

¹Central Research Laboratories, Museum of Natural History, Vienna, Austria; ²Department of Evolutionary Biology, University of Vienna, Vienna, Austria; ³Institute of Biology and Soil Science, Russian Academy of Sciences, Vladivostok, Russia; ⁴1st Zoological Department, Museum of Natural History, Vienna, Austria

Genetic divergences and intraspecific variation in corvids of the genus *Corvus* (Aves: Passeriformes: Corvidae) – a first survey based on museum specimens

ELISABETH HARING^{1,2}, BARBARA DÄUBL¹, WILHELM PINSKER¹, ALEXEY KRYUKOV³ and ANITA GAMAUF^{2,4}

Abstract

The first comprehensive overview of intra- and interspecific variation within the genus *Corvus* as well as first insights into the phylogenetic relationships of its species is presented. DNA sequences of the mitochondrial control region were obtained from 34 of the 40 described species (including subspecies: 56 taxa). As the study was based mainly on museum material, several specimens did not yield the full length marker sequence. In these cases, only a short section of the control region could be analysed. Nevertheless, even these individuals could be assigned tentatively to clades established on the full length marker sequence. Inclusion of sequences of other corvid genera as available in GenBank clearly confirmed the monophyly of the genus *Corvus*. Within the *Corvus* clade several distinct subclades can be distinguished. Some represent lineages of single species or species pairs while other clades are composed of many species. In general, the composition of the clades reflects geographical contiguity and confirms earlier assumptions of a Palearctic origin of the genus *Corvus* with several independent colonizations of the Nearctic and the Aethiopia. The Australasian radiation seems to be derived from a single lineage. The distribution of plumage colour in the phylogenetic tree indicates that the pale markings evolved several times independently. The white/grey plumage colour pattern – which is found also in other genera of the family Corvidae, for example, in *Pica* – occurs already in the species pair representing the first split within the genus *Corvus* (*Corvus monedula*, *Corvus dauuricus*). Thus, reversal to full black colour seems to have occurred as well. The use of colour traits as a phylogenetic marker within *Corvus* should be considered with severe caution.

Key words: *Corvus* – mitochondrial control region – molecular phylogeny – phylogeography – colour patterns

Introduction

The crows, rooks and ravens of the genus *Corvus* are a successful group of song birds that is world-wide distributed except South America and Antarctica (Goodwin 1976; Madge and Burn 1993; dos Anjos et al. 2009). Among corvids, *Corvus* is the species richest genus. It comprises 40 (Dickinson 2003) to 44 (dos Anjos et al. 2009) species, among them 23 monotypic species and 17 polytypic species. Altogether the genus comprises 92 taxa (dos Anjos et al. 2009). Twenty-two species cover large distribution ranges, 18 species occur on continental (3) or oceanic (15) islands. The highest taxon density (19 species) is found in the region from south-east Asia to Australasia including adjacent Pacific islands, representing about half of the described species.

The ancestors of the Corvidae appear to have originated on the Australo-Papuan tectonic plate in the early Tertiary (Ericson et al. 2005; Jönsson et al. 2011). Based on DNA–DNA hybridization Sibley and Ahlquist (1990) ranked the Corvidae as a branch of the Australasian corvid radiation. The phylogenetic relationships among species of the genus *Corvus*, which is in the centre of this study, as well as the evolution of the genus itself, have been a matter of debate for decades (Meinertzhagen 1926; Stresemann 1943; Amadon 1944; Goodwin 1976; Schodde and Mason 1999). Yet, sequence-based molecular genetic studies including members of the family Corvidae mainly dealt with specific questions

concerning selected species or subspecies (e.g. Tarr and Fleischer 1999; Fok et al. 2002; Iwasa et al. 2002; Lee et al. 2003; Kryukov et al. 2004, 2005; Baker and Omland 2006; Haring et al. 2007; Kryukov et al. 2012).

In our previous study (Haring et al. 2007), we investigated the mitochondrial control region (mt CR) of several widely distributed Palearctic corvids, among them five species of the genus *Corvus*. Some of them (*C. corone*, *C. frugilegus* and the species pair *Corvus monedula/Corvus dauuricus*) show an interesting phylogeographical pattern, each being divided into a western and an eastern group of populations within a Palearctic distribution range. We designated this pattern ‘west–east’ pattern. The fifth species, *Corvus corax*, does not show such a phylogeographical pattern within its Palearctic range (‘single-group’ pattern). Omland et al. (2000), however, could show that a distinct lineage of *C. corax* exists within its Nearctic distribution range and that *C. corax* seems to be paraphyletic (see also Feldman and Omland 2005). Some more examples for both phylogeographical patterns were found in other corvid species (Haring et al. 2007). A comprehensive study of the whole genus *Corvus* has, however, not been attempted so far.

