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Inter-generic relationships of the crows, jays, magpies and allied groups (Aves: Corvidae) based on nucleotide sequence data

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Phylogenetic relationships were studied based on DNA sequences obtained from all recognized genera of the family Corvidae *sensu stricto*. The aligned data set consists 2589 bp obtained from one mitochondrial and two nuclear genes. Maximum parsimony, maximum-likelihood, and Bayesian inference analyses were used to estimate phylogenetic relationships. The analyses were done for each gene separately, as well as for all genes combined. An analysis of a taxonomically expanded data set of cytochrome *b* sequences was performed in order to infer the phylogenetic positions of six genera for which nuclear genes could not be obtained. Monophyly of the Corvidae is supported by all analyses, as well as by the occurrence of a deletion of 16 bp in the β-fibrinogen intron in all ingroup taxa. *Temnurus* and *Pyrrhocorax* are placed as the sister group to all other corvids, while *Cissa* and *Urocissa* appear as the next clade inside them. Further up in the tree, two larger and well-supported clades of genera were recovered by the analyses. One has an entirely New World distribution (the New World jays), while the other includes mostly Eurasian (and one African) taxa. Outside these two major clades are *Cyanopica* and *Perisoreus* whose phylogenetic positions could not be determined by the present data. A biogeographic analysis of our data suggests that the Corvidae underwent an initial radiation in Southeast Asia. This is consistent with the observation that almost all basal clades in the phylogenetic tree consist of species adapted to tropical and subtropical forest habitats.

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The family Corvidae (*sensu* Morony et al. 1975) consists of more than 100 species of crows, jays, magpies and allies, arranged in 25 genera (*Cissilopha* is here considered a subgenus of *Cyanocorax* following Madge and Burn 1994). Sibley and Monroe (1990) called this group Corvini, while their Corvidae was a taxonomically much larger group that included also many other traditional families, e.g., vangas, drongos, whistlers, orioles and monarch flycathchers. The Corvidae *sensu stricto* has a worldwide distribution, and the family is represented in almost all habitats. Corvids are renowned for an unusual intelligence among birds and a wide range of fascinating behavioural adaptations have been documented in the group, including cooperative breeding. Corvids thus attract considerable attention from general biologists, and are favoured study objects of many ethologists and ecologist. Despite this broad interest the patterns of evolution and the phylogenetic relationships of the Corvidae are inadequately known. The early history of the classification of the Corvidae has been summarized elsewhere (Goodwin 1976, Hope 1989, and Sibley and Ahlquist 1990) and here we will focus only on previous

ideas about the higher-level relationships within the group.

Most corvid genera are well defined and little controversy exists about their monophyly. Most taxonomists acknowledge the traditional delimitations of genera (e.g., Sibley and Monroe 1990), although Amadon (1944) argued for reducing the number of genera of New World jays and Southeast Asian magpies and treepies. Certain monophylethic groups of corvid genera are also widely recognized. The largest of these consists of the five genera of New World jays (*Calocitta*, *Cyanocorax*, *Cyanolyca*, *Gymnorhinus* and *Psilorhinus*), and it has been suggested that the Holarctic *Perisoreus* and the Palearctic *Garrulus* are closely related to this group. Another assumingly monophyletic group consists of *Nucifraga* and the species-rich genus *Corvus*. Also the Southeast Asian magpies and treepies (*Cissa*, *Dendrocitta, Temnurus* and *Urocissa*) are often regarded to form a monophyletic group of genera to which *Platysmurus* and sometimes *Cyanopica* and *Pica* have been added.

Most proposals about higher-level relationships among corvids have been based on studies in comparative anatomy (e.g., Amadon 1944). The few phylogenetic analyses of intergeneric relationships that exist mostly utilize DNA sequence data obtained from mitochondrial genes (Espinosa de los Monteros and Cracraft 1997, Cibois and Pasquet 1999, Saunders and Edwards 2000), and only one is based on morphology (Hope 1989). Also, molecular and morphological informations are rarely analysed together, with the exception of an analysis of the New World jays by Espinosa de los Monteros and Cracraft (1997) where parts of Hope's morphological data set were added to their cytochrome *b* data set.

It has long been discussed which taxa constitute the earliest radiation within the Corvidae, and both the crows and the jays have been suggested based on their possession of purportedly primitive characters. On the other hand, crows and jays are not supposed to be particularly close to each other (Goodwin 1976). Furthermore, osteological data supports neither crows nor jays as basal radiations of corvids, but places the Southeast Asian magpies and treepies in this position (Hope 1989). Yet another hypothesis places the choughs (*Pyrrhocorax*) as the most basal branch of the family based on an analysis of cytochrome *b* sequence data (Cibois and Pasquet 1999). However, these authors noted that the phylogenetic relationships suggested by the cytochrome *b* data set were very sensitive to which model for nucleotide substitutions and weighting scheme were employed, as well as to which analytical method was used.

Herein we present a hypothesis of the intergeneric relationships of the Corvidae based on DNA sequence data obtained from one mitochondrial, protein-coding (cytochrome *b*) gene and two introns positioned in the nuclear myoglobin and β-fibrinogen genes, respectively. The occurrence of the three loci in three linkage groups is based on their known positions in the human genome. This means that they have evolved independently, thus providing three independent estimates of the true branching patterns within the Corvidae. In addition to this large data set, we also studied a cytochrome *b* data set consisting of representatives from all genera of corvids. In order to estimate the phylogenetic position of the six genera for which we were unable to sequence the nuclear markers, we also studied a data set including only cytochrome *b* but representing all genera of corvids.

Materials and methods

Examined taxa and choice of outgroups

A total of 32 species representing 23 genera included in the Corvidae have been included in the analyses (Table 1). These taxa represent all genera traditionally included in this family (Madge and Burn 1994), with the exception of *Pseudopodoces* and *Platylophus*. *Pseudopodoces* has recently been shown to be a ground-adapted tit (Paridae) based on morphological and molecular data (James et al. 2003), and the corvid affinity of *Platylophus* has long been questioned (Amadon 1944, Goodwin 1976). Sibley and Monroe (1990), based on DNA-DNA hybridization data, retained *Platylophus* in their Corvini (i.e., Corvidae in traditional classifications), but both Clench (1985) and Hope (1989), based on their respective analyses of the pterylosis and osteology, concluded that it is not a corvid. This is also confirmed from an analysis of mitochondrial and nuclear sequence data (P. G. P. Ericson pers. obs.). *Pseudopodoces* and *Platylophus* are thus both excluded from the present analysis. It should also be pointed out that the genus *Psilorhinus* often is synonymized with *Cyanocorax* (AOU 1998), a combination consistent with the present analysis.

It was not possible to amplify nuclear DNA from the study skin samples. We therefore conducted analyses on two different data sets. The first consists of data from both mitochondrial and nuclear genes obtained from fresh samples. A total of 18 corvid species representing 17 genera are included in this data set. We also investigated a taxonomically more inclusive data set comprising 31 species representing all recognized corvid genera. Only cytochrome *b* sequences were included in this data set.

