contains also two African species, *Serinus canicollis* and *S. alario* (Arnaiz-Villena et al., 1999; Ryan et al., 2004; Nguembock et al., 2009). The same group was also supported by the morphological and behavioral analysis of van den Elzen and Khoury (1999), although they further added *Carduelis citrinella*. The latter species was included in *Carduelis* until Vaurie (1959) transferred it to *Serinus*, a decision followed by all subsequent authors. However, all molecular data indicate that it forms a distinct lineage

together with *Carduelis carduelis* in the *Serinus–Carduelis* complex (clade 13), supporting its return to *Carduelis*.

Geographically disjunct, *Serinus estherae*, a poorly known species of montane habitats, is the only serin species occurring in the Oriental region, with isolated populations in Sumatra, Java, Sulawesi and the Philippines (Clement et al., 1993). Following traditional opinion, it has been generally included in *Serinus* (e.g. Ripley and Rabor, 1961; Paynter, 1968; Clement et al., 1993; Dickinson, 2003), although White and Bruce (1986) noted that it might belong elsewhere. Delacour (1946) was the only author who dismissed a relationship with *Serinus*, suggesting instead a link with *Carduelis monguilloti*, the geographically nearest finch, occurring in South Vietnam. Our results indicate that *S. estherae* has close relationships with neither *Serinus* nor *Carduelis monguilloti*. In our combined dataset *Serinus estherae* is closest to the *Carduelis carduelis–C. citrinella* lineage, but the node has no support, while in the mitochondrial dataset the node collapses in a large polytomy (clade 12). It therefore seems more appropriate to regard *Serinus estherae* as an isolated lineage, deserving the recognition of a separate genus in agreement with Wolters (1967).

The last species in *Serinus*, *S. thibetanus*, is restricted to the Eastern Himalayas and Western China. It couples a serin-like general plumage with the habits of *Carduelis* siskins, and indeed it has been alternately shifted between *Serinus* (e.g. Paynter, 1968; Voous, 1977; Ripley, 1982; Clement et al., 1993; Dickinson, 2003) and *Carduelis* (e.g. Hartert, 1910; Vaurie, 1959; Ripley, 1961; Cheng, 1976; Eck, 1996; Rasmussen and Anderton, 2005). Our results indicate that it is sister to the large "American" *Carduelis* clade (clade 15), which also includes the Palearctic *Carduelis spinus*. In this lineage, the North American taxa branch off first, while the Central and South American species form a more recent radiation that rapidly colonized the entire continent. Our topology is consistent with the hypothesis of progressive lineage diversification paralleling the north to south colonization of the Americas (van den Elzen et al., 2001), although it does not fully agree with previous results. In Arnaiz-Villena et al.'s topology (1998), the American *Carduelis* clustered in two distinct clades, one for the Central-South American species plus *Carduelis pinus* and *C. spinus*, and a second for the other North American species. Their use of a single, quite rapidly evolving marker, cytochrome *b*, might be responsible for the differences in the more basal nodes in Arnaiz-Villena et al.'s tree and our own. Instead our tree shows a better agreement with the topology of Nguembock et al. (2009). However in the combined analysis they found *Carduelis spinus* outside the "American" clade and closer to *Carduelis hornemanni* and *Loxia*. In this context, we note that Nguembock et als' ND3 *Carduelis spinus* sequence (EU881008) is identical to ours, and in their ND3 topology the species is indeed placed in the "American" *Carduelis* clade. However, their myoglobin sequence (EU878702) is surprisingly similar to our *Loxia* sequences (*p*-distance < 0.005) but quite different from *Carduelis pinus*, the sister species of *C. spinus* in our tree (*p*-distance = 0.023). We were not able to investigate the other sequences used, but it seems likely that Nguembock et al.'s result is due to their use for *Carduelis spinus* of sequences that in part do not belong to this species.

