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Phylogeny of Passerida (Aves: Passeriformes) based on nuclear and mitochondrial sequence data

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Abstract

Passerida is a monophyletic group of oscine passerines that includes almost 3500 species (about 36%) of all bird species in the world. The current understanding of higher-level relationships within Passerida is based on DNA–DNA hybridizations [C.G. Sibley, J.E. Ahlquist, Phylogeny and Classification of Birds, 1990, Yale University Press, New Haven, CT]. Our results are based on analyses of 3130 aligned nucleotide sequence data obtained from 48 ingroup and 13 outgroup genera. Three nuclear genes were sequenced: c-*myc* (498–510 bp), RAG-1 (930 bp), and myoglobin (693–722 bp), as well one mitochondrial gene; cytochrome *b* (879 bp). The data were analysed by parsimony, maximum-likelihood, and Bayesian inference. The African rockfowl and rockjumper are found to constitute the deepest branch within Passerida, but relationships among the other taxa are poorly resolved—only four major clades receive statistical support. One clade corresponds to Passeroidea of [C.G. Sibley, B.L. Monroe, Distribution and Taxonomy of Birds of the World, 1990, Yale University Press, New Haven, CT] and includes, e.g., flowerpeckers, sunbirds, accentors, weavers, estrilds, wagtails, finches, and sparrows. Starlings, mockingbirds, thrushes, Old World flycatchers, and dippers also group together in a clade corresponding to Muscicapoidea of Sibley and Monroe [op. cit.]. Monophyly of their Sylvioidea could not be corroborated—these taxa falls either into a clade with wrens, gnatcatchers, and nuthatches, or one with, e.g., warblers, bulbuls, babblers, and white-eyes. The tits, penduline tits, and waxwings belong to Passerida but have no close relatives among the taxa studied herein.

1. Introduction

The oscine passerines constitute a morphologically homogeneous group, essentially varying only in plumage and in characters relating to feeding adaptations. As similar feeding specializations have evolved convergently in different phylogenetic lineages, the potential of morphology to outline higher-level relationships among oscine birds has been seriously limited (Ames, 1971; Beecher, 1953; Raikow, 1978; Tordoff, 1954). In reality, only two oscine families (larks—Alaudidae, and swallows and martins—Hirundinidae) can be unambiguously defined by morphology (Mayr, 1958). The remaining oscines are often grouped into three categories: (1) Old World insect-eaters and their relatives, (2) New World insect-eaters and finches, and (3) crows, birds-of-paradise, and associated families (Mayr and Greenway, 1956; Voous, 1985). In mid-1900s most systematists recognized these three groups, but their interrelationships were much disputed. At issue was whether the crows and their allies constitute the deepest branch of oscines, or if they are a highly derived group (Voous, 1985).

Oscine relationships on the family-level and above were still insufficiently understood and partly controversial in the 1980s when Charles G. Sibley and coworkers began to publish the results based on analyses of their DNA–DNA hybridizations (cf. Sibley and Ahlquist, 1990). In many ways their interpretations of the data turned previous ideas upside-down. They not only dismissed the much favored idea that the crows and allies were the "crown-group" of oscine passerines, but also suggested that the oscines consists of two

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sistergroups, named Corvida and Passerida (Sibley and Ahlquist, 1990). This systematic arrangement was novel and, according to Sibley and Ahlquist (1990, p. 628), "no other discovery based on DNA hybridization evidence has solved more problems in avian systematics".

The suggested division of the oscines into a corvid and a passerid group has not been corroborated by any other line of evidence, however. While monophyly of Passerida has been supported by parsimony and maximum-likelihood analyses of DNA sequence data (Ericson et al., 2002a,b), as well as by an autapomorphic insertion of one codon in a conserved region of the c-*myc* gene (Ericson et al., 2000), Corvida appear to be a paraphyletic taxon within which the Passerida is nested (Barker et al., 2002; Ericson et al., 2002a,b). In addition, a study of the systematic relationships of the lyrebirds (genus *Menura*) indicates that this taxon is the sistergroup to all other oscine passerines (Ericson et al., 2002b).

Sibley and Ahlquist (1990) further divided Passerida into the three "superfamilies" Muscicapoidea (e.g., waxwings, dippers, thrushes, Old World flycatchers, starlings, and mockingbirds), Sylvioidea (e.g., nuthatches, tits, wrens, swallows, bulbuls, babblers, and sylviine warblers), and Passeroidea (e.g., larks, pipits, wagtails, waxbills, weavers, finches, sparrows, cardinals, tanagers, woodwarblers, and blackbirds). It was suggested that Muscicapoidea is the sistergroup of the other two groups (Sibley and Ahlquist, 1990, Fig. 344), although this relationship was not corroborated by a reanalysis of the original data set (Harshman, 1994). Furthermore, monophyly of the two "superfamilies" Passeroidea and Sylvioidea could not be confirmed when employing a more sophisticated experimental design and rigorous statistical methods to analyze DNA–DNA hybridization data (Sheldon and Gill, 1996).

Despite the taxonomically sparse sampling, the experimental and analytical approach employed by Sheldon and Gill (1996) resulted in the yet most reliable hypothesis of relationships among oscines based on the DNA–DNA hybridization method. In their analysis, three sylvioid clades were recognized (Fig. 1): one "parid-remizid" (tits and penduline tits) clade; one "nuthatch–creeper–gnatcatcher–wren" clade; and one "Old World wablers–bulbuls–babblers–swallows" clade. The few muscicapoid and passeroid taxa included in the analysis formed two other clades that largely agreed with the results of Sibley and Ahlquist (1990). A major exception was that the presumed passeroid larks grouped with the sylvioid warbler clade, instead of with the other passeroids.

Hitherto, few phylogenetic studies utilizing DNA sequence data have been undertaken explicitly to test hypotheses of higher-level relationships within Passerida based on the DNA–DNA hybridization results. The most inclusive investigations on the family level and

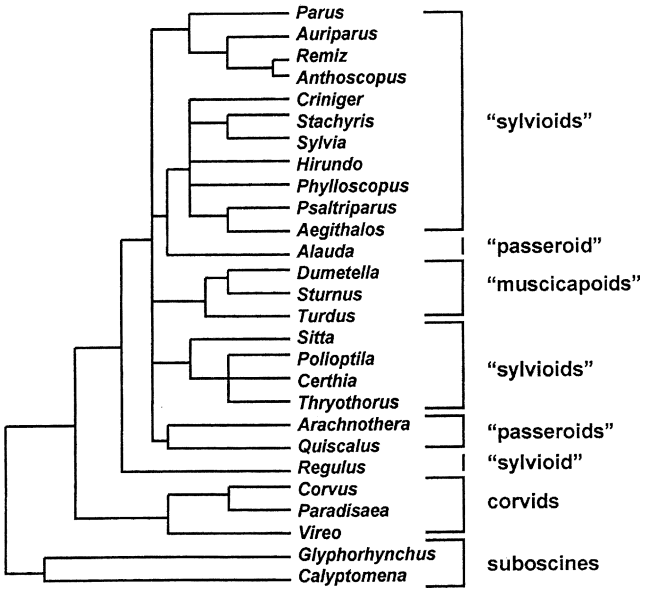

Fig. 1. Hypothesis of relationships within Passerida based on DNA–DNA hybridization data (Sheldon and Gill, 1996). The differences between these results and those previously presented based on DNA–DNA hybridizations (Sibley and Ahlquist, 1990) can probably be explained by the more sophisticated experimental design and statistical analysis employed in the study of Sheldon and Gill. The taxa fall into three groups: one "parid-remizid" (tits and penduline tits), one "nuthatch–creeper–gnatcatcher–wren" clade; and one "Old World wablers–bulbuls–babblers–swallows"clade.