Three outgroups were used: *Lanius* (Laniidae) represented by *L. ludovicianus* and *L. collurio*, *Vireo olivaceus* (Vireonidae) and *Epimachus albertisi* (Paradisaeidae). The outgroups were chosen to represent close relatives of the corvid clade as suggested by analyses of DNA-DNA hybridisation (Sibley and Ahlquist 1990) and DNA sequences (P. G. P. Ericson pers. obs.). Due to problems

Table 1. The studied species (taxonomy follows Madge and Burn 1994). FMNH: Field Museum of Natural History, Chicago; MNHN: Muséum National d'Histoire Naturelle (Paris); NRM: Swedish Museum of Natural History; UWBM: Burke Museum of Natural History and Culture (Seattle). References: 1: Espinosa de los Monteros and Cracraft (1997), 2: Cibois and Pasquet (1999), 3: Helm-Bychowski and Cracraft (1993), 4: Nunn and Cracraft (1996), 5: Cracraft and Feinstein (2000), 6: Cicero and Johnson (1998), 7: Härlid and Arnason (1999), 8: Ericson et al. (2002a), and 9: Ericson and Johansson (2003).

Species	Vernacular name	Gene sequenced	Source	Voucher no.	GenBank no.
Aphelocoma coerulescens	Scrub jay	myoglobin, β-fibrinogen	muscle	FMNH 333861	AY395580, AY395598
		cytochrome *b*			U77335 (ref. 1)
Calocitta formosa	White-throated magpie-jay	myoglobin, β-fibrinogen	muscle	FMNH 393683	AY395581, AY395599
		cytochrome *b*			U77336 (ref. 1)
Cissa chinensis	Green magpie	myoglobin, β-fibrinogen	muscle	MNHN uncat.	AY395582, AY395600
		cytochrome *b*			U86037 (ref. 2)
Corvus corax	Common raven	cytochrome *b*			U86031 (ref. 2)
Corvus corone cornix	Hooded crow	cytochrome *b*			U86032 (ref. 2)
Corvus coronoides	Australian raven	cytochrome *b*			AF197837 (ref. 5)
Corvus frugilegus	Rook	myoglobin, β-fibrinogen	muscle	NRM 986396	AY395583, AY395601
		cytochrome *b*			NC 002069 (ref. 7)
Corvus monedula	Western jackdaw	myoglobin, β-fibrinogen	muscle	NRM 986450	AY395584, AY395602
		cytochrome *b*			U86033 (ref. 2)
Crypsirina temia	Racket-tailed treepie	cytochrome *b*	study skin	NRM 568802	AY395618
Cyanocitta cristata	Blue jay	myoglobin, β-fibrinogen	muscle	FMNH 356957	AY395585, AY395603
		cytochrome *b*			X74258 (ref. 3)
Cyanocorax chrysops	Plush-crested jay	myoglobin, β-fibrinogen	muscle	NRM 956615	AY395586, AY395604
		cytochrome *b*			U77334 (ref. 1)
Cyanolyca viridicyana	Black-collared jay	cytochrome *b*			U77333 (ref. 1)
Cyanopica cyana	Azure-winged magpie	myoglobin, β-fibrinogen	muscle	UWBM 59859	AY395587, AY395605
		cytochrome *b*	study skin	NRM 568808	AY395619
Dendrocitta formosae	Grey treepie	cytochrome *b*	study skin	NRM 568803	AY395620
Garrulus glandarius	Eurasian jay	cytochrome *b*			U86034 (ref. 2)
Garrulus lidthi	Lidthi's jay	myoglobin, β-fibrinogen	muscle	MNHN uncat.	AY395588, AY395606
		cytochrome *b*			U86035 (ref. 2)
Gymnorhinus cyanocephala	Pinyon jay	myoglobin, β-fibrinogen	muscle	FMNH 334283	AY395589, AY395607
		cytochrome *b*			U77332 (ref. 1)
Nucifraga caryocatactes	Spotted nutcracker	myoglobin, β-fibrinogen	muscle	NRM 976114	AY395590, AY395610
		cytochrome *b*			U86041 (ref. 2)
Perisoreus canadensis	Grey jay	cytochrome *b*			U77331 (ref. 1)
Perisoreus infaustus	Siberian jay	myoglobin, β-fibrinogen	muscle	NRM 976543	AY395591, AY395608
		cytochrome *b*			U86042 (ref. 2)
Perisoreus internigrans	Sichuan jay	cytochrome *b*	study skin	NRM 568809	AY395621
Pica pica	Magpie	myoglobin, β-fibrinogen	muscle	NRM 986309	AY395592, AY395609
		cytochrome *b*			U86036 (ref. 2)
Platysmurus leucopterus	Black magpie	cytochrome *b*	study skin	NRM 568801	AY395622
Podoces biddulphi	Xinjiang ground-jay	cytochrome *b*	study skin	NRM 568806	AY395623
Podoces hendersoni	Henderson's ground-jay	myoglobin, β-fibrinogen	muscle	UWBM 57967	AY395593, AY395611
		cytochrome *b*	study skin	NRM 568804	AY395624
Psilorhinus morio	Brown jay	cytochrome *b*	study skin	NRM 568805	AY395625
Ptilostomus afer	Piapiac	myoglobin, β-fibrinogen	muscle	MNHN uncat.	AY395594, AY395613
		cytochrome *b*			U86040 (ref. 2)
Pyrrhocorax graculus	Yellow-billed chough	cytochrome *b*			U86043 (ref. 2)
Pyrrhocorax pyrrhocorax	Red-billed chough	myoglobin, β-fibrinogen	muscle	UWBM 58057	AY395595, AY395612
		cytochrome *b*			U86044 (ref. 2)

Table 1 (*Continued*)

Species	Vernacular name	Gene sequenced	Source	Voucher no.	GenBank no.
Temnurus temnurus	Ratchet-tailed treepie	myoglobin, β-fibrinogen	muscle	NRM 947306	AY395596, AY395614
		cytochrome *b*	study skin	NRM 568807	AY395626
Urocissa erythrorhyncha	Blue magpie	myoglobin, β-fibrinogen	blood	MNHN uncat.	AY395597, AY395615
		cytochrome *b*			U86038 (ref. 2)
Zavattariornis stresemanni	Stresemann's bush-crow	cytochrome *b*	study skin	NRM 552443	AY395627
Epimachus albertisi	Black-billed sicklebill	myoglobin, β-fibrinogen	muscle	MV C148	AY064735 (ref. 8), AY395616
		cytochrome *b*			U15205 (ref. 4)
Lanius collurio	Red-backed shrike	myoglobin, β-fibrinogen	muscle	NRM 986403	AY228328 (ref. 9), AY395617
Lanius ludovicianus	Loggerhead shrike	cytochrome *b*			X74259 (ref. 3)
Vireo cassinii	Red-eyed vireo	cytochrome *b*			AF081990 (ref. 6)

in sequencing nuclear genes from our sample of *Vireo olivaceus*, only *Lanius* and *Epimachus* were used as outgroups in the analyses of the nuclear data sets.