Two Holarctic groups form a strongly supported clade, the *Loxia* crossbills and the redpolls *Carduelis flammea* and *C. hornemanni* (clade 11). The same topology has been recovered in all previous molecular studies (Arnaiz-Villena et al., 1998; Ryan et al., 2004; Yang et al., 2006; Nguembock et al., 2009). Less clear are their relationships with *Carduelis flavirostris* and *C. cannabina* (clade 10). These four *Carduelis* species have sometimes been separated in the genus *Acanthis* (Vaurie, 1959; Paynter, 1968; Rasmussen and Anderton, 2005) and indeed *Carduelis flavirostris* is remarkably similar to *C. flammea* and *C. hornemanni* in proportion, habitat and plumage pattern (Clement et al., 1993). Our molecular data provide discrepant evidence, with support for a sister-relationship of clades 10 and 11 according to the nuclear and combined datasets, but with the mitochondrial genes pointing instead to a relationship of the *C. flavirostris–C. cannabina* pair to the "American" siskins (clade 15). The latter is also indicated in part by the findings of Arnaiz-Villena et al. (1998), whereas Nguembock et al. (2009) recovered *C. cannabina* as a lineage isolated from the other taxa.

4.3. Taxonomic recommendations

On the basis of both our results and previous studies we suggest a number of changes in the taxonomic treatment of the family Fringillidae relative to the classification used in Dickinson (2003).

(a) The family Fringillidae should comprises three subfamilies: Fringillinae Leach, 1820, including only the genus *Fringilla*; Euphoniinae Cabanis, 1847, including the genera *Euphonia* and *Chlorophonia*; and Carduelinae Vigors, 1825, for the remaining genera, including the Hawaiian drepanids. The name Drepanidinae Cabanis, 1847, is subsumed as a junior synonym of Carduelinae Vigors, 1825.

(b) The genus *Carpodacus* Kaup, 1829 (type species *Fringilla rosea* Pallas, 1776), should be redefined to include the species *Carpodacus pulcherrimus* (F. Moore, 1856), *C. puniceus* (Blyth, 1845), *C. rhodochlamys* (J. F. Brandt, 1843), *C. rodochroa* Vigors, 1831, *C. rodopeplus* (Vigors, 1831), *C. roseus* (Pallas, 1776), *C. rubicilla* (Güldenstädt, 1775), *C. rubicilloides* Przevalski, 1876, *C. synoicus* (Temminck, 1825), *C. thura* Bonaparte and Schlegel, 1850, *C. trifasciatus* J. Verreaux, 1871 and *C. vinaceus* J. Verreaux, 1871, following Yang et al. (2006), our own results and, in part, Arnaiz-Villena et al. (2001). Pending molecular analyses we also suggest that *C. edwardsii* J. Verreaux, 1871, *C. eos* (Stresemann, 1930) and *C. grandis* Blyth, 1849, be retained in *Carpodacus*. We further propose merging into *Carpodacus* the following species: *Kozlowia roborowskii* (Przevalski, 1887), *Uragus sibiricus* (Pallas, 1773) and *Pinicola subhimachala* (Hodgson, 1836) (which becomes *subhimachalus* in combination with the masculine name *Carpodacus*).

(c) *Carpodacus erythrinus* (Pallas, 1770) falls outside the core rosefinch clade and should be transferred to a monotypic genus, for which we propose to resurrect the genus name *Erythrina* Brehm, 1829 (type species *Erythrina albifrons* Brehm, 1829 = *Loxia erythrina* Pallas, 1770, gender feminine, thus requires emending the specific name to *erythrina*).

(d) The genus *Pinicola* Vieillot, 1807, should be restricted to *Pinicola enucleator* (Linnaeus, 1758).

(e) *Carpodacus nipalensis* (Hodgson, 1836) should be transferred to a monotypic genus, for which we propose to resurrect the genus name *Procarduelis* Blyth, 1843 (type species *Carpodacus nipalensis* Hodgson, 1836, gender feminine).

(f) The species *Carpodacus rubescens* (Blanford, 1872) belongs to a distinct lineage not related to the other rosefinches. We propose to separate this species in the monotypic genus

Agraphospiza gen. n.

Type species: *Procarduelis rubescens* Blanford, 1872. Gender feminine.