above have all focussed on relationships within the superfamily Passeroidea (Grapputo et al., 2001; Groth, 1998; Klicka et al., 2000; Seutin and Bermingham, 1997; Yuri and Mindell, 2002). Examples of studies that use representatives of several muscicapoid and sylvioid families as ingroups, include analyses of the relationships among Malagasy babblers (Timaliidae) and warblers (Sylviidae) (Cibois et al., 1999); the taxonomic status of the vangas, Vangidae (Yamagishi et al., 2001) and mockingbirds and allies, Mimidae (Hunt et al., 2001); the systematic position of the kinglets (*Regulus*) (Sturmbauer et al., 1998); the relationships of white-eyes (*Zosterops*) (Slikas et al., 2000); the relationships among sylvioid taxa (Dunipace and Spicer, unpublished); and general relationships of the oscines (Chikuni et al., 1996; Honda and Yamagishi, 2000). In these studies the suggested inter-familial relationships often received no, or little bootstrap support. One possible explanation is that the analyses included mitochondrial genes only (the exceptions being those of Hunt et al., who also used the nuclear myoglobin gene, and Chikuni et al., who added data from the 18S ribosomal RNA gene). It is becoming widely accepted that most mitochondrial regions (and definitely those used in the cited studies) evolve at rates that cause them to reach saturation too soon to make them optimally useful to resolve ancient branching patterns among passerines. For example, Moore and DeFillippis (1997) warned that the cytochrome *b* gene

only gives reliable information in birds for divergencies younger than 9 million years.

In this study we use 3130 bp aligned nucleotide sequence data obtained from one mitochondrial (cytochrome *b*) and three nuclear (c-*myc*, RAG-1, and myoglobin) genes, to outline major patterns of diversification within the Passerida. The ambition is to identify and delimit monophyletic groups of taxa that can be resolved in greater detail through a denser taxon sampling and a proper selection of molecular markers in the future.

2. Materials and methods

The ingroup taxa were selected to represent as many as possible of the traditionally recognized families of Passerida. A total of 48 genera of Passerida were studied (Table 1). As outgroups served a selection of 13 representatives of Corvida *sensu* Sibley and Ahlquist (1990) (Table 1). The chosen outgroups do not form a monophyletic group, but includes the lyrebird which is supposed to belong to the most basal clade of oscines (following Ericson et al., 2002a,b).

Genomic DNA was prepared from tissue or blood specimens using the QIAamp DNA Mini Kit (QIAGEN). Nucleotide sequence data were obtained from the three nuclear genes c-*myc* exon 3, RAG-1, and myoglobin intron 2, and from the mitochondrial cytochrome *b* gene. Ericson et al. (2000), Irestedt et al. (2001), and Johansson et al. (2001) describe protocols for the PCR amplification and sequencing of c-*myc* and RAG-1. The myoglobin gene (intron 2) was amplified as a single fragment and sequenced using primers and conditions described by Heslewood et al. (1998) and Irestedt et al. (2002). The amplification and sequencing of cytochrome *b* follow Ericson et al. (2002b).

The sequences obtained from the nuclear protein-coding genes correspond to the regions between, respectively, positions 759 and 1235 (*c-myc*, exon 3) and 1054 and 1983 (RAG-1) in chicken (Carlson et al., 1991; Watson et al., 1983). The complete myoglobin intron 2 was sequenced, along with 13 and 10 bp of the flanking regions of exon 2 and exon 3, respectively. The analysed cytochrome *b* sequences correspond to the region between positions 15037 and 15915 in chicken (Desjardin and Morais, 1990). The cytochrome *b* sequence was amplified as one fragment to minimize the risk of amplifying nuclear copies of the gene. No unexpected start, stop or nonsense codons, that could indicate the presence of a nuclear copy, were observed in the cytochrome *b* sequences. All sequences are deposited in GenBank (Table 1).

For each taxon multiple sequence fragments obtained by sequencing with different primers were assembled to complete sequences with SeqMan II (DNASTAR). The sequences of all genes were aligned by eye. Most indels in the myoglobin intron 2 could readily be aligned across taxa. The phylogenetic information from indels was not used in the parsimony analysis. Statistics for nucleotide variation and pairwise genetic distances were computed with MEGA 2.0 (Kumar et al., 2001) and PAUP* 4.0b8 (Swofford, 1998).

Parsimony and maximum-likelihood analyses were performed using the heuristic search option in PAUP* 4.0b8 (Swofford, 1998). The maximum-likelihood tree was calculated using the GTR + I + G time-reversible model for nucleotide substitutions with the proportions of invariable sites $(I) = 0.342$ and $\alpha = 0.446$. This model was selected using the likelihood-ratio test implemented in Modeltest 3.06 (Posada and Crandall, 1998).

Likelihood trees were also calculated by iterations using a Bayesian inference of phylogeny with the program MrBayes 2.01 (Huelsenbeck et al., 2001). Each analysis were initiated from a random starting tree and the program were set to run four (three heated and one cold) Markov chain Monte Carlo iterations simultaneously for 400,000 generations with trees sampled every 100th generation. The likelihood scores increased until they stabilized after ca. 260,000 generations. After this, another 140,000 generations were run with trees sampled every 100th generation. Posterior probabilities for clades, estimated by a majority-rule consensus tree based on the saved 1400 trees, were used to indicate branch supports in the maximum-likelihood tree.

Searches for maximum parsimony trees were performed with all characters coded as unordered. Previous analyses of intra-familial relationships in passerine birds have shown that transition substitutions at third codon positions in the cytochrome *b* gene exhibit high degree of saturation (Ericson et al., 2002b; Irestedt et al., 2002). In the present data set this is also true for third position transversions (Fig. 2), and all variation at third codon positions in cytochrome *b* was excluded from the parsimony analysis. To reduce the risk of finding local optima only, multiple analyses were performed with taxa added in a randomized order. Nodal supports were assessed by parsimony jackknifing analysis using the program Xac (Farris et al., 1996; Farris, 1997) with 10,000 replicates.