Laboratory procedures

Blood and tissue samples were obtained from the collections at the Swedish Museum of Natural History, Muséum National d'Histoire Naturelle (Paris), the Burke Museum of Natural History and Culture (Seattle), and the Field Museum of Natural History (Chicago). As no blood or tissue samples of the genera *Crypsirina*, *Cyanolyca*, *Dendrocitta*, *Platysmurus*, *Psilorhinus* and *Zavattariornis* could be located, we instead extracted DNA from museum study skins for these taxa. Although the nuclear introns failed to amplify, the cytochrome *b* gene could be sequenced from the study skins.

All extractions were carried out using the QIAamp™ DNA Mini Kit (QIAGEN®) following the manufacturer's instructions. Genomic DNA was prepared from tissue for all taxa except *Urocissa* for which blood was used. From the study skins the DNA was extracted from small pieces (2–3 mm^3) of the foot papillae. After being cut from the study skins the samples were temporarily placed in ethanol. After digestion in Proteinase K for 24 h, DNA was extracted through the QIAamp™ tissue extraction kit (QIAGEN®) as described by Mundy et al. (1997). The DNA was degraded in all samples and several primers were used to amplify and sequence shorter segments of cytochrome *b* (Table 2).

The protocol of Ericson et al. (2002a) was used for the amplification of cytochrome *b* from fresh material. No stop codons or non-coding regions, indicating the presence of nuclear pseudogenes, were observed in the sequences. 924 bp of cytochrome *b* were selected for analysis, corresponding to the region between positions 14992 to 15915 in the chicken mitochondrial genome (Desjardins and Morais 1990). For several taxa cytochrome *b* sequences were obtained from GenBank (Table 1).

An approximately 700 bp long fragment of the myoglobin gene was amplified using the protocol of Ericson (2002a) and Irestedt et al. (2002). The amplified fragment corresponds to the entire intron 2 and 13 bp and 10 bp of the flanking second and third exons, respectively. The maximum length of the intron 2 of the myoglobin gene was 696 bp (observed in most ingroup taxa) and the minimum length was 670 bp (in *Lanius*).

PCR-amplification and sequencing of the β-fibrinogen gene following Prychitko and Moore (1997) resulted in an approximately 900 bp long fragment of intron 7. The sequencing posed some problems for *Corvus frugilegus* of which seven basepairs in the beginning of the sequence could not be determined and these were coded as missing in the analyses. The minimum length of the β-fibrinogen intron 7 was 862 bp (*Urocissa*) and the maximum length was 922 bp (*Lanius*).

Table 2. Primer sequences for amplifying and sequencing shorter segments of cytochrome *b* from museum study skins.

Name	Primer sequence (5′ to 3′)	Sequencing direction
L14850	AAC ATC TCC GCT GGA TGA AAC TTC GGA TC	Forward
L413	AAT ATC CTT CTG AGG AGC TAC AGT CAT	Forward
L658	CCA TTC CAC CCC TAC TAC TCC ATC AAA GA	Forward
L799	CCT CAC ATC AAA CCA GAA TGA TAC TTC C	Forward
H454	TGT TTG TCC AAT GTA TGG GAT TGC TGA	Reverse
H598	GTT GTT TGA GCC TGT TTC GTG TAG GAA	Reverse
H658	TCT TTG ATG GAG TAG TAG GGG TGG AAT GG	Reverse
H814	ATG GCG TAT GCA AAT AGG AAG TAT CAT TC	Reverse
H952	AAT AGG ATT TGT GAT AGG GGT CGG AA	Reverse

Alignment and phylogenetic analyses

The sequences could readily be aligned by eye using MegAlign™ (DNASTAR®). The aligned sequences include 2589 base pairs (bp) of homologous nucleotides, of which 924 bp derive from the cytochrome *b* gene, 721 bp from myoglobin intron 2 and flanking regions, and 944 bp from β-fibrinogen intron 7. There were a few indels observed in the aligned sequences. In the myoglobin intron, three autapomorphic indels were observed in the ingroups after alignment. For β-fibrinogen, all ingroup taxa share a 16 bp deletion relative to the outgroups. *Urocissa* further showed two major deletions (17 bp and 12 bp, respectively), but only a few additional (all autapomorphic) indels were observed in the ingroup. The alignments of the myoglobin and β-fibrinogen data sets are available as PopSets in GenBank. Nucleotide frequencies, uncorrected sequence divergences (p-distances) and inferred numbers of transitions and transversions were determined with Mega 1.0 (Kumar et al. 1993).

Both parsimony and maximum-likelihood analyses were performed in PAUP* 4.0b10 (Swofford 1998). The heuristic search option with TBR-branch swapping, and ten random additions of taxa were used in the parsimony analysis. These analyses were done for the genes independently, and for all genes combined. The cytochrome *b* gene was analysed with both all codon positions unweighted, and after removal of transition substitutions at third codon positions. Nodal supports in the parsimony analyses were estimated by doing 1000 bootstrap replicates.

The maximum-likelihood analyses were based on the unweighted, combined dataset using a general time-reversible model for nucleotide substitutions proposed by the likelihood-ratio test in MODELTEST (Posada and Crandall 1998). The GTR+I+Γ model uses six types of substitutions and estimates the proportions of invariable sites and the shape parameter (alpha) of the gamma distribution for evolutionary rate heterogeneity. Bayesian inference was calculated with MRBAYES 2.01, using the Markov chain Monte Carlo method (Huelsenbeck et al. 2001). A total of 400,000 generations were run. Stabilisation in the likelihood scores was reached after about 100,000 generations after which every hundred tree was saved. Posterior probabilities for clades were estimated from a majority-rule consensus tree calculated in PAUP* based on all the saved trees. A maximum-likelihood analysis was also performed on the taxonomically more inclusive cytochrome *b* data set.

Biogeographical analysis

Molecular analyses of the oscine passerines give strong support to an east Gondwanan origin of the group (Sibley and Ahlquist 1990, Barker et al. 2002, Ericson et al. 2002b, 2003). To test if our phylogeny is consistent with such an origin of the corvid clade we made an analysis of the ancestral distribution within the phylogeny. To reconstruct the ancestral distribution we used the dispersal-vicariance (DIVA) algorithm (Ronquist 1996, 1997). The DIVA analysis is an event-based approach that makes no assumptions about a general area relationship. Hence, there are no area configuration constraints on the ancient distributions. This means that the DIVA analysis allows for geological events to have generated and eliminated dispersal barriers. Therefore the DIVA analysis can handle both hierarchical and reticulate area relationships within the phylogeny.