Diagnosis: the new taxon differs from the other rosefinches of the genera *Carpodacus*, *Erythrina* and *Haemorhous* (as here restricted) by the totally unstreaked plumage in both sexes, the much longer and thinner, more rounded and less conical bill, the short but very pointed wing and the short tail with very long coverts. It differs also from *Procarduelis* in morphological proportions as shown by the PCA (Fig. 3), the

presence of a well-developed, loud, musical territorial song, and in laying blue eggs (vs. white eggs in *Procarduelis*). Etymology: *Agraphospiza* = unstreaked finch, from ἄγραφος (Greek: *a* – not; *graphos* – lines) and σπίζα (Greek: *spiza* – finch).

(g) The North American species of rosefinches, *Carpodacus mexicanus* (Statius Müller, 1776) and *C. purpureus* (Gmelin, 1789), belong to a distinct lineage not related to the Palearctic taxa, so they must be separated in a different genus, for which we propose to resurrect the genus name *Haemorhous* Swainson, 1837 (type species *Fringilla purpurea* Gmelin, 1789, gender masculine). *Carpodacus cassinii* Baird, 1854 is included here, on grounds of morphological similarity with *C. purpureus*, biogeography and protein allozyme data (Marten and Johnson, 1986).

(h) The genus *Serinus* Koch, 1816 (type species *Serinus hortulanus* Koch, 1816 = *Fringilla serinus* Linnaeus, 1766), is polyphyletic. We propose to restrict the genus *Serinus* to the species *Serinus alario* (Linnaeus, 1758), *S. canaria* (Linnaeus, 1758), *S. canicollis* (Swainson, 1838), *S. pusillus* (Pallas, 1811), *S. serinus* (Linnaeus, 1766) and *S. syriacus* Bonaparte, 1850, following our results and the analyses of Arnaiz-Villena et al. (1999), Ryan et al. (2004) and Nguembock et al. (2009).

(i) The remaining African and Arabian species of *Serinus* form a monophyletic clade, for which we propose to resurrect the genus name *Crithagra* Swainson, 1827 (type species *Loxia sulphurata* Linnaeus, 1766, gender feminine, multiple specific name changes required). The inclusion of these species is supported by our results, by the analyses of Ryan et al. (2004) and Nguembock et al. (2009) and, in part, by Arnaiz-Villena et al. (1999). Although some African species have never been subject to a molecular analysis, they are included here on grounds of morphological similarity to the analyzed species and biogeography. The monotypic genus *Neospiza* Salvadori, 1903, is synonymised with *Crithagra* following the results of Melo (2007) and** Melo and Jones (in press).

(j) *Serinus estherae* (Finsch, 1902) appears to belong to an isolated lineage in the *Serinus–Carduelis* complex, for which we propose to resurrect the genus name *Chrysocorythus* Wolters, 1967 (type species *Serinus mindanensis* Ripley and Rabor, 1961 = *Crithagra estherae* Finsch, 1902, gender masculine).

(k) The genus *Carduelis* Brisson, 1760 (type species *Fringilla carduelis* Linnaeus, 1758), is polyphyletic. We propose here to restrict the genus *Carduelis* to the species *Carduelis carduelis* (Linnaeus, 1758) and *C. citrinella* (Pallas, 1764), following our results and the analyses of Arnaiz-Villena et al. (1998, 2001) and Nguembock et al. (2009).

(l) The greenfinches *Carduelis ambigua* (Oustalet, 1896), *C. chloris* (Linnaeus, 1758), *C. monguilloti* (Delacour, 1926), *C. sinica* (Linnaeus, 1766) and *C. spinoides* Vigors, 1831, form a distinct clade not related to other *Carduelis*, for which we propose to resurrect the genus name *Chloris* Cuvier, 1800 (type species *Loxia chloris* Linnaeus, 1758, gender feminine). The inclusion of these species is supported by our results and by the analyses of Arnaiz-Villena et al. (1998) and Nguembock et al. (2009).