3. Results

After alignment, the concatenated sequences became 3130 bp long. A total of between 498 and 510 bp were obtained from c-*myc* exon 3, 930 bp from RAG-1, between 693 and 722 from myoglobin intron 2, and 879 bp from cytochrome *b*. The observed, pairwise genetic distances between ingroup taxa range between 0.4 and 5.3% (median 3.0%) in *c-myc*, 0.8 and 7.2% (median 3.9%) in

Table 1
Taxon names (family/subfamily names follow Sibley and Monroe, 1990), identification and GenBank numbers for samples used in the study

Species	Family (subfamily) – tribe	Sample no.	c-*myc*	RAG-1	cyt *b*	Myoglobin
Ingroup taxa						
Aegithalos caudatus	Aegithalidae	NRM 976089	**AY227974**	**AY228001**	**AY228044**	**AY228281**
Aethopyga flagrans	Nectariniidae – Nectariniini	ZMCU O1346	AF377266 Ref. 4	**AY228002**	**AY228045**	**AY228282**
Agelaius cyanopus	Emberizinae – Icterini	NRM 966916	AF377253 Ref. 4	AY037854 Ref. 2	**AY228046**	**AY228283**
Alauda arvensis	Alaudidae	NRM 966614	AF377269 Ref. 4	**AY228003**	**AY228047**	**AY228284**
Anthus trivialis	Motacillinae	NRM 976393	AF377254 Ref. 4	**AY228004**	**AY228048**	**AY228285**
Bombycilla garrulus	Bombycillidae – Bombycillini	NRM 986044	**AY227975**	**AY228005**	**AY228049**	**AY228286**
Calcarius lapponicus	Emberizinae – Emberizini	NRM 976550	**AY227976**	**AY228006**	**AY228050**	**AY228287**
Campylorhynchus fasciatus	Troglodytinae	ZMCU O2444	**AY227977**	**AY228007**	**AY228051**	**AY228288**
Chaetops frenatus	Picathartidae	PFI uncat.	**AY227978**	**AY228008**	**AY228052**	**AY228289**
Chlorocichla flaviventris	Pycnonotidae	ZMCU O1789	AF377268 Ref. 4	**AY228009**	**AY228053**	**AY228290**
Cinclus cinclus	Cinclidae	NRM 20016138	**AY227979**	**AY228010**	**AY228054**	**AY228291**
Coccothraustes coccothraustes	Fringillinae – Fringillini	NRM 976374	AY037844 Ref. 2	AY037855 Ref. 2	**AY228055**	**AY228292**
Cryptospiza reichenovii	Estrildinae	ZMCU O785	**AY227980**	**AY228012**	**AY228056**	**AY228293**
Dicaeum australe	Nectariniidae – Dicaeini	ZMCU O3737	**AY227981**	**AY228013**		**AY228294**
Dicaeum trigonostigma	Nectariniidae – Dicaeini				AF290138 Ref. 7	
Emberizoides herbicola	Emberizinae – Thraupini	NRM 976735	**AY227982**	**AY228014**	**AY228057**	**AY228295**
Erithacus rubecula	Muscicapinae – Saxicolini	NRM 976377	AF377260 Ref. 4	**AY228015**	**AY228058**	**AY228296**
Eucometis penicillata	Emberizinae – Thraupini	NRM 966968	**AY227983**	**AY228016**	**AY228059**	**AY228297**
Euphonia chlorotica	Emberizinae – Thraupini	NRM 956750	**AY227984**	**AY228017**	**AY228060**	**AY228298**
Euplectes progne	Ploceinae	ZMCU O3876	**AY227985**	**AY228011**	**AY228061**	**AY228299**
Ficedula hypoleuca	Muscicapinae – Muscicapini	NRM 976132	AF377261 Ref. 4	**AY228018**	**AY228062**	**AY228300**
Geothlypis aequinoctialis	Emberizinae – Parulini	NRM 956574	AF377256 Ref. 4	**AY228019**	**AY228063**	**AY228301**
Hirundo rustica	Hirundinidae	NRM 976238	AF377270 Ref. 4	AY064271 Ref. 3		AY064258 Ref. 3
Hirundo rustica	Hirundinidae				AF074577 Ref. 6	
Lamprotornis corruscus	Sturnidae – Sturnini	ZMCU O3713	**AY227986**	**AY228020**	**AY228064**	**AY228302**
Loxia curvirostra	Fringillinae – Fringillini	NRM 976546	AF377257 Ref. 4	AY037856 Ref. 2	**AY228065**	**AY228303**
Mimus saturinus	Sturnidae – Mimini	NRM 966912	AF377265 Ref. 4	AY037852 Ref. 2	**AY228066**	**AY228304**
Molothrus badius	Emberizinae – Icterini	NRM 976783	**AY227987**	**AY228021**	**AY228067**	**AY228305**
Montifringilla ruficollis	Passerinae	IZAS uncat.	**AY227988**	**AY228022**	**AY228068**	**AY228306**
Motacilla alba	Motacillinae	NRM 976193	**AY227989**	**AY228023**	**AY228069**	**AY228307**
Panurus biarmicus	Sylviinae – Timaliini	NRM 966576	AF377271 Ref. 4	**AY228024**	**AY228070**	**AY228308**

Table 1 (*continued*)