The DIVA analysis can only handle fully bifurcate trees, and it requires that the distribution of extant species and their ancestors is described from a set of exclusive areas. Speciation is allowed to take place either within unit areas or as vicariance events separating the continuous range of a mother species into two mutually exclusive ranges of daughter species. Neither of these processes changes the set of unit areas that are used. In contrast dispersal into new areas expands the set of areas while at extinction unit areas are deleted. The DIVA algorithm, allocates a "cost" to dispersal and extinction events that entail a change in the set of unit areas and produces an optimal solution for the ancestral distribution based on the phylogeny of extant species and their distribution. Given the information contained in the distribution of extant species, the optimal solution identifies the ancestral distribution as a unique area or several unit areas as the location for branching events in the phylogeny.

Selection of the set of unit areas is crucial to the DIVA analysis. Herein we choose to divide the distribution of the extant species in seven unit areas to reflect the current dispersal barriers and habitat distributions (Table 3). Some of these have well defined borders, while in other cases the definition has to be somewhat arbitrary. Given the somewhat arbitrary delimitation of ranges we considered a species as present in an area only if its distribution there encompassed more than 5% of its range.

Results

The combined data set − two nuclear introns and the mitochondrial cytochrome *b*

Molecular variation and analyses of saturation. The unweighted cytochrome *b* data set consisted of 397 (43%) characters that vary between taxa of which 298 (32%) were phylogenetically informative. After the exclusion of transitions at third codon positions (see below), the cytochrome *b* data set consisted of 397 (43%) variable characters of which 250 (27%) were phylogen-

Table 3. Definition of the set of unit areas used in the dispersal-vicariance (DIVA) biogeographical analysis.

Biogeographic region	Definition
Australian	Australian continent and Tasmania, New Guinea
Oriental	Indonesia, south and southeast lowland China, Indochina, India, Bangladesh, Pakistan, Nepal
Western and Central Asia	Highland China, Mongolia and west to Red Sea/Mediterranean Sea
Ethiopian	Africa south of the Sahara, and Madagascar
North Asia	Asia (western border of Ural mountains) north of western and Central Asia, and the Oriental region
Western Palearctic	Europe (eastern border Ural mountains), North Africa
New World	North and South America

etically informative. The corresponding values for myoglobin intron 2 were 113 (16%) variable characters of which 34 (5%) were phylogenetically informative, and for β-fibrinogen intron 7, 236 (25%) and 66 (7%), respectively.

Nucleotide substitutions in cytochrome *b* were saturated for transitions at third codon positions, as indicated when plotted against the observed sequence distances of both the myoglobin and β-fibrinogen data set (Fig. 1). Transitions at third codon positions in cytochrome *b* thus were excluded from the parsimony analyses (but not from the maximum-likelihood analyses).

Plotting nuclear substitutions observed in the two nuclear introns against each other indicates that the β-fibrinogen intron evolves about 40% faster than the myoglobin intron (Fig. 2). As evident from the pairwise sequence divergences observed for the three genes across taxa, both nuclear introns evolve considerably slower than does cytochrome *b*.

Pairwise sequence distances. The observed pairwise sequence distances for the unweighted cytochrome *b* data set range from 9.8% (*Corvus monedula* – *Corvus frugilegus*) to 18.6% (*Perisoreus* – *Lanius*). Among ingroup taxa the maximum divergence is 17.2% (*Garrulus* – *Pyrrhocorax*); Table 4). Pairwise sequence distances in myoglobin intron 2 range between 0.3% (*Cyanocitta* – *Gymnorhinus*) and 4.7% (*Aphelocoma* – *Epimachus*, and *Pica* – *Lanius*), with the maximum observed distance among ingroup taxa is 3.7% (*Pica* – *Aphelocoma*). For intron 7 of β-fibrinogen the distances range from 1.1% (*Calocitta* – *Cyanocorax*) to 8.0% (*Corvus monedula* – *Lanius*, *Pica* – *Lanius*, and *Epimachus* – *Lanius*). The maximum distance among ingroup taxa is 5.3% (*Perisoreus* – *Pica*); Table 5).

Phylogenetic results. The general topologies of the phylogenetic trees obtained in the parsimony and maximum-likelihood analyses of the combined dataset agree well (Fig. 3A and B). Note that the weighted data set, with 3rd position transitions in cytochrome *b* excluded, was used in the parsimony analysis (but not in the maximum-likelihood analysis). The topologies can be summarised as follows (bootstrap support values for the parsimony analysis and posterior probabilities from the Bayesian analysis, respectively, are given in brackets): 1) the family Corvidae is recovered as monophyletic (MP: 100%, Bayesian: 100%), 2) *Pyrrhocorax* and *Temnurus*

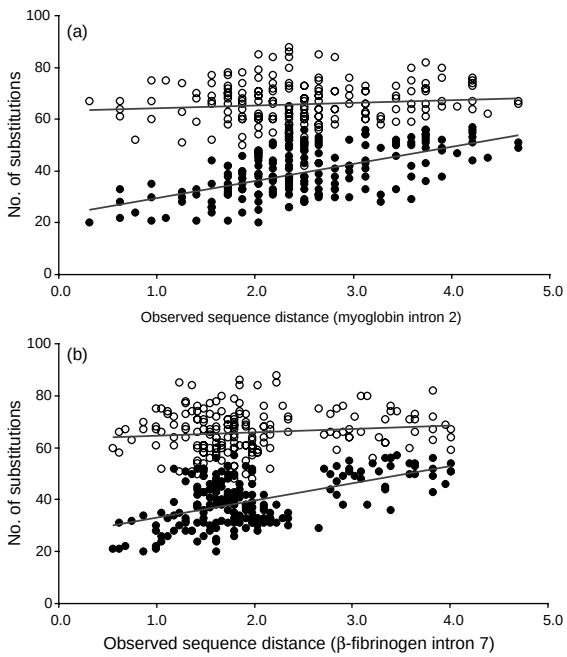

Fig. 1. Saturation plots of cytochrome *b* substitutions at third positions of the codon, against the observed pairwise sequence distances of a) the myoglobin gene, and b) the β-fibrinogen gene. The plots shows that transitions (open circles) in the cytochrome *b* sequences clearly reach saturation (also indicated by the almost horizontal regression line), whereas transversions (closed circles) do not.

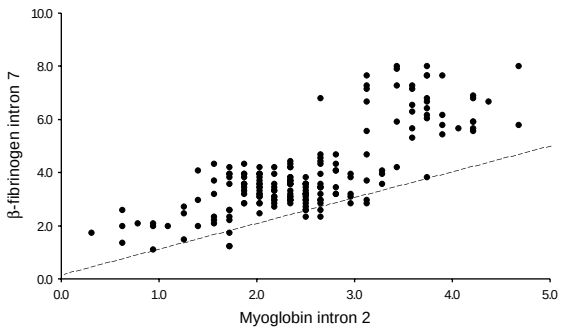

Fig. 2. Pairwise sequence distances observed in the two nuclear introns are plotted against each other. The line shows the 1:1 ratio, which gives an indication of a faster mutation rate in β-fibrinogen than in myoglobin.

Table 4. Pairwise. uncorrected sequence divergencies (p-distances) for the unweighted cytochrome *b* dataset (below diagonal). and for the same dataset but with tranversions only at third codon positions (above diagonal).