(m) The American *Carduelis*, together with *Carduelis spinus* (Linnaeus, 1758) and *Serinus thibetanus* (Hume, 1872), form a distinct clade, for which we propose to resurrect the genus name *Spinus* Koch, 1816 (type species *Fringilla spinus* Linnaeus, 1758, gender masculine, multiple specific name changes required). The inclusion of these species is supported by our results and by the analyses of Arnaiz-Villena et al. (1999, 2001), van den Elzen et al. (2001) and Nguembock et al. (2009). Only two American species, *Carduelis atriceps* (Salvin, 1863) and *C. dominicensis* (Bryant H, 1867), have never been included in a molecular analysis, but are deemed to belong to this clade on grounds of morphological similarity and biogeography.

(n) *Carduelis cannabina* (Linnaeus, 1758) and *C. flavirostris* (Linnaeus, 1758) form a monophyletic lineage for which we propose to resurrect the genus name *Linaria* Bechstein, 1802 (type species *Fringilla cannabina* Linnaeus, 1758, gender feminine). The same clade has been recovered by Arnaiz-Villena et al. (1999, 2001), Yang et al. (2006) and Nguembock et al. (2009). Although not included in any molecular analysis, we suggest that *Carduelis johannis* (S. Clarke, 1919) and *C. yemenensis* (Ogilvie-Grant, 1913) also belong in this group, on grounds of plumage similarity to *Carduelis cannabina*.

(o) The redpolls *Carduelis flammea* (Linnaeus, 1758) and *C. hornemanni* (Holböll, 1843) form a distinct lineage, also recovered by Arnaiz-Villena et al. (1999) and Nguembock et al. (2009), for which we propose to resurrect the genus name *Acanthis* Borkhausen, 1797 (type species *Fringilla linaria* Linnaeus, 1758 = *Fringilla flammea* Linnaeus, 1758, gender feminine).

Acknowledgments

We are grateful to the institutions and curators that provided samples used in this study: Göran Sjöberg (Ajtte Swedish Mountain and Sami Museum, Jokkmokk), Fu Min Lei (Institute of Zoology, Chinese Academy of Science, Beijing), Jan T. Lifjeld and Arild Johnsen (Natural History Museum, University of Oslo), Mark Adams (Natural History Museum, Tring), Hein van Grouw (Naturalis, Leiden), and Göran Frisk (Swedish Museum of Natural History, Stockholm). Martim Melo suggested helpful comments and corrections on a first draft of the manuscript. The Swedish Research Council provided financial support (Grant No. 621-2007-5280 to PE).

Appendix A

The GAPDH and myoglobin sequences of *Chaunoproctus ferreorostris* that we obtained are shorter than the minimum length currently accepted by Genbank (200 bp). The sequences are provided here.

Chaunoproctus ferreorostris glyceraldehyde-3-phosphate dehydrogenase (GAPDH) gene, intron 11 partial sequence

GCAGGAAGAATGGAAGAAGAGGGTGCAAGAAATGGGTCAGCCCTGACATGCTTGTTTTCTGTCCCCAG

Chaunoproctus ferreorostris myoglobin gene, intron 2 partial sequence

AGGACCATGGCCTACTCAAGGTCATGAAGCAGATCAGCGTCAGAGCTAG GAATAGAGCCCAGTGCTTCTGCC

References

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

Arnaiz-Villena, A., Alvarez-Tejado, M., Ruiz-del-Valle, V., Garcia-de-la-Torre, C., Varela, P., Recio, M.J., et al., 1998. Phylogeny and rapid northern and southern hemisphere speciation of goldfinches during the Miocene and Pliocene epochs. Cell. Mol. Life Sci. 54, 1031–1041.

Arnaiz-Villena, A., Alvarez-Tejado, M., Ruíz-del-Valle, V., Garcia-de-la-Torre, C., Varela, P., Recio, M.J., Ferre, S., Martinez-Laso, J., 1999. Rapid radiation of canaries (genus *Serinus*). Mol. Biol. Evol. 16, 2–11.

Arnaiz-Villena, A., Guillen, J., Ruiz-del-Valle, V., Lowy, E., Zamora, J., Varela, P., Stefani, D., Allende, L.M., 2001. Phylogeography of crossbills, bullfinches, grosbeaks, and rosefinches. Cell. Mol. Life Sci. 58, 1159–1166.

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 (30), 11040–11045.

Beecher, W.J., 1953. A phylogeny of the Oscines. Auk 70, 270–333.