Members of the genus *Corvus* are robust built and morphologically quite uniform, with long tarsi adapted to the movements on ground and trees, and large bills to probe and grasp prey. Body size varies between 120 g in *C. monedula/dauuricus* and 2000 g in *C. corax*, the largest of all passerines. Sex dimorphism does not occur in many species but is pronounced in some (Ludwig et al. 2009). Their omnivorous life style allowed the representatives of *Corvus* to live in any habitat type, from closed primary rain forest up to semi-open habitats and deserts. Island species, especially those inhabiting rain forests, are prone to extinction, particularly in connection

Corresponding author: Elisabeth Haring (elisabeth.haring@nhm-wien.ac.at)

Contributing authors: Barbara Däubel (barbara.daeubl@nhm-wien.ac.at), Wilhelm Pinsker (wilhelm.pinsker@univie.ac.at), Alexey Kryukov (kryukov@ibss.dvo.ru), Anita Gamauf (anita.gamauf@nhm-wien.ac.at)

with habitat loss. Several island species are therefore endangered (*C. florensis*), critically endangered (*C. unicolor*, *C. kubaryi*) or even extinct in the wild (*C. hawaiiensis*; BirdLife International 2011). As reflection of their intelligence and adaptability some species have also learned to live as commensals alongside with man. Because of their extraordinary mental abilities some species (*C. corax*, *C. moneduloides*) are considered as ideal study objects in cognition research (Heinrich 1999; Schloegl et al. 2008; Wimpenny et al. 2009). Regarding plumage colouration, 10 of 40 *Corvus* species are bicoloured (combinations of black with white, grey or brownish), while the others are completely black with a metallic gloss. So far it is unknown to which extent these plumage patterns correspond to phylogenetic relationships or other factors such as sociality (Marzluff and Angell 2005).

Here we present the first comprehensive survey on the genetic differentiation in the genus *Corvus* based on DNA sequence data. One difficulty in this species-rich, almost worldwide distributed group of birds was to get samples from a wide variety of taxa. For several species/subspecies it was not easy or even impossible to obtain fresh tissue. As our aim was to include as many taxa as possible, the study had to be based mainly on museum material including many rather old specimens. Consequently we used a comparatively short marker sequence, approximately 650 bp of the mt CR, which has been already employed in previous studies (Kryukov et al. 2004; Haring et al. 2007). For that reason, the present analysis is not an ideal system for resolving the phylogeny of the genus, as this would require analysing longer sequences and, in addition, nuclear marker sequences suitable to resolve the earlier ramifications within the genus. Nevertheless, the CR sequences can provide information on the differentiation of species and on intraspecific variation, and a first glimpse into the phylogenetic relationships of the various taxa.

Specifically we addressed the following questions: (1) Are the molecular relationships in accordance with the current taxonomy? Can the described and currently accepted taxa be clearly differentiated with the highly variable non-coding CR sequence? (2) What is the magnitude of genetic differentiation between species and subspecies? (3) Are there any differences in the amount of intraspecific variation? (4) What can we deduce from the distribution of colour patterns within the genus? Are taxa with similar plumage more closely related or have similar plumage patterns arisen independently?

Materials and Methods

Samples, DNA extraction, PCR amplification, and sequencing

We follow the classification of Dickinson (2003). We extracted DNA from the majority of species and subspecies of the genus *Corvus* from five continents. Only from the six 'island' taxa, *C. imparatus*, *C. sinaloe*, *C. nasicus*, *C. kubaryi*, *C. insularis* and *C. unicolor*, the quality of the DNA was not sufficient for sequence analysis. In addition to our samples, we included 103 previously published sequences of several species in the phylogenetic analysis (Kryukov et al. 2004; Haring et al. 2007): *C. corone*, *C. corax*, *C. frugilegus* and *C. monedula*. Altogether 339 samples were processed. PCR amplification was successful with 227 samples (67%) of the genus *Corvus* representing 34 species (including subspecies: 56 taxa; Appendix). We took any effort to obtain DNA from as many taxa/individuals as possible, for example, from the 12 samples of *Corvus pectoralis* only two yielded DNA of sufficient quality, and from the six samples of *C. nasicus* none was positive. As outgroup species we used *Cyanocorax cyanomelas*, *Cyanocorax chrysops*, *Pica pica*, *Cyanopica cyanus*, *Cyanopica cooki*, *Nucifraga caryocatactes*, *Perisoreus infaustus* (see Appendix).