	Aphelocoma	*Calocitta*	*Cissa*	*Corvus frug.*	*Corvus mon.*	*Cyanocitta*	*Cyanocorax*	*Cyanopica*	*Garrulus*	*Gymnorhinus*	*Perisoreus*	*Pica*	*Nucifraga*	*Podoces*	*Pyrrhocorax*	*Ptilostomus*	*Temnurus*	*Urocissa*	*Epimachus*	*Lanius*
Aphelocoma		7.47	8.55	6.60	6.60	5.41	6.93	7.27	7.68	4.98	7.47	6.49	7.14	8.13	9.20	6.93	6.91	8.01	8.87	10.93
Calocitta	14.37		9.74	8.23	8.23	7.36	5.19	8.25	9.31	6.49	8.55	8.77	8.33	9.32	10.93	8.44	8.89	9.20	9.09	10.50
Cissa	16.07	15.65		7.14	6.82	8.01	9.09	6.95	8.33	8.44	6.93	6.39	6.60	6.28	8.44	6.60	7.76	5.74	8.55	10.17
Corvus frugilegus	13.94	13.51	13.51		3.90	5.63	7.79	7.27	5.84	5.84	5.95	4.87	4.22	5.63	8.12	5.09	6.49	6.28	8.33	8.87
Corvus monedula	13.66	15.36	12.66	9.82		5.41	7.58	6.62	5.74	5.52	5.84	4.76	4.44	5.53	7.58	5.09	7.05	6.49	8.01	9.52
Cyanocitta	13.23	13.66	15.65	12.80	11.66		6.06	7.49	7.90	4.00	6.60	6.60	6.39	6.28	8.33	5.95	6.91	7.36	7.25	10.50
Cyanocorax	13.51	11.38	16.64	13.66	14.94	13.51		8.69	8.55	5.74	8.44	8.33	7.90	8.88	9.74	8.01	9.31	8.87	8.33	10.39
Cyanopica	13.51	14.51	13.23	13.80	12.66	14.22	15.79		8.47	6.73	6.62	5.54	6.30	6.85	8.79	6.30	7.08	7.60	8.47	9.55
Garrulus	14.79	16.22	15.08	12.94	12.66	15.79	17.07	16.36		7.36	7.25	6.39	6.49	7.26	8.87	6.49	7.48	7.14	8.66	9.63
Gymnorhinus	12.23	13.66	16.93	13.09	13.51	11.38	12.23	13.37	15.50		6.49	6.17	6.28	7.15	8.66	6.17	7.05	7.58	6.93	9.85
Perisoreus	15.65	14.08	14.08	13.09	12.66	14.79	16.07	14.65	15.79	15.50		5.41	5.84	5.74	7.36	5.63	6.49	5.74	8.87	10.17
Pica	12.52	15.22	12.38	11.38	11.95	14.22	15.08	12.38	13.51	13.94	13.37		4.98	5.53	7.58	4.98	6.63	6.82	7.79	9.63
Nucifraga	14.65	14.37	13.80	11.95	12.23	13.37	14.94	14.65	14.65	14.37	15.36	12.66		6.18	7.58	5.19	6.35	6.39	8.44	9.20
Podoces	17.07	16.36	15.50	13.94	13.94	13.66	16.79	14.08	15.93	15.65	14.65	13.23	14.37		8.78	4.88	8.19	6.39	9.43	9.86
Pyrrhocorax	15.93	17.07	16.22	15.22	14.37	14.51	16.36	14.94	17.21	15.08	15.79	14.94	15.36	16.79		8.44	5.64	7.79	8.98	10.06
Ptilostomus	15.22	14.65	12.80	13.09	10.95	13.37	15.79	12.52	13.66	13.94	12.38	10.81	12.66	13.37	15.65		6.49	6.28	8.23	10.17
Temnurus	12.94	14.79	15.36	14.08	13.94	14.08	16.36	14.37	16.07	14.79	14.65	14.94	15.22	16.50	12.38	14.65		6.21	8.89	9.59
Urocissa	15.65	14.79	12.66	12.23	13.94	14.79	15.65	15.08	14.65	14.08	12.66	13.37	14.37	16.07	15.36	13.51	14.65		8.12	9.20
Epimachus	15.93	15.65	15.50	15.65	15.79	15.93	16.07	15.08	17.21	16.36	16.79	14.65	16.64	17.21	17.07	14.94	17.35	13.66		9.31
Lanius	18.07	18.21	17.92	15.36	15.50	16.50	17.78	16.07	16.07	16.07	18.63	15.93	16.36	17.35	16.22	16.64	17.21	16.22	16.36	

Table 5. Pairwise, uncorrected sequence divergencies (p-distances) for myoglobon intron 2 (below diagonal) and β-fibrinogen intron 7 (above diagonal).

	Aphel-ocoma	*Calo-citta*	*Cissa*	*Corvu-sfru*	*Corvu-smon*	*Cyano-citta*	*Cyano-corax*	*Cyano-pica*	*Garr-ulus*	*Gymno-rhinu*	*Periso-reus*	*Pica*	*Nuci-fraga*	*Podo-ces*	*Pyrrh-ocora*	*Ptilos-tomu*	*Temn-urus*	*Uroc-issa*	*Epima-chus*	*Lanius*
Calocitta	1.72		3.58	3.58	3.95	2.59	1.11	2.96	3.33	2.10	3.95	3.95	3.58	3.21	3.46	3.21	3.46	3.83	5.93	6.79
Cissa	2.81	2.34		3.95	4.32	3.95	2.96	3.09	3.83	3.46	4.20	4.32	3.95	3.58	3.58	3.58	2.84	1.98	5.93	7.28
Corvusfru	2.96	2.50	2.03		2.10	3.95	2.96	3.33	2.84	3.46	4.69	3.09	1.98	2.59	3.58	2.35	3.58	4.20	5.93	7.65
Corvusmon	2.50	2.03	1.56	0.78		4.07	3.33	3.46	2.96	3.58	4.32	3.21	1.36	2.72	3.95	2.47	3.95	4.32	6.17	8.02
Cyanocitta	1.40	0.62	1.72	1.87	1.40		1.98	3.33	3.70	1.73	4.20	4.57	3.95	3.58	3.83	3.58	3.83	4.20	6.30	7.65
Cyanocorax	1.72	0.94	2.34	2.50	2.03	0.94		2.35	2.72	1.48	3.46	3.58	2.96	2.59	2.84	2.59	2.84	3.21	5.56	6.67
Cyanopica	2.65	2.50	2.03	2.50	1.87	1.87	2.50		3.09	2.84	3.09	3.95	3.09	2.96	2.84	2.96	2.72	3.58	5.43	6.54
Garrulus	2.65	2.18	1.72	1.87	1.40	1.56	2.18	2.18		3.21	4.44	3.46	2.59	2.47	3.33	2.22	3.21	3.70	6.17	7.16
Gymnorhinu	1.72	0.94	2.03	2.18	1.72	0.31	1.25	2.18	1.87		3.70	3.83	3.46	2.84	3.09	3.09	3.33	3.70	5.80	7.16
Perisoreus	3.12	2.65	2.34	2.81	2.34	2.03	2.65	2.50	2.34	2.34		5.31	4.44	4.07	3.83	4.32	4.07	4.69	6.79	7.65
Pica	3.74	2.96	2.81	2.03	1.56	2.65	3.28	3.28	2.65	2.96	3.59		2.84	2.59	4.20	2.96	4.07	4.69	6.67	8.02
Nucifraga	2.81	2.34	1.87	1.09	0.62	1.72	2.34	2.34	1.72	2.03	2.65	1.87		2.35	3.58	2.10	3.58	4.20	6.05	7.65
Podoces	2.96	2.50	2.03	1.72	1.25	1.87	2.50	2.18	2.03	2.03	2.81	2.50	1.56		2.96	2.22	2.96	3.70	5.68	7.28
Pyrrhocora	3.12	2.65	1.87	2.65	2.18	2.03	2.65	2.34	2.34	2.34	2.34	3.43	2.50	2.65		3.21	3.21	3.58	5.56	6.67
Ptilostomu	3.12	2.50	1.87	1.72	1.25	2.03	2.65	2.34	1.72	2.18	2.65	2.34	1.56	1.56	2.50		3.21	3.83	5.68	7.28
Temnurus	2.96	2.50	2.03	2.50	2.03	1.87	2.50	2.50	2.50	2.18	2.81	3.28	2.34	2.18	2.03	2.65		3.21	5.68	6.79
Urocissa	2.81	2.34	0.62	2.34	1.87	1.72	2.34	2.34	2.34	2.03	2.65	3.12	2.18	2.34	2.18	2.50	2.03		6.42	7.90
Epimachus	4.68	4.21	3.43	4.21	3.74	3.59	4.21	3.90	3.90	3.90	4.21	4.37	3.74	4.21	3.12	4.06	3.59	3.74		8.02
Lanius	4.21	3.74	3.12	3.90	3.43	3.12	3.74	3.59	3.59	3.12	3.74	4.68	3.74	3.43	3.12	3.59	2.65	3.43	3.74	