BirdLife International, 2000. Threatened Birds of the World. Lynx Edicions and BirdLife International, Barcelona and Cambridge, UK.
Bledsoe, A.H., 1988. Nuclear DNA evolution and phylogeny of the new world nine-primaried oscines. Auk 105, 504–515.
Bock, W.J., 1960. The palatine process of the premaxilla in the Passeres. Bull. Mus. Comp. Zool. 122, 361–488.
Burns, K.J., 1997. Molecular systematics of tanagers (Thraupinae): evolution and biogeography of a diverse radiation of neotropical birds. Mol. Phylogen. Evol. 8, 334–348.
Cheng, T.H., 1976. Distributional List of Chinese Birds, revised ed. Science Press, Academia Sinica, Beijing.
Chesser, R.T., 1999. Molecular systematics of the rhinocryptid genus *Pteroptochos*. Condor 101, 439–446.
Chu, P.C., 2002. A morphological test of the monophyly of the cardueline finches (Aves: Fringillidae, Carduelinae). Cladistics 18, 279–312.
Clegg, S.M., Owens, P.F., 2002. The 'island rule' in birds: medium body size and its ecological explanation. Proc. Roy. Soc. London B 269, 1359–1365.
Clement, P., Harris, A., Davis, J., 1993. Finches and Sparrows. An Identification Guide. Christopher Helm, London.
Collar, N.J., Newton, I., 2010. Family Fringillidae (finches). In: del Hoyo, J., Elliott, A., Christie, D.A. (Eds.), Handbook of the Birds of the World, Weavers to New World Warblers, vol. 15. Lynx Edicions, Barcelona, pp. 440–617.
Cramp, S., Perrins, C. (Eds.), 1994. Handbook of the Birds of Europe, the Middle East and North Africa, vol. VIII. Oxford University Press, Oxford.
Delacour, J., 1946. Notes on the taxonomy of the birds of Malaysia. Zoologica 31, 1–8.
Dementiev, G.P., Gladkov, N.A., 1954. Ptitsy Sovietskogo Soiuza, vol. 5. Sovietskaya Nauka, Moscow.
Desfayes, M., 1969. Remarques sur les affinités des fringillides des genres *Rhodopechys* et *Callacanthis*. Ois. Rev. Fran. Orn. 39, 21–27.
Desfayes, M., 1971. Revision generique des carduelides. Ois. Rev. Fran. Orn. 41, 130–147.
Dickinson, E.C., 2003. The Howard and Moore Complete Checklist of the Birds of the World, third ed. Christopher Helm, London.
Drovetski, S.V., Zink, R.M., Mode, N.A., 2009. Patchy distributions belie morphological and genetic homogeneity in rosy-finches. Mol. Phylogen. Evol. 50, 437–445.
Eck, S., 1996. Die palaearktischen Vögel – Geospezies und Biospezies. Zool. Abhandl. Staatl. Mus. Tierkunde Dresden 49 (Suppl.), 1–103.
Ericson, P.G.P., Johansson, U.S., 2003. Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data. Mol. Phylogen. Evol. 29, 126–138.
Fjeldså, J., Zuccon, D., Irestedt, M., Johansson, U.S., Ericson, P.G.P., 2003. *Sapayoa aenigma*: a New World representative of 'Old World suboscines'. Proc. Roy. Soc. London 270 (Suppl.), S238–S241.
Fjeldså, J., Irestedt, M., Ericson, P.G.P., Zuccon, D., 2010. The Cinnamon Ibon *Hypocryptadius cinnamomeus* is a forest canopy sparrow. Ibis 152, 747–760.
Fleischer, R.C., McIntosh, C.E., 2001. Molecular systematics and biogeography of the Hawaiian avifauna. Studies Avian Biol. 22, 51–60.
Fleischer, R.C., Tarr, C.L., James, H.F., Slikas, B., McIntosh, C.E., 2001. Phylogenetic placement of the Po'ouli, *Melamprosops phaeosoma*, based on mitochondrial DNA sequence and osteological characters. Studies Avian Biol. 22, 98–103.
French, N.R., 1954. Notes on breeding activities and on gular sacs in the Pine Grosbeak. Condor 56, 83–85.
Fry, C.H., Keith, S. (Eds.), 2004. The Birds of Africa, vol. VII. Academic Press, London.