Liver and muscle samples stored in ethanol, skin samples from foot pads of museum specimens (41% of the successfully analysed samples were obtained from museum material), as well as feathers collected in the field were used for DNA extraction. Specimens investigated in this study, their geographical origins and types of tissue are listed in the Appendix. Different protocols were used for DNA extractions. For muscle and liver tissues the DNeasy Blood and Tissue kit (Qiagen, Hilden, Germany) was used according to the manufacturer's instructions. Until 2007 DNA extractions from museum material were performed in a 10% Chelex (BioRad, Hercules, CA, USA) solution containing proteinase K (0.5 mg ml⁻¹) as described in Haring et al. (2007). From 2007 on the AGOWA sbeadex Forensic Kit (AGOWA, Berlin, Germany) was used according to the manufacturer's instructions with an incubation time of up to 24 h depending on visible progress of tissue digestion. The final elution volume was 30 µl. Optimal amounts of template DNA were determined empirically (2–10 µl of the DNA solution in 25 µl PCR volume). If necessary, re-amplifications were performed with 1–2 µl template DNA. Negative controls for PCR were carried out to screen for contaminated reagents: (1) control extractions (without DNA) instead of template and (2) reaction with distilled water instead of template.

As a large part of the samples analysed was obtained from museum collections (study skins and feathers), a comparatively short marker sequence was analysed: a partial sequence of the mt CR (positions 693–1308 of the reference sequence of *C. c. cyanus*, AJ458536) as well as 21 bp of the adjacent *tRNA-Phe* gene (length of PCR fragment approximately 680 bp). This section was amplified with the primers CR-Cor+ (ACCCTTCAAGTGCCTAGCAG) and Phe-Cor- (TTGACATCTTCAGTGTCATGC). To obtain the CR sequence from old samples with bad DNA quality two overlapping PCR fragments were amplified using various primers: for the left fragment CR-Cor3- (TAAAATTGTTGTTTATTTT) or CR-Cor6- (GATGATTTGGACAATCTAGG) was used in combination with CR-Cor+, and for the right fragment CR-Cor5+ (ACTAGGAATATCACCRAAA), CR-Cor2+ (TCGTTTATTTTATTTTGTAA) or CR-Cor4+ (ATTTTTATCTGTCAATTTA) was used in combination with Phe-Cor-. For some samples additional primers were used to combine the whole sequence from three overlapping sections: CR-Cor8+ (AACCTTCCTCCATTTTCCCC), CR-Cor11+ (ACTAGGAATTATCACCYAAACC), CR-Cor7- (TTTTATATTGTTTAAATTGATT), CR-Cor9- (GGCTAAGTTGGTGGTTGTG), CR-Cor10- (TTTAATTGAATTTATAGTTGTG). From some samples only the 5'-section (SF1) or the 3'-section (SF2) of the CR could be isolated (both approximately 280 bp). These sequences were used to assign the individuals to specific clades. From two samples (Crhista1, Crhista2) a section of 61 bp could not be determined, the missing part in these sequences was coded with *N* in the alignments.

PCR was performed on a Mastercycler gradient thermocycler (Eppendorf, Hamburg, Germany) in 25 µl with 0.5 units DynazymeII DNA polymerase (OY, Finnzymes, Vantaa, Finland), 1 µM of each primer and 0.2 mM of each dNTP (Mannheim, Roche, Mannheim, Germany); annealing temperature: 58°C, 35 reaction cycles. PCR products were either sequenced directly or extracted from agarose gels using the QIAquick Gel Extraction Kit (Qiagen) and cloned (TOPO TA Cloning kit; Invitrogen, Paisley, UK). Sequencing of both strands was performed by MWG-Biotech (Germany) and LGC Genomics-AGOWA (Berlin, Germany).