Species	Family (subfamily) – tribe	Sample no.	c-*myc*	RAG-1	cyt *b*	Myoglobin
Parula pitiayumi	Emberizinae – Parulini	NRM 947170	**AY227990**	**AY228025**	**AY228071**	**AY228309**
Parus major	Paridae – Parinae	NRM 956363	AF377263 Ref. 4	**AY228026**	**AY228072**	**AY228310**
Passer montanus	Passerinae	NRM 976359	AF295171 Ref. 1	**AY228027**	**AY228073**	**AY228311**
Petronia petronia	Passerinae	IZAS uncat.	**AY227991**	**AY228028**	**AY228074**	**AY228312**
Peucedramus taeniatus	Peucedraminae	LSU B-9874	**AY227992**	**AY228029**	**AY228075**	**AY228313**
Picathartes gymnocephalus	Picathartidae	LSU B-19213	**AY227993**	**AY228030**	**AY228076**	**AY228314**
Plectrophenax nivalis	Emberizinae – Emberizini	NRM 986392	**AY227994**	**AY228031**	**AY228077**	**AY228315**
Ploceus velatus	Ploceinae	SA uncat.	AF377258 Ref. 4	**AY228032**	**AY228078**	**AY228316**
Polioptila dumicola	Polioptilinae	NRM 956689	**AY227995**	**AY228033**	**AY228079**	**AY228317**
Prunella modularis	Prunellinae	NRM 976138	AF377259 Ref. 4	**AY228034**	**AY228080**	**AY228318**
Remiz pendulinus	Paridae – Remizinae	NRM 966576	AF377280 Ref. 4	**AY228035**	**AY228081**	**AY228319**
Saltator atricollis	Emberizinae – Cardinalini	NRM 966978	**AY227996**	**AY228036**	**AY228082**	**AY228320**
Sitta europea	Sittidae	NRM 976163	AF377267 Ref. 4	AY064272 Ref. 3	AF378102 Ref. 4	AY064257 Ref. 3
Stachyris nigriceps	Sylviinae – Timaliini	NRM 947308	**AY227997**	**AY228037**		**AY228321**
Stachyris whiteheadi	Sylviinae – Timaliini				AF094633 Ref. 5	
Sturnus vulgaris	Sturnidae – Sturnini	NRM 966615	AF377264 Ref. 4	AY037853 Ref. 2	AF378103 Ref. 4	**AY228322**
Sylvia atricapilla	Sylviinae – Sylviini	NRM 976380	**AY227998**	**AY228038**		**AY228323**
Sylvia atricapilla	Sylviinae – Sylviini				AF074596 Ref. 6	
Tangara seledon	Emberizinae – Thraupini	NRM 956580	**AY227999**	**AY228039**	**AY228083**	**AY228324**
Troglodytes troglodytes	Troglodytinae	NRM 986416	AF377272 Ref. 4	**AY228040**	**AY228084**	**AY228325**
Zosterops nigrorum	Zosteropidae	ZMCU O2663	AY037843 Ref. 2	AY037851 Ref. 2	**AY228085**	**AY228326**
Outgroup taxa						
Campephaga flava	Corvinae – Oriolini	ZMCU O11	AF295162 Ref. 1	AF295162 Ref. 1	**AY228086**	**AY165803** Ref. 10
Corvus corone cornix	Corvinae – Corvini	NRM 986167	AF377274 Ref. 4	**AY228041**	**AY228087**	**AY228327**
Eopsaltria australis	Eopsaltridae	MV 1390	AY064283 Ref. 3	AY064262 Ref. 3	AY064273 Ref. 3	AY064732 Ref. 3
Gymnorhina tibicen	Corvinae – Artamini	AM LAB1107	AY064284 Ref. 3	AY064263 Ref. 3		
Gymnorhina tibicen	Corvinae – Artamini	MV AC78				AY064741 Ref. 3
Gymnorhina tibicen	Corvinae – Artamini				AF197867 Ref. 9	
Lanius collurio	Laniidae	NRM 986403	**AY228000**	**AY228042**		**AY228328**
Lanius ludovicianus	Laniidae				AY030105 Ref. 8	
Malurus amabilis	Maluridae	MV C803	AY037840 Ref. 2	AY037847 Ref. 2	**AY228088**	AY064729 Ref. 3
Menura novaehollandiae	Menuridae	AM LAB1112	AF295169 Ref. 1	AF295191 Ref. 1	AY064276 Ref. 3	AY064744 Ref. 3

Table 1 (*continued*)

Species	Family (subfamily) – tribe	Sample no.	c-*myc*	RAG-1	cyt *b*	Myoglobin
Oriolus oriolus	Corvinae – Oriolini	ZMCU O1376	AF377276 Ref. 4	**AY228043**		**AY228329**
Oriolus xanthornus	Corvinae – Oriolini				AF094615 Ref. 5	
Orthonyx temminckii	Orthonychidae	MV B831	AY064286 Ref. 3	AY064265 Ref. 3	AY064275 Ref. 3	AY064728 Ref. 3
Pachycephala pectoralis	Pachycephalinae	MV 1419	AY064287 Ref. 3	AY064266 Ref. 3	**AY228089**	AY064727 Ref. 3
Pomatostomus temporalis	Pomatostomidae	MV D257	AY064288 Ref. 3	AY064267 Ref. 3	**AY228090**	AY064730 Ref. 3
Ptiloprora plumbea	Meliphagidae	MV C173	AY037841 Ref. 2	AY037848 Ref. 2	**AY228091**	AY064736 Ref. 3
Ptiloris magnificus	Corvinae – Paradisaeini	MV C784	AY064290 Ref. 3	AY064269 Ref. 3	**AY228092**	AY064740 Ref. 3

Acronyms are AM, Australian Museum, Sydney; IZAS, Institute of Zoology, Academia Sinica, Beijing; LSUMZ, Louisiana State University, Museum of Natural Science; MV, Museum Victoria, Melbourne; NRM, Swedish Museum of Natural History; PFI, Percy FitzPatrick Institute, Cape Town; SA, Staffan Andersson; and ZMCU, Zoological Museum of the University of Copenhagen. References for sequences published in GenBank are 1: Irestedt et al. (2001), 2: Ericson et al. (2002a), 3: Ericson et al. (2002b), 4: James et al. (2003), 5: Cibois et al. (1999), 6: Sheldon et al. (1999), 7: Klicka et al. (2000), 8: Cicero and Johnson (2001), 9: Cracraft and Feinstein (2000), and 10: Johansson and Ericson (2003).