Fuller, E., 2001. Extinct Birds. Oxford University Press, Oxford.
Gebauer, A., Kaiser, M., Wassmann, C., 2006. Remarks on biology, vocalisations and systematics of *Urocynchramus pylzowi* Przewalski (Aves, Passeriformes). Zootaxa 1325, 75–98.
Grant, P.R., 1968. Bill size, body size, and the ecological adaptations of bird species to competitive situations on islands. Syst. Zool. 17, 319–333.
Grant, P.R., 1998. Patterns on islands and microevolution. In: Grant, P.R. (Ed.), Evolution on Islands. Oxford University Press, Oxford, pp. 1–17.
Groth, J.G., 2000. Molecular evidence for the systematic position of *Urocynchramus pylzowi*. Auk 117, 787–791.
Hartert, E., 1910. Die Vögel der paläarktischen Fauna, vol. I. Friedländer und Sohn, Berlin.
Howard, R., Moore, A., 1980. A Complete Checklist of the Birds of the World, second ed. Macmillan, London.
Huelsenbeck, J.P., Ronquist, F., 2001. MrBayes: Bayesian inference of phylogeny. Biometrics 17, 754–755.
Irestedt, M., Fjeldså, J., Johansson, U.S., Ericson, P.G.P., 2002. Systematic relationships and biogeography of the tracheophone suboscines (Aves: Passeriformes). Mol. Phylogen. Evol. 23, 499–512.
Irestedt, M., Fjeldså, J., Ericson, P.G.P., 2004. Phylogenetic relationships of woodcreepers (Aves: Dendrocolaptinae): incongruence between molecular and morphological data. J. Avian Biol. 35, 280–288.
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.
Isler, M.L., Isler, P.R., 1987. The Tanagers: Natural History, Distribution and Identification. Smithsonian Institution Press, Washington, DC.
James, H.F., 2004. The osteology and phylogeny of the Hawaiian finch radiation (Fringillidae: Drepanidini), including extinct taxa. Zool. J. Linn. Soc. 141, 207–255.
Kirwan, G.M., Gregory, S.M.S., 2005. A new genus for the Mongolian Finch *Bucanetes mongolicus* (Swinhoe, 1870). Bull. Brit. Orn. Club 125, 68–80.
Klicka, J., Johnson, K.P., Lanyon, S.M., 2000. New world nine-primaried oscine relationships: constructing a mitochondrial DNA framework. Auk 117, 321–336.
Klicka, J., Burns, K., Spellman, G.M., 2007. Defining a monophyletic cardinalini: a molecular perspective. Mol. Phylogen. Evol. 45, 1014–1032.
Liang, G., Li, T., Yin, Z., Lei, F.M., 2008. Molecular phylogenetic analysis of some Fringillidae species based on mitochondrial COI gene sequences. Zool. Res. 29 (5), 465–475.
Marten, J.A., Johnson, N.K., 1986. Genetic relationships of North American cardueline finches. Condor 88, 409–420.
Melo, M., 2007. Bird Speciation in the Gulf of Guinea. Ph.D. Thesis. School of Biological Sciences, Institute of Evolutionary Biology – University of Edinburgh, Edinburgh.
Melo, M., Jones, P.J. in press. Bird speciation in the Gulf of Guinea island system. In: Harebottle, D.M., Craig, A.J.F.K., Anderson, M.D., Rakotomanana, H., Muchai, M. (Eds.), Proceedings of the 12th Pan-African Ornithological Congress, 2008. Animal Demography Unit, Cape Town, pp. xx–xx.
Miller, A.H., 1941. Buccal food-carrying pouches in the Rosy Finch. Condor 43, 72–73.
Morioka, H., 1992. Relationships of the Ogasawara Islands Grosbeak *Chaunoprotus ferreorostris* (Aves, Fringillidae). Bull. Natl. Sci. Mus. Tokyo Ser. A 18 (1), 45–49.
Nguembock, B., Fjeldsa, J., Couloux, A., Pasquet, E., 2009. Molecular phylogeny of Carduelinae (Aves, Passeriformes, Fringillidae) proves polyphyletic origin of the genera *Serinus* and *Carduelis* and suggests redefined generic limits. Mol. Phylogen. Evol. 51, 169–181.