Phylogenetic analysis

Editing and alignment of sequences were performed using the BIOEDIT software package version 5.0.9 (Hall 1999). Neighbour-joining (NJ; Saitou and Nei 1987) and Maximum parsimony (MP) dendrograms were calculated with the software package PAUP (version 4.0b10; Swofford 2002). MP analyses were based on heuristic searches with the TBR (tree bisection reconnection) branch swapping algorithm and a random taxon addition sequence (1000 replicates) and delayed character transformation (DELTRAN). Gaps were treated as fifth character state. Bootstrap analyses were carried out with 1000 replicates for MP (10 random addition replicates) and NJ trees. Bayesian trees were calculated using MRBAYES 3.1.2 (BI, Huelsenbeck and Ronquist 2001) by MCMC sampling for 6 million generations

(four simultaneous MC chains, sample frequency 100, burn-in 10 000). We used the Software TRACER v1.5.0. (Rambaut and Drummond 2004) for assessing when the chains reached stationarity. Those trees generated prior to stationarity were discarded as burn-in and were not included in the calculation of the consensus trees. The substitution model TIM2 + G was determined with JMODELTEST v. 0.1.1. (Posada 2008) applying the Akaike information criterion. The average p distances between and within clades and subclades were calculated with the software MEGA5 (Tamura et al. 2011) using the pairwise deletion option.

The sequences determined in the course of this study as well as those from our previous study are registered under the GenBank accession numbers listed in the Appendix.

Results

The alignment of the 199 CR sequences (191 representatives of the genus *Corvus* and eight outgroup sequences) has a length of 704 bp (long fragment; LF). Tree calculations with the LF data set performed with NJ and BI algorithms resulted in the same major topology with one difference concerning the succession of basal splits. However, these nodes are poorly supported in both analyses. Figure 1 shows the NJ tree illustrating the relationships among species or groups of related species. The variation within the terminal groups is indicated by the triangle at the end of each branch representing the deepest split within each clade. The relationships among individuals are depicted in partial trees (Figs 2–4), which also include branch support values of all analyses. From several individuals only short sections of the CR (short fragment SF1 or SF2) could be obtained, three of them representing species

not present in the LF data set. To integrate this data, sequence similarities (especially informative synapomorphies) were inspected and, based on a NJ tree (not shown) calculated with this short alignment, individuals were assigned to clades obtained with the LF data set. Their tentative positions in the tree are indicated in the partial trees (Figs 2–4).

Clades within *Corvus*

The genus *Corvus* appears as a highly supported monophyletic group with respect to the five outgroup genera. Within *Corvus* seven major clades can be distinguished, six of which are highly supported. Whereas clades 1, 2, 3 and 5 contain only a few species or species pairs, clades 4, 6 and 7 are composed of more species. Here we will first describe the seven clades in general, their species composition and sister group relationships. More detailed descriptions of the relationships within the clades are presented together with taxonomic considerations in the discussion. Of several taxa of which LF sequences were obtained, additional individuals were analysed yielding short sequences (SF1) only. These sequences cluster with their conspecifics in the respective clades (Figs 2 and 3).

The basal split within *Corvus* separates the Palearctic species pair *C. monedula*/*C. dauuricus* (clade 1) from the rest (Fig. 2). The next split separates the African *C. capensis* (clade 2) from the remaining five clades, among which the relationships are not well supported. The weakly supported clade 3 consists of the Nearctic species *C. palmarum* and *C. ossifragus*, two quite distinct lineages that cluster with clade 4, but only with low support. *Corvus jamaicensis*, from which only a partial