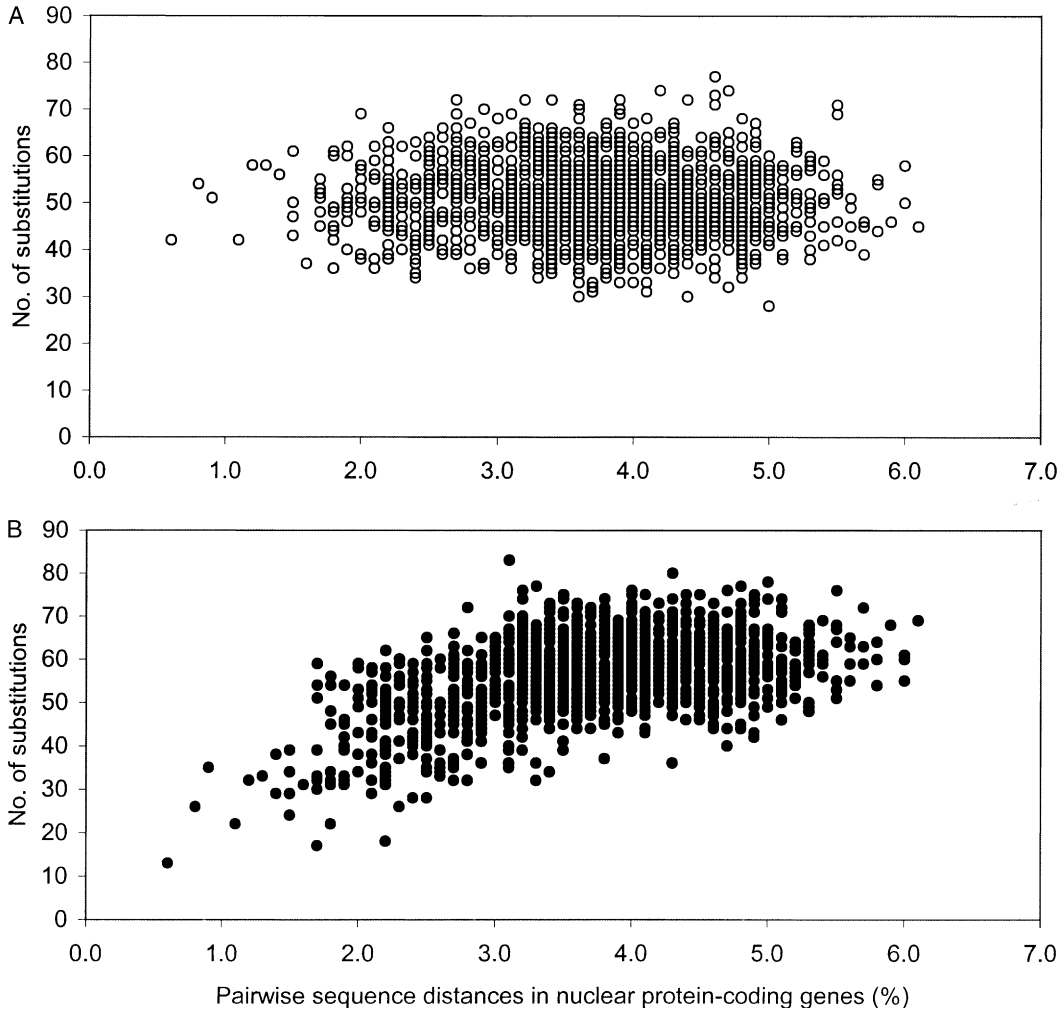

Fig. 2. The observed number of transitions (A) and transversions (B) at third codon positions in the cytochrome *b* gene, plotted against the pairwise genetic distances calculated for the combined c-*myc* and RAG-1 genes. The low correlation between the two axes in A and B suggests that third codon positions are saturated for both transitions and transversions, and these were excluded from the parsimony analysis.

RAG-1, 0.6 and 9.3% (median 5.8%) in myoglobin, and 7.0 and 19.2% (median 15.5%) in cytochrome *b*.

Three indels in the c-*myc* gene were observed. Two of these have been reported elsewhere (Ericson et al., 2000), and the third is an autapomorphic insertion of five codons in *Euplectes*. Several of the indels observed in the myoglobin intron 2 are autapomorphic singletons, or occur in especially variable regions of the gene. Potentially synapomorphic indels include a two bp deletion in *Campylorhynchus*, *Polioptila*, and *Troglodytes*, a two bp insertion in *Chaetops* and *Picathartes*, and a one bp deletion in *Erithacus*, *Ficedula*, *Lamprotornis*, *Mimus*, and *Sturnus*.

3.1. Phylogenetic analyses

Monophyly of Passerida is recognized by both the parsimony and maximum-likelihood analyses (Fig. 3). The node receives a 100% support in the Bayesian analyses, but less than 50% in the parsimony jackknifing analysis. Two African taxa, the rockfowl (*Picathartes*) and the rockjumper (*Chaetops*) group together and constitute the deepest branch within Passerida. The clade consisting of all other Passerida representatives receives strong support (99% in the Bayesian analysis and 94% in parsimony jackknifing), but the higher-level relationships above this node are not well resolved. The four large, and mostly well-supported clades of taxa recovered correspond roughly to the superfamilies of Sibley and Ahlquist (1990). One clade (A) consists of all passeroid taxa, except the larks. Most of the sylvioid representatives grouped into either clade B or clade C, while most muscicapoid taxa grouped together into clade D.

Monophyly of clade A is supported in both the Bayesian analysis (100%) and parsimony jackknifing (94%). Several of the traditionally recognized families and subfamilies in this clade are represented by more than one species. These higher-level taxa were all recovered as monophyletic with strong nodal supports (Fig. 4). The first two branches to split from the other taxa in clade A consist of the flowerpeckers and sunbirds, and the accentor and olive warbler, respectively. Both these clades are strongly supported. The next clade up in the tree (with 100% support by the Bayesian analysis and 91% by parsimony jackknifing) comprises the wagtails, pipits, Old World finches, and sparrows, along with all emberizid taxa (buntings, tanagers, woodwarblers, and blackbirds). The maximum-likelihood analysis groups the Old World finches and sparrows into one clade, and the wagtails, pipits and emberizids into another, but neither receives any nodal supports. Within the emberizid clade, the longspur-snow sparrow clade forms a well-supported sistergroup to the rest, and the blackbirds and woodwarblers form a monophyletic group. The tanager-cardinal-bunting clade is monophyletic, but largely unresolved.

Clade B consists of taxa representing sylvioid groups as babblers, white-eyes, Old World Warblers, bulbuls, swallows, long-tailed tits, larks, and parrotbills (Fig. 5). One hundred percent support by the Bayesian analysis and 86% by parsimony jackknifing support the mono-

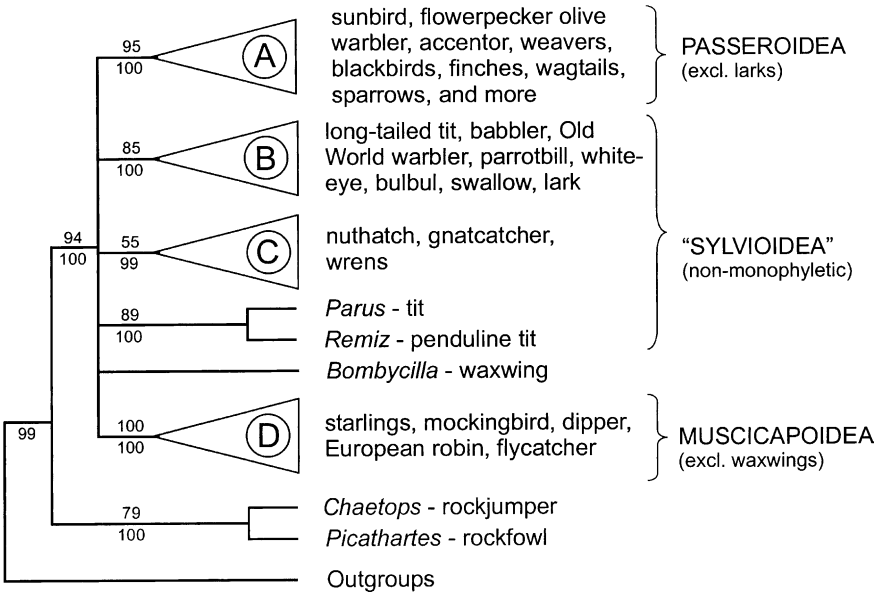

Fig. 3. Phylogenetic relationships among major groups of Passerida. The tree summarizes the parsimony and maximum-likelihood analyses of DNA sequence data obtained from three nuclear and one mitochondrial gene for 48 ingroup taxa. All 3130 nucleotide positions are included in the likelihood analyses, while third codon positions in cytochrome *b* (293 bp) are excluded from the parsimony analyses. Nodal supports are estimated by parsimony jackknifing (above nodes) and Bayesian inference analysis (below nodes).