Nicolai, J., 1956. Zur Biologie und Ethologie des Gimpels (*Pyrrhula pyrrhula* L.). Zeitschr. Tierpsych. 13, 93–132.
Niethammer, G., 1966. Über die Kehltaschen des Rotflügelgimpels, *Rhodopechys sanguinea*. J. Orn. 107, 278–282.
Nylander, J.A.A., 2004. MrModeltest v.2.2. [Program Distributed by the Author]. Department of Systematic Zoology, Uppsala University, Uppsala.
Nylander, J.A.A., Wilgenbush, J.C., Warren, D.L., Swofford, D.L., 2008. AWTY (Are We There Yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. Bioinformatics 24, 581–583.
Oates, E.W., 1890. The Fauna of British India, Including Ceylon and Burma. Birds, vol. II. Taylor and Francis, London.
Ottaviani, M., 2008. Monographie des Fringilles. Histoire naturelle et photographies, vol. 1. Edition Prin.
Paynter Jr., R.A., 1968. Check-list of Birds of the World, vol. XIV. Museum of Comparative Zoology, Cambridge.
Paynter Jr., R.A., Storer, R.W., 1970. Check-list of Birds of the World, Vol. XIII. Museum of Comparative Zoology, Cambridge.
Pratt, H.D., 2005. The Hawaiian Honeycreepers. Oxford University Press, Oxford.
Raikow, R.J., 1976. Pelvic appendage myology of the Hawaiian honeycreepers (Drepanididae). Auk 93, 774–792.
Raikow, R.J., 1978. Appendicular myology and relationships of the New World nine-primaried oscines (Aves: Passeriformes). Bull. Carnegie Mus. Nat. Hist. 7, 1–43.
Rasmussen, P.C., Anderton, J.C., 2005. Birds of South Asia. The Ripley Guide, vols. 1 and 2. Smithsonian Institution and Barcelona: Lynx Edition, Washington, DC.
Ridgely, R.S., Tudor, G., 1989. The Birds of South America. The Oscine Passerines, vol. 1. University of Texas, Austin.
Ripley, S.D., 1961. Synopsis of the Birds of India and Pakistan. Bombay Natural History Society, Bombay.
Ripley, S.D., 1982. Synopsis of the Birds of India and Pakistan. Bombay Natural History Society, Bombay.
Ripley, S.D., Bond, G.M., 1966. The birds of Socotra and Abd-el-Kuri. Smithsonian Miscellanious Collection 151 (7), 1–37.
Ripley, S.D., Rabor, D.S., 1961. The avifauna of Mount Katanglad. Postilla 50, 1–20.
Ronquist, F., Huelsenbeck, J.P., 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19, 1572–1574.
Ryan, P.G., Wright, D., Oatley, G., Wakeling, J., Cohen, C., Nowell, T.L., Bowie, R.C.K., Ward, V., Crowe, T.M., 2004. Systematics of *Serinus* canaries and the status of Cape and Yellow-crowned Canaries inferred from mtDNA and morphology. Ostrich 75, 288–294.
Sato, A., Tichy, H., O'hUigin, C., Grant, P.-R., Grant, B.R., Klein, J., 2001. On the Origin of Darwin's Finches. Mol. Biol. Evol. 18, 299–311.
Sharpe, R.B., 1909. A Hand-list of the Genera and Species of Birds, vol. V. British Museum (Natural History), London.
Shimodaira, H., Hasegawa, M., 1999. Multiple comparisons of log-likelihoods with applications to phylogenetic inference. Mol. Biol. Evol. 16, 1114–1116.
Sibley, C.G., Ahlquist, J.E., 1982. The relationships of the Hawaiian honeycreepers (Drepaninini) as indicated by DNA–DNA hybridization. Auk 99, 130–140.
Sibley, C.G., Ahlquist, J.E., 1990. Phylogeny and Classification of Birds. Yale University Press, New Haven.
Stamatakis, A., 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics 22, 2688–2690.
Stuart Baker, E.C., 1930. The Fauna of British India, including Ceylon and Burma, vol. VII, 2nd ed. Taylor and Francis, London.
Sushkin, P.P., 1924. On the Fringillidae. Bull. Brit. Orn. Club 45, 36–39.
Sushkin, P.P., 1925. The Evening Grosbeak (*Hesperiphona*), the only American genus of a Palaearctic group. Auk 42, 256–261.