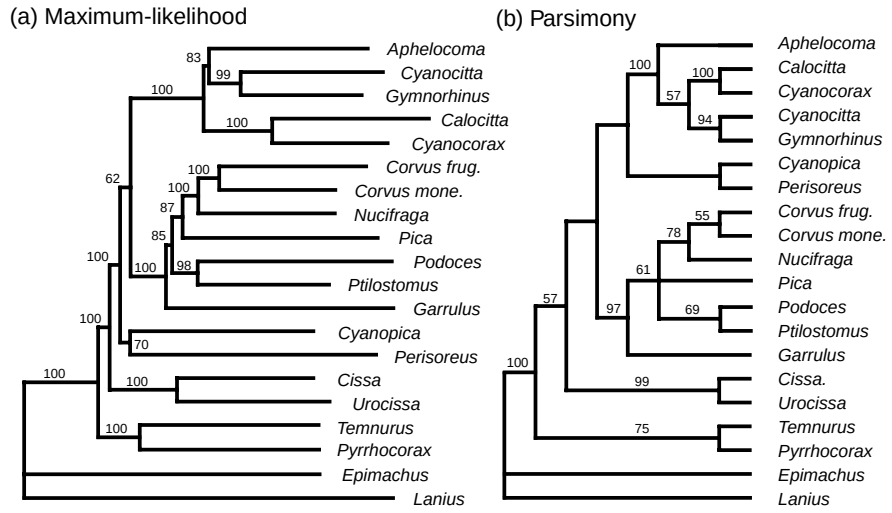

Fig. 3. Phylogenetic trees of the three genes (cytochrome *b*, myoglobin and β-fibrinogen) combined resulting from a maximum-likelihood analysis (left) and a parsimony analysis (right). The maximum-likelihood tree shows the best-fit tree (−ln likelihood = 12413.62). The numbers indicated on the branches are posterior probabilities (> 50%) estimated from the Bayesian inference analysis. The parsimony tree is a strict consensus tree based on the two shortest trees (length 1092, C.I: 0.42, R.I: 0.45) with nodal support values calculated by 1000 bootstrap replicates.

fall outside a clade consisting of all other ingroup taxa (MP: 57%, Bayesian: 100%), 3) further up in the tree, *Cissa* and *Urocissa* form a clade that is the sister group to the remaining ingroup taxa (MP: this node is present in the strict consensus tree but receives no bootstrap support, Bayesian: 100%), 4) the New World jays (*Aphelocoma*, *Calocitta*, *Cyanocorax*, *Cyanocitta* and *Gymnorhinus*) are monophyletic (MP: 100%, Bayesian: 100%), 5) the genera *Corvus*, *Garrulus*, *Nucifraga*, *Pica*, *Podoces,* and *Ptilostomus* form a clade (MP: 97%, Bayesian: 100%), and 6) *Cyanopica* and *Perisoreus* may be sister taxa (MP: the clade occurs in the strict consensus tree without bootstrap support, Bayesian: 70%), but their positions in relation to other corvid genera cannot be conclusively determined.

Within the clade of New World jays, *Calocitta* groups strongly with *Cyanocorax* (MP: 100%, Bayesian: 100%) in the analyses of the combined data set, as does *Cyanocitta* with *Gymnorhinus* (MP: 94%, Bayesian: 99%). *Aphelocoma* is positioned basal of these four genera, but this arrangement receives only moderate support (MP: 57%, Bayesian: 83%).

The two *Corvus* representatives group together (MP: 55%, Bayesian: 100%), with *Nucifraga* outside these (MP: 78%, Bayesian: 100%). A clade with *Podoces* and *Ptilostomus* also receives high support (MP: 69%, Bayesian: 98%). The maximum-likelihood analysis places *Pica* as the next taxon outside these (with 87% posterior probability in the Bayesian analysis) but the parsimony analyses is ambiguous on this point. In both analysis *Garrulus* is the basal-most member of this clade of Eurasian and African taxa although the support for this is moderate (MP: 61%, Bayesian: 85%).

The resolution of the individual gene trees is low, with few nodes receiving bootstrap support (Fig. 4). The topologies of the individual gene trees are congruent with most of the general phylogenetic patterns found in the analysis of the combined data set, or at least alternative relationships do no receive a bootstrap support exceeding 50%. The single exception is that in the β-fibrinogen tree where *Temnurus* groups with the *Cissa*/*Urocissa* clade on the exclusion of *Pyrrhocorax*, an arrangement that receives 79% bootstrap support.

The taxonomically expanded cytochrome *b* data set

The maximum-likelihood and Bayesian analyses of the taxonomically more inclusive, cytochome *b* data set generally corroborate the results of the combined nuclear and mitochondrial genes (Fig. 5). The genera *Crypsirina*, *Dendrocitta* and *Platysmurus* group with *Temnurus*, and they form, together with the two species of *Pyrrhocorax*, the sister group of all other corvids in the maximum-likelihood analysis. However, in the Bayesian analysis of the cytochrome *b* data set *Pyrrhocorax* is positioned in the most basal position, with the *Temnurus*-group as the next branch up in the tree. In both analyses *Cissa* and *Urocissa* group together and are placed as the sister taxon to all other corvids (except *Pyrrhocorax* and the *Temnurus*-group).