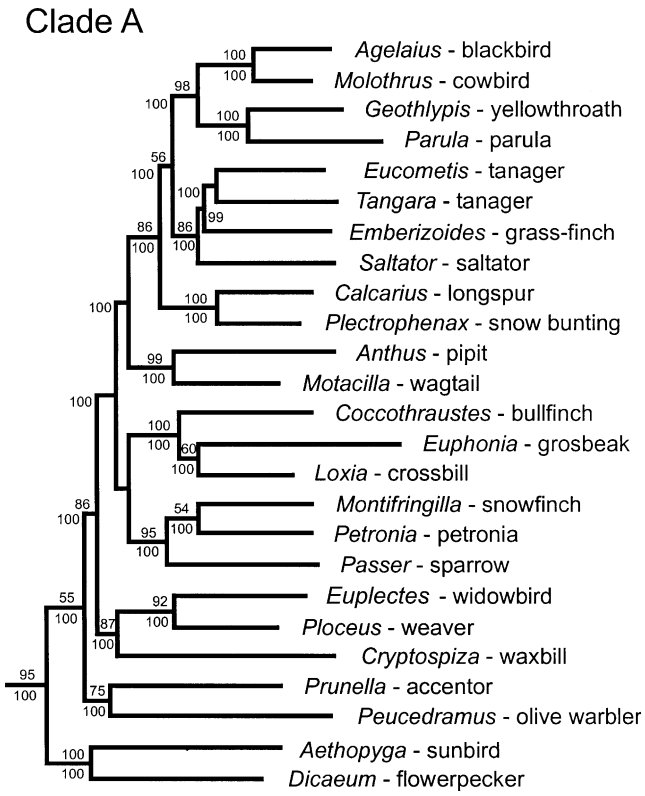

Fig. 4. Clade A—Passeroidea (*sensu* Sibley and Ahlquist (1990), excluding larks). Maximum-likelihood tree with nodal support values estimated as described in the legend of Fig. 3.

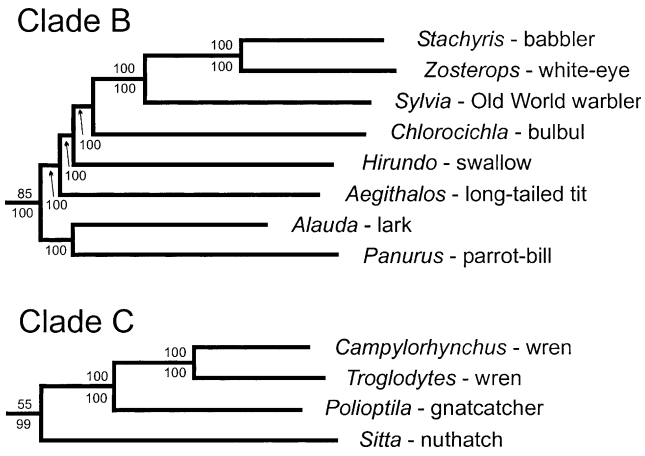

Fig. 5. Clades B and C—Sylvioidea (*sensu* Sibley and Ahlquist (1990), but excluding tits and penduline tits, and including larks). The trees are calculated by maximum-likelihood analysis, while nodal support values are estimated as described in the legend of Fig. 3. The two clades with sylvioid taxa are most likely not sisters rendering Sylvioidea non-monophyletic. In Clade B, the relationships between the babblers, white-eyes, Old World warblers, and bulbuls are well supported in all analyses. While all deep branches in this clade get 100% support in the Bayesian analysis (values indicated below the nodes), they recieve less than 50% support parsimony jackknifing supports (values indicated above the nodes). In Clade C the wrens and gnatcatcher group confidently together, with the nuthatch as their sister.

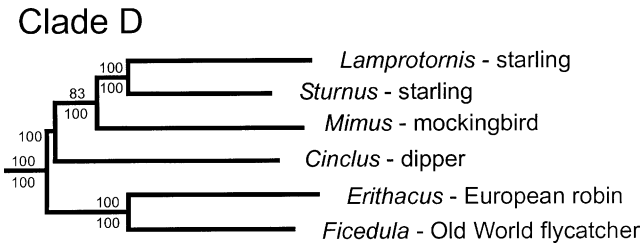

Fig. 6. Clade D—Muscicapoidea (*sensu* Sibley and Ahlquist (1990), excluding waxwings). Maximum-likelihood tree with nodal support values estimated as described in the legend of Fig. 3. Monophyly of these muscicapoid taxa is strongly supported, but their internal relationships are less resolved. The thrushes and Old World flycatchers form one well-supported group, and the starlings and mockingbird another, while the dipper cannot be confidently allocated to any of them.

phyly of this clade. The babbler and white-eye group together with the warbler next to them. Outside this clade are the bulbul, swallow, and long-tailed tit, respectively. The lark, which was placed in Passeroidea by Sibley and Ahlquist (1990), group together with the sylvioid parrotbill with strong support in the Bayesian inference analysis. This tree topology is rather poorly resolved by the parsimony jacknife analysis, while the Bayesian analysis gives 100% support to all nodes.

Other sylvioid taxa (wrens, gnatcatchers, and nuthatch) grouped into clade C with 100% by the Bayesian analysis but only 53% by parsimony jackknifing (Fig. 5). Within clade C, a group with the wrens and the gnatcatcher is strongly supported, and the Bayesian analysis supports the nuthatch as sistergroup to this wren–gnatcatcher clade.

The strongly supported (100% in both analyses) muscicapoid clade D consists of representatives of the families of starlings, mockingbirds, thrushes, Old World flycatchers, and dippers (Fig. 6). The thrush and the flycatcher form a monophyletic sistergroup to the other muscicapoids. Among these, the startlings and mockingbird group together with high support, while the dipper is the sister to them.

A few groups of Passerida cannot be confidently grouped with other taxa. These include the sylvioid tits and penduline tits, which form a strongly supported clade (Fig. 3). The muscicapoid waxwing was also left without close relatives among the other Passerida taxa.

4. Discussion

4.1. Passerida sensu Sibley and Monroe (1990)—Fig. 3

The analyses by Ericson et al. (2002a,b) and Barker et al. (2002) have confidently proven that although the Passerida is monophyletic, the postulated sistergroup relationship between this taxon and Corvida is not correct. Instead Passerida is nested within Corvida and

the taxonomic delimitation of Passerida may be uncertain, as no morphological synapomorphy is known for this taxon. The only character yet described that could be used to define Passerida is the common possession of an insertion of one codon in a conserved region of the c-*myc* gene. This insertion has been scanned for in some 170 passerine species, representing almost all families and subfamilies *sensu* Sibley and Monroe (1990). To date, the insertion has only been found in representatives of Passerida, as well as in the rockfowl (*Picathartes*) and rock-jumpers (*Chaetops*). Sibley and Ahlquist (1990) tentatively placed the African rockfowl and rockjumpers in Corvida, despite that these taxa were never included in the DNA–DNA hybridization analyses. However, they cautionally remarked that the rockfowl and rockjumpers were "on the border" to Passerida (Sibley and Ahlquist, 1990, 627)—a suggestion in agreement with the results of the present analysis. Taxonomically we believe it is well justified to keep the taxon Passerida as this may be the only interfamilial group of oscines for which a synapomorphy character is known (the insertion in c-*myc*, but if diagnosed by this synapomorphy it shall also include the rockfowl and rockjumpers.