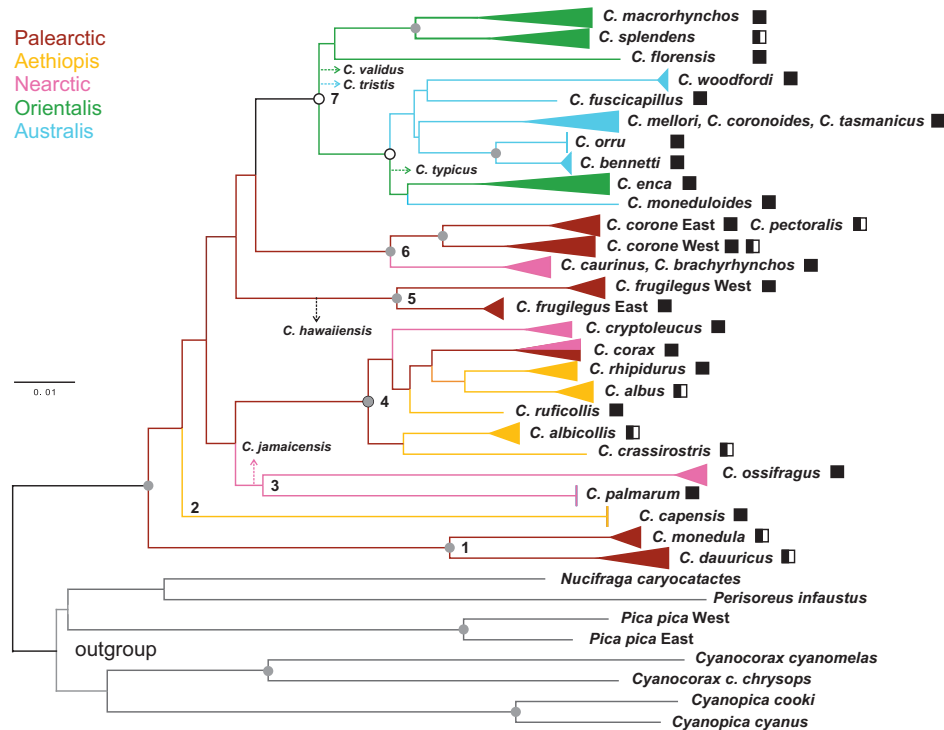


Fig. 1. Comprehensive tree (NJ) illustrating the major lineages of the genus *Corvus* and geographical occurrences. Terminal clades are depicted as triangles (illustrating the variation in clades consisting of >2 individuals) or vertical bars (2 individuals). These nodes obtained maximum support in all analyses. High node support (bootstrap value >90% and BI value 1.0) is indicated by grey dots. Two nodes with bootstrap value >70% and BI value 1.0 are indicated by white circles. For detailed support values of all analyses see Figs 2–4. Taxa with bicoloured (black and grey/white) visible plumage are indicated with bicoloured squares. Unicoloured black or dark brown taxa are indicated with black squares. Colours of terminal branches indicate geographical affiliation of taxa, while colouring of basal branches illustrate our hypothetical scenario of a Palearctic origin of the genus *Corvus*