Above this node are two clades that are also recognised in the combined nuclear and mitochondrial data set. A long branch in the maximum-likelihood tree leads to the first of these clades, the New World jays, and the monophyly of this group receive 100% posterior probability in the Bayesian analysis. The second clade unites a group of mostly Eurasian and African taxa that do not yield support exceeding 50% in the Bayesian analysis. The African *Zavattariornis*, of which no fresh material was available, evidently belong to this group, which also includes the genera *Corvus*, *Garrulus*, *Nucifraga*, *Pica*, *Podoces,* and *Ptilostomus*. The short internodes between

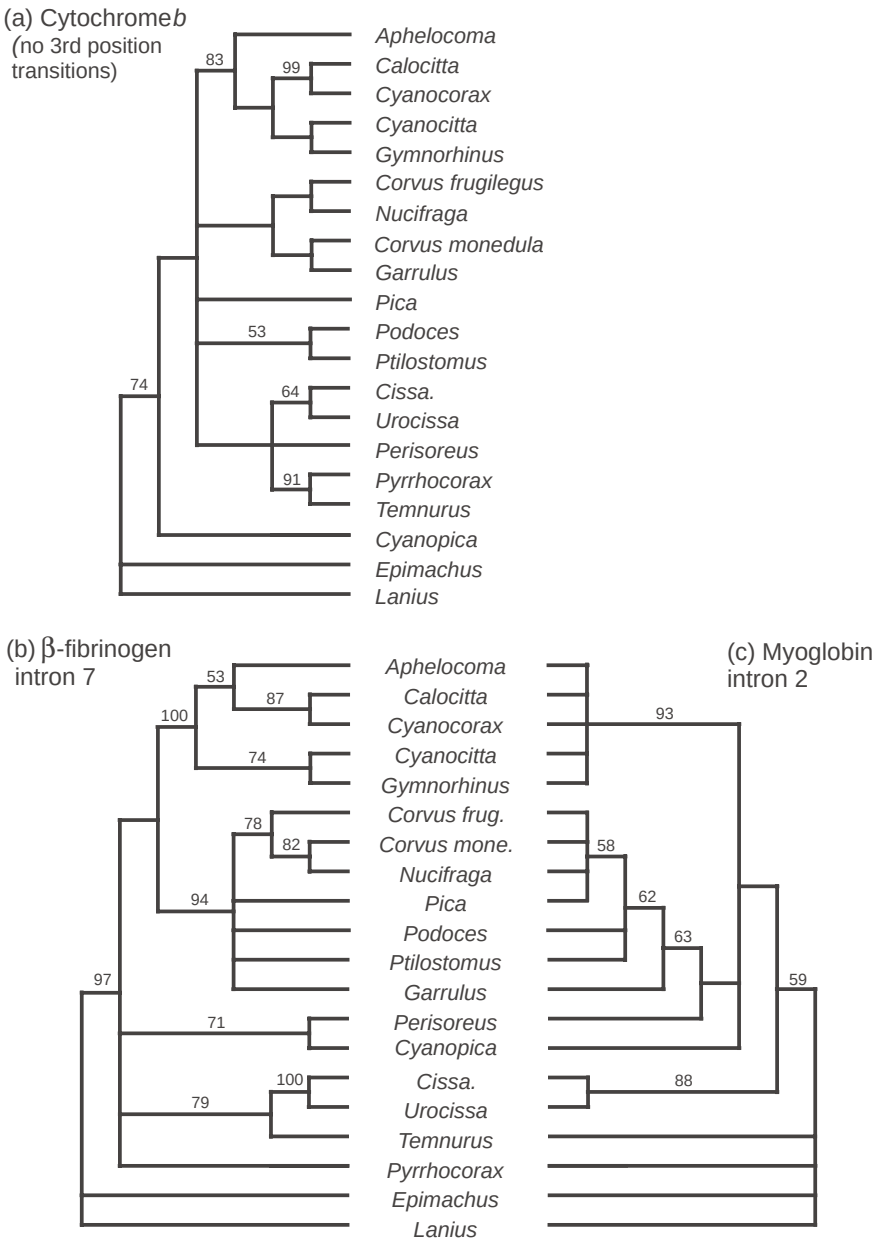

Fig. 4. Gene trees calculated in parsimony analyses of DNA sequences obtained from the (a) cytochrome *b*, (b) β-fibrinogen, and (c) myoglobin genes. The gene trees are strict consensus trees based on six original trees (length 639, C.I: 0.35, R.I: 0.36) for cytochrome *b*, 292 original trees for β-fibrinogen (length 292, C.I: 0.65, R.I: 0.71), and 288 original trees (length 144, C.I: 0.65, R.I: 0.74) for myoglobin, respectively. Support values were obtained from 1000 bootstrap replicates.

these taxa in the maximum-likelihood tree cast doubts about the basal relationships among them. As in the analyses of the combined nuclear and mitochondrial data set, *Cyanopica* and *Perisoreus* weakly group together. The precise relations of these taxa to other corvids are obscure also with the cytochrome *b* data set.

Ancestral distributions

The outcome of the DIVA analysis was unambiguous in identifying the Oriental region (as defined in Table 3), as the area of ancestral corvid radiations. All four basal nodes in the corvid phylogeny based on maximum likelihood for the combined data for cytochrome b, myoglobin, and β-fibrinogen (Fig. 3a) were unambiguously identified as of Oriental origin. The position of the *Cyanopica*/*Perisoreus* branch receives weak support in our analysis. In line with the recommendation for such situations (Ronquist 1997), we ran separate analyses with the alternate positions for this branch in our phylogeny. Shifting the position of the *Cyanopica*/*Perisoreus* branch did, however, not alter the outcome of the DIVA analysis.

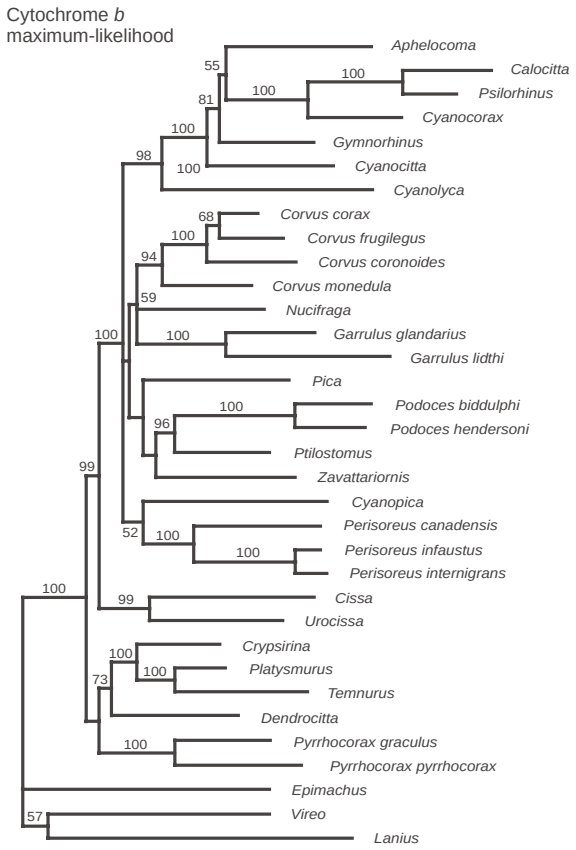

Fig. 5. Maximum-likelihood tree calculated for cytochome *b* data obtained from the taxonomically more inclusive data set. The numbers indicated on the branches are posterior probabilities (>50%) estimated from the Bayesian inference analysis.