4.2. Passeroidea sensu Sibley and Monroe (1990)—Fig. 4

Monophyly. The analyses strongly corroborate monophyly of Passeroidea, with the understanding that the larks are not part of this taxon, as already shown by Sheldon and Gill (1996). No morphological synapomorphy of Passeroidea is known.

Higher-level relationships. Although the passeroids seemingly stem from an insectivorous ancestor, this group is characterized by the evolution of many specialized feeding adaptations, most prominently seed-eating. Other passerine groups have also developed granivorous habits, but Passeroidea is unparalleled in this respect. However, the deepest passeroid branch consists of the primarily frugivorous flowerpeckers (Dicaeidae) and nectarivorous sunbirds (Nectariniidae). These two groups have been regarded as closely related based on both morphology (Beecher, 1953; Delacour, 1944) and DNA-DNA hybridization data (Sibley and Ahlquist, 1990).

The systematic position of the accentors (Prunellidae) has long been a matter of discussion. Both the parsimony and maximum-likelihood analyses herein suggest them to group together with the olive warbler (*Peucedramus*) and to be basal among all passeroids except flowerpeckers and sunbirds. The results may best be interpreted as that the accentors is part of a yet unresolved node that also includes the Old World finches (Fringillidae), sparrows (Passeridae), waxbills (Estrildidae), weavers (Ploceidae), and the New World buntings and allies (Emberizinae, Thraupinae, Cardinalinae, Icterinae, and Parulinae). Many of the taxa at this node in the phylogenetic tree have a much-reduced tenth primary (Fig. 7). Based on the results of the present study it cannot be unambiguously determined whether this is due to a single, synapomorphic event, or if it has been reduced independently two or more times. Immediately outside this clade, the flowerpeckers likewise have a much-reduced tenth primary, while the sunbirds have all primaries fully developed. Although reduction of the tenth primary is known to have occurred independently in a few lineages of oscine birds (see Sibley and Ahlquist, 1990, for summaries), it is most widespread within the

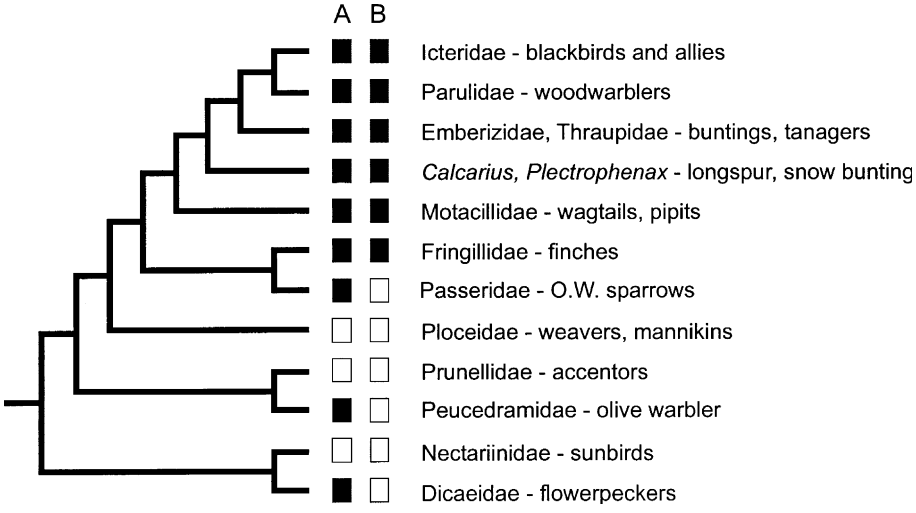

Fig. 7. The occurrences of a much-reduced tenth primary (A), and an insertion of three codons in the c-*myc* gene (B) within Passeroidea mapped onto the best-fit tree (generalized) from the maximum-likelihood analysis. Filled rectangles indicate (A) reduction of the tenth primary, and (B) possession of the insertion in c-*myc*.

passeroid clade. When mapped onto the maximum-likelihood tree, the reduction of the tenth primary seems to have occurred at least three times within the Passeroidea (Fig. 7).

The highly conserved c-*myc* gene may contribute little to resolving the relationships among the passeroids, but the insertion of three codons at one position in the gene seems to bear on this problem. This insertion occurs in all investigated representatives of the Old World finches, wagtails and pipits, and New World buntings and allies, but not outside this group (Fig. 7, Ericson et al., 2000). As with the reduction of the tenth primary, the phylogenetic tree can be constrained to fit the distribution of this insertion with a nonsignificant deterioration of the likelihood score (data not shown). The taxonomic distributions of the insertion and the reduction, respectively, are not in conflict. An analysis of a subset of the Passeroidea with the flowerpeckers and sunbirds as outgroups, and with the phylogenetic tree constrained to fit these distributions, resulted in the tree shown in Fig. 8. This tree is only one step longer and not significantly worse fit (data not shown) than the unconstrained tree.

The results suggest that the genus *Euphonia* is not a tanager but a fringillid, corroborating the results of Klicka et al. (2000). Within the emberizid clade, the blackbirds and woodwarblers are sisters, with the buntings, cardinals and tanagers grouping outside them. The close relationship between blackbirds and woodwarblers was suggested by an analysis of nuclear DNA data (Barker et al., 2002) but not by mitochondrial DNA (Groth, 1998). The systematic relationships within the bunting-cardinal-tanager clade is complicated (cf. Burns, 1997; Groth, 1998; Klicka et al., 2000; Sibley and Ahlquist, 1990) and the small taxon sample herein adds no information to this matter.

4.3. Sylvioidea sensu Sibley and Monroe (1990)—Fig. 5

Monophyly. The nucleotide sequence data do not support monophyly of the sylvioids, but the Bayesian likelihood analysis provided weak support to a group consisting of the clades B and C, along with the parrotbill and the presumed muscicapoid waxwing. The group thus contains all sylvioids, except the tits and penduline tits, and the waxwing for which the systematic position long has been a matter of discussion. However, this largely sylvioid group was not recognized neither by the best-fit likelihood tree, nor by parsimony jackknifing.