Swofford, D.L., 2003. PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.
Taka-Tsukasa, N., Hachisuka, M.U., 1907. A contribution to Japanese ornithology. Ibis 49, 898–908.
Töpfer, T., Haring, E., Birkhead, T.R., Lopes, R.J., Severinghaus, Liu L., Martens, J., Päckert, M., 2011. A molecular phylogeny of bullfinches Pyrrhula Brisson, 1760 (Aves: Fringillidae). Mol. Phylogen. Evol. 58, 271–282.
van den Elzen, R., 2000. Systematics and distribution patterns of Afrotropical Canaries (*Serinus* species group, Aves, Passeriformes, Carduelidae). Bonn. Zool. Monograph. 46, 133–143.
van den Elzen, R., Khoury, F., 1999. Systematik, phylogenetische Analyse und Biogeographie der Großgattung *Serinus* Koch, 1816. Courier Forschungsinstitut Senckenberg 215, 55–65.
van den Elzen, R., Guillen, J., Ruiz-del-Valle, V., Allende, L.M., Lowy, E., Zamora, J., et al., 2001. Both morphological and molecular characters support speciation of South American siskins by sexual selection. Cell. Mol. Life Sci. 58, 2117–2128.
Van der Meij, M.A., de Bakker, M.A., Bout, R.G., 2005. Phylogenetic relationships of finches and allies based on nuclear and mitochondrial DNA. Mol. Phylogen. Evol. 34, 97–105.
Vaurie, C., 1959. The Birds of the Palearctic Fauna. Passeriformes. H. F. & G. Witherby, London.
Voous, K.H., 1977. List of Holarctic bird species. Passerines. Ibis 119 (223–250), 376–406.
White, C.M.N., Bruce, M.D., 1986. The birds of Wallacea. British Ornithological Union Checklist 7, 1–524.
Wolters, H.E., 1967. Über einege asiatische Carduelinae. Bonn. Zool. Beitr. 18, 169–172.
Yang, S.J., Lei, F.M., Yin, Z.H., 2006. Molecular phylogeny of rosefinches and rose bunting (Passeriformes, Fringillidae, Urocynchramidae). Acta Zootax. Sinica 31, 453–458.
Yuri, T., Mindell, D.P., 2002. Molecular phylogenetic analysis of Fringillidae, "New World nine-primaried oscines" (Aves: Passeriformes). Mol. Phylogen. Evol. 23, 229–243.
Ziswiler, V., 1964. Neue Aspekte zur Systematik körnerfressender Singvögel. Verhand. Schweizerisch. Naturforsch. Gesellsch. 144, 133–134.
Ziswiler, V., 1965. Zur Kenntnis des Samenöffnens und der Struktur des hörneren Gaumens bei körnerfressenden Oscines. J. Orn. 106, 1–48.
Zuccon, D., 2005. A Molecular Phylogeny of Starlings (Aves: Sturnini): Evolution, Biogeography and Diversification in a Passerine Family. Ph.D. thesis. Università degli Studi di Torino.
Zuccon, A., Zuccon, D., 2010. MrEnt v.2.2. Program Distributed by the Authors. <http://www.mrent.org>.
Zuccon, D., Cibois, A., Pasquet, E., Ericson, P.G.P., 2006. Nuclear and mitochondrial sequence data reveal the major lineages of starlings, mynas and related taxa. Mol. Phylogen. Evol. 41, 333–344.
Zusi, R.L., 1978. The interorbital septum in cardueline finches. Bull. Brit. Orn. Club 98, 5–10.