Discussion

The ancestor of the oscine passerines, to which the Corvidae belongs, appears to have been isolated on the Australo-Papuan tectonic plate when this split from Antarctica in the early Tertiary (Ericson et al. 2002b, 2003). The subsequent spread of oscines into other parts of the world began when the Australo-Papuan plate came close enough to Asia to allow dispersals. It is unknown how many successful dispersal events of oscines have taken place but the family Corvidae belongs to these. It is intriguing that the oldest branches of corvids, as identified in the present study, include taxa that almost all are geographically confined to the southeastern parts of Asia, i.e., the area to which the corvid ancestor presumably first arrived from the Australo-Papuan region. The genera *Crypsirina*, *Dendrocitta*, *Platysmurus*, *Temnurus*, *Cissa* and *Urocissa* all inhabit tropical and subtropical forests in Southeast Asia and nearby areas. *Pyrrhocorax* is an exception to this pattern in being distributed in mountain areas from the Himalayas to western Europe. An analysis of osteological and other morphological characters suggested *Pyrrhocorax* to be closely related to *Corvus* and *Nucifraga* (Hope 1989), which conform to the traditional opinion about the relationships of this taxon. Unexpectedly, Cibois and Pasquet (1999) based on an analysis of cytochrome *b* data found *Pyrrhocorax* to be basal among the corvids. In our analysis, this was confirmed not only by the cytochrome *b* data, but by the myoglobin and β-fibrinogen data as well.

Despite the Australo-Papuan origin of the oscine radiation, there is among genera belonging to the basal branches of the corvids a complete lack of species with a distribution on Australia proper. The almost total prevalence of species with forest-living habits among the basal clades sits well with the Corvidae having radiated only after the exodus of an ancestral passerine from Australia. There seems to be little reason to doubt that the Corvidae originated from forest living ancestors. Its closest relatives (e.g., Paradisaeidae, Oriolidae) are forest adapted, and the basal groups within the Corvidae consist almost exclusively of forest living species, once again with the exception of genus *Pyrrhocorax*. By the time that the oscines started to radiate extensively in late Oligocene and Miocene (Feduccia 1995), the early Tertiary rainforests of Australia had become largely replaced by more open savanna-like forests or under extreme conditions even by desert like conditions. Hence, by the time the Corvidae started to radiate the Australian continent had already become less suitable habitat for a forest adapted ancestor.

Later radiations of Corvidae seem to be associated with an adaptation to drier habitats allowing an expansion out of the Southeast Asian range into more open habitats and resulting in the current almost ubiquitous distribution. However, as a legacy of their origin the clades of later radiations contain taxa with a distribution encompassing southeast Asia (e.g., *Cyanopica, Perisoreus internigrans, Garrulus lidthi, Pica pica*). The adaptation to arid conditions is at its most extreme in the desert adapted Asian genus *Podoces* while the African genera *Ptilostomus* and *Zavattariornis* inhabit dry grassland. Within the "Old World" clade, *Podoces* and *Ptilostomus* unexpectedly grouped together, considering their different geographical distributions. This clade yields 98% posterior probability in the Bayesian analysis, but only 69% in the parsimony analysis. Within this clade the adaptation to truly arid conditions thus appears to be a single evolutionary event according to the phylogenetic analysis. The disjunct distribution of the extant species should then reflect later dispersal events coupled to further specialisation.

Soon after the initial radiation of corvids in the southeast Asian region, the ancestors to the New World jays spread to the Americas, presumably by following the trans-Beringian route. In North America, and later in South and Middle America, the New World jays underwent significant adaptive radiations. Unlike most

Palearctic jays that are confined to forested areas, several New World jays inhabit open terrain. In the Old World most corvids living in open areas belong to the crows (e.g., *Corvus*) and the New World jays may have had little competition from these in the beginning. Today, the three genera *Corvus, Perisoreus* and *Nucifraga* occur in the Americas, but these all have their core-distribution in other parts of the world. These three groups presumably radiated in the Palearctic and later immigrated to the New World, while the magpies (*Pica*) appear to have speciated after immigration to the New World (Lee et al. 2003).

Monophyly of the New World jays is strongly supported herein and has been established based on DNA sequence data before (Espinosa de los Monteros and Cracraft 1997, Cibois and Pasquet 1999). The overall topology of the New World jay clade differs somewhat between the parsimony and likelihood analyses of the combined data set. In both analyses *Cyanocitta* groups with *Gymnorhinus*, and *Calocitta* with *Cyanocorax*. In the parsimony analysis *Aphelocoma* is basal to these four genera (57% support), while it groups with the *Cyanocitta–Gymnorhinus* clade in the maximum-likelihood analysis (with 83% posterior probability in the Bayesian analysis). The latter topology agrees with that of Espinosa de los Monteros and Cracraft (1997) based on cytochrome *b* sequences obtained from a larger number of New World jay species. Based on the finding that the *Cyanocorax–Calocitta* clade is basal in their phylogenetic tree, they hypothesized that the ancestor of the New World jays dispersed from Eurasia via Beringia to the Americas. The group later underwent a rapid radiation in South America giving rise to the *Cyanocorax–Calocitta* clade. A more recent, secondary radiation further north should then have given rise to the *Cyanocitta–Gymnorhinus–Aphelocoma* clade.

A widely held theory about the systematic relationships among jays postulates that the Palearctic jays (*Garrulus* and *Perisoreus*) form a monophyletic group together with the New World jays. This is not supported in the present analysis: *Garrulus* clearly is a member of a clade consisting of several Old World core-groups, while the systematic position of old world core in groups *Perisoreus* can not be conclusively determined. Furthermore, *contra* the suggestion made by Madge and Burn (1994), and in agreement with the results of Cibois and Pasquet (1999), our analyses do not support a close relationship between *Garrulus* and *Perisoreus*. Instead, *Perisoreus* seems to be closest to *Cyanopica*, and the clade of these two in turn form a trichotomy with the New World jays on one hand, and the large group of core-Old World taxa on the other. The short internodes in this part of the tree in general, and between the three major clades in particular, suggest a rather rapid cladogenesis.

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