Higher-level relationships. Clade B, one of the two large subclades of sylvioids recognized by the analyses, contains the representatives of babblers, white-eyes, Old World warblers, bulbuls, swallows, long-tailed tits, larks, and parrotbills. DNA–DNA hybridization data also suggested these groups to be related (Sheldon and Gill, 1996; Sibley and Ahlquist, 1990), and the reconstructed inter-relationships of the group are largely similar to those presented herein (Fig. 9). The only difference being in the position of the white-eyes, which are recovered as sisters to the babblers in the present analysis, while DNA–DNA hybridization data suggested them to be closer to the Old World warblers. It should be noted that DNA–DNA hybridization analyses indicate that the Old World warbler subfamily (Sylviinae) as traditionally recognized (e.g., Morony et al., 1975) is not monophyletic (Sheldon and Gill, 1996; Sibley and

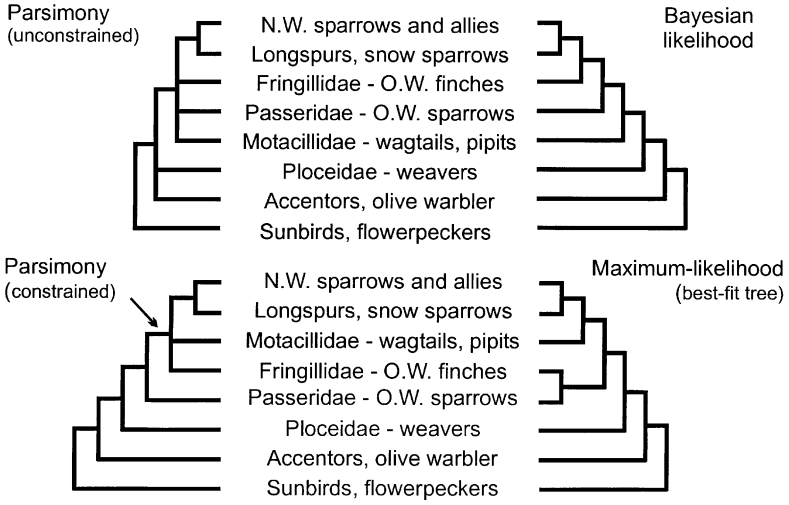

Fig. 8. Alternative phylogenetic relationships for Passeroidea. All differences between the trees obtained with different analytical methods concern the relative positions of fringillids, motacillids, and passerids. The lower left tree was calculated after first having constrained the tree topology to fit a postulated, synapomorphic insertion of three codons in the c-*myc* gene in all emberizid, fringillid, and motacillid taxa. The most parsimonious tree calculated from this data set is only one step longer than that calculated from the unconstrained data, and the likelihood score for that tree is not significantly worse than that for the unconstrained tree.

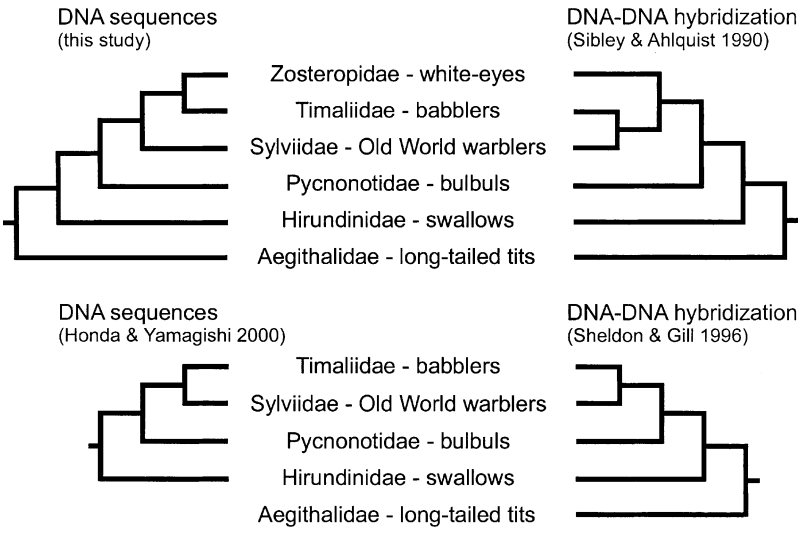

Fig. 9. Several molecular analyses of the phylogenetic relationships among the taxa that form Clade B have produced almost identical tree topologies (allowing for the differences in taxonomic representation).

Ahlquist, 1990). It should thus be borne in mind that only one "sylviine" taxon was included here, *Sylvia atricapilla*. A topology similar to clade B was arrived at by Barker et al. (2002) in an analysis of 3524 bp of aligned sequences from RAG-1 and c-*mos*. Their results are identical to ours regarding the relationships of white-eyes, babblers, Old World warblers, and bulbuls, but differ in the relationships of long-tailed tits, swallows and larks.

Barker et al.'s (2002) analysis is one of few phylogenetic analyses based on DNA sequence data that have included representatives of several sylvioid families as ingroups. Another example is an analysis of eight sylvioid genera with the primary aim to investigate the systematic position of the kinglets (*Regulus*) based on a 385 bp segment of the mitochondrial 16S gene (Sturmbauer et al., 1998). The results differed from those based on DNA–DNA hybridizations (Sheldon and Gill, 1996) in that the tree-creepers and nuthatches, and not the kinglets, were placed basal among the sylvioids. The short sequences and sparse taxon sampling of this study makes it less useful for comparisons with the present analysis, however.

The topology of clade C is fully compatible to the less resolved tree obtained based on DNA–DNA hybridizations (Sheldon and Gill, 1996). It is also not contradicted by the results based on the nuclear DNA data set of Barker et al. (2002), although the taxon selection differ somewhat (they did not include a gnatcatcher but did have a treecreeper, unlike herein).

4.4. *Muscicapoidea sensu Sibley and Monroe (1990)—Fig. 6*

Monophyly. All muscicapoid taxa included in the study, except the waxwing, group together with strong nodal supports. The waxwings have long been difficult to place systematically and their inclusion in Muscicapoidea was a novel suggestion based on DNA–DNA hybridization data (Sibley and Ahlquist, 1990). However, the waxwings constitute the deepest branch within Muscicapoidea at delta T_{50}H 10.6 (op. cit. Figs. 349 and 379). Neither the present data set of DNA sequences, nor that of Barker et al. (2002), supports a close relationship between the waxwings and "core"-muscicapoids.

Higher-level relationships. The close relationship between the starlings and mockingbirds was first suggested by DNA–DNA hybridization data (Sibley and Ahlquist, 1990), and it has later been confirmed by analyses of nucleotide sequences (Barker et al., 2002; Ericson et al., 2002a,b). The study also strongly suggests a sistergroup relationship between thrushes and Old World flycatchers, corroborating previous results based on DNA–DNA hybridization data (Sibley and Ahlquist, 1990). The dipper is placed as the sister to the starling-mockingbird lineage by the likelihood analysis, but its position is left unresolved by parsimony. In the parsimony analysis of Barker et al. (2002) the dipper grouped with the thrush-flycatcher clade, while it got a position basal to both this and the starling-mockingbird clade in the maximum-likelihood analysis. The bootstrap supports are less than 50% for all alternative placements of the dipper in both their analysis and ours, and its systematic position within Muscicapoidea must be regarded as unresolved.

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