Partial tree clades 1, 2, 3, 4

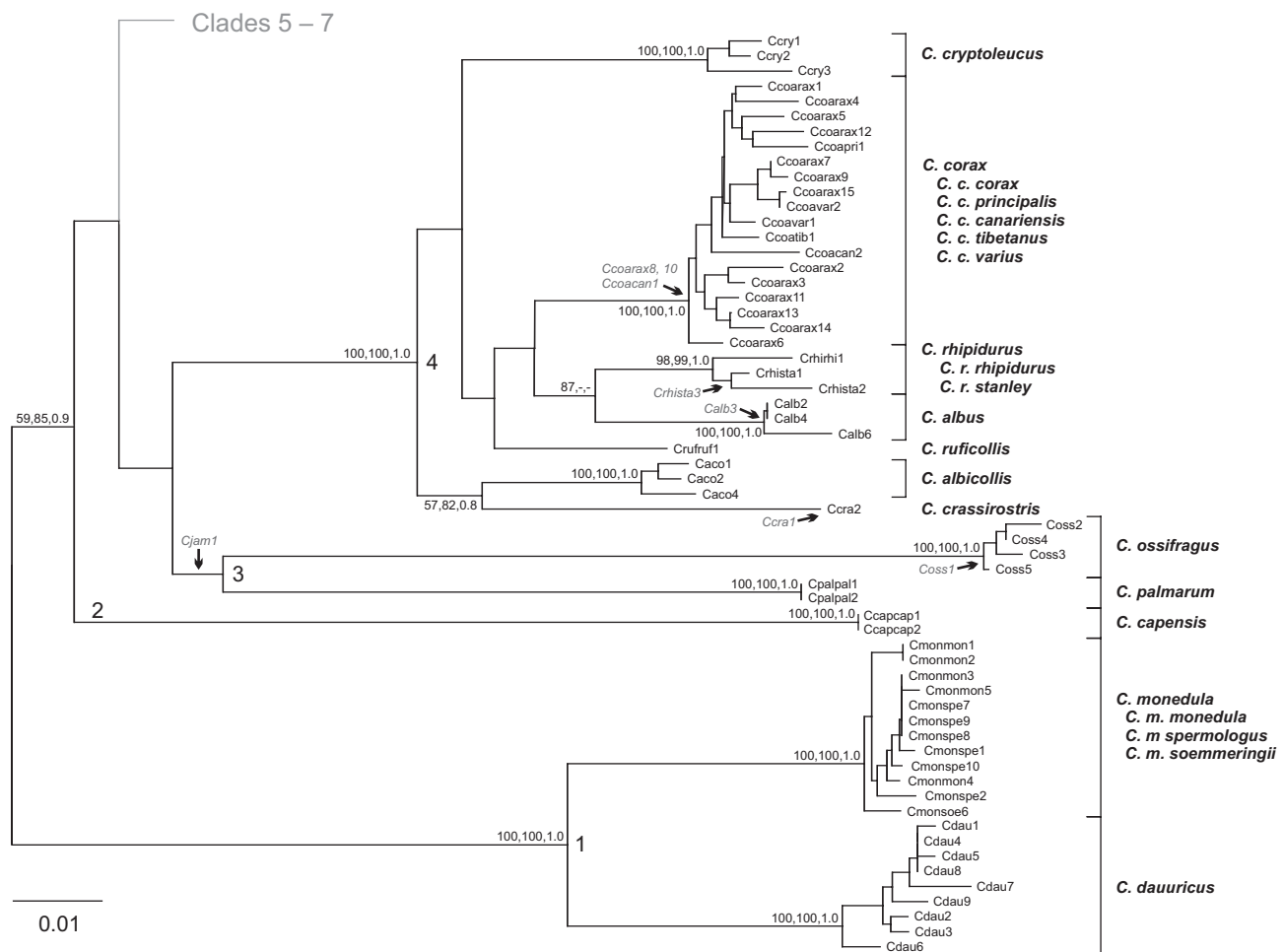


Fig. 2. Detailed view of clades 1, 2, 3 and 4. Node support values are given for NJ, MP, BI analyses at the major nodes (up to species level). Bootstrap values < 50% and BI values < 0.9 are not indicated. Individuals assigned to lineages according to short sequences are indicated with labcodes in italics and arrows

sequence of the 3'-end of the CR (SF2; 282 bp) could be analysed, clusters with *C. palmarum* and *C. ossifragus*, although with low support. Anyway, the sequences of the latter three species are quite distinct from all other lineages (average pairwise distances ranging from 11.2% to 15.2%) and their phylogenetic relationships remain unclear given the low node support. Clade 4 includes the African taxa *C. albus*, *C. rhipidurus*, *C. ruficollis*, *C. albicollis* and *C. crassirostris*, the Holarctic *C. corax* as well as the Nearctic *C. cryptoleucus*. Within *C. corax* the subspecies *C. c. tibetanus*, *C. c. principalis*, *C. c. varius* and *C. c. canariensis* are nested within the *C. c. corax* clade.

Clade 5 (Fig. 3) includes the two subspecies of *Corvus frugilegus* (the western *C. f. frugilegus* and the eastern *C. f. pastinator*). Clade 5 is the sister group of clades 6 + 7 in the NJ analysis, while in the BI tree it is the sister group of clades 3 + 4. However, the nodes defining the relationships between more basal branches are in general poorly supported in both the analyses. The Hawaiian *C. hawaiiensis* stands close to this clade according to the short sequence obtained from two individuals (SF1, approximate position indicated in Fig. 3).

Clade 6 is divided into two subclades. One comprises the Palearctic *C. corone/cornix* complex that is divided into two groups, as already known from our previous studies: one

(Clade West in Haring et al. 2007) includes five subspecies (*corone*, *cornix*, *sardonius*, *capellanus*, *orientalis*), while the other one (Clade East) includes only *C. c. orientalis*. Surprisingly, the East Palearctic species *Corvus pectoralis* is also part of this group and appears not differentiated. The second subclade of clade 6 consists of the Nearctic species *C. caurinus* and *Corvus bennetti* group together. With *Corvus enca* and *Corvus moneduloides* they form the second well-supported subclade of clade 7. Finally, *Corvus florensis* forms a separate lineage within clade 7. Its relationship to one of the two subclades has to be considered as unresolved. The three Australasian species *Corvus validus*, *Corvus tristis* and *Corvus typicus*, from which only a short sequence (SF1) could be determined, can be assigned to clade 7, which is in

Partial tree clades 5 and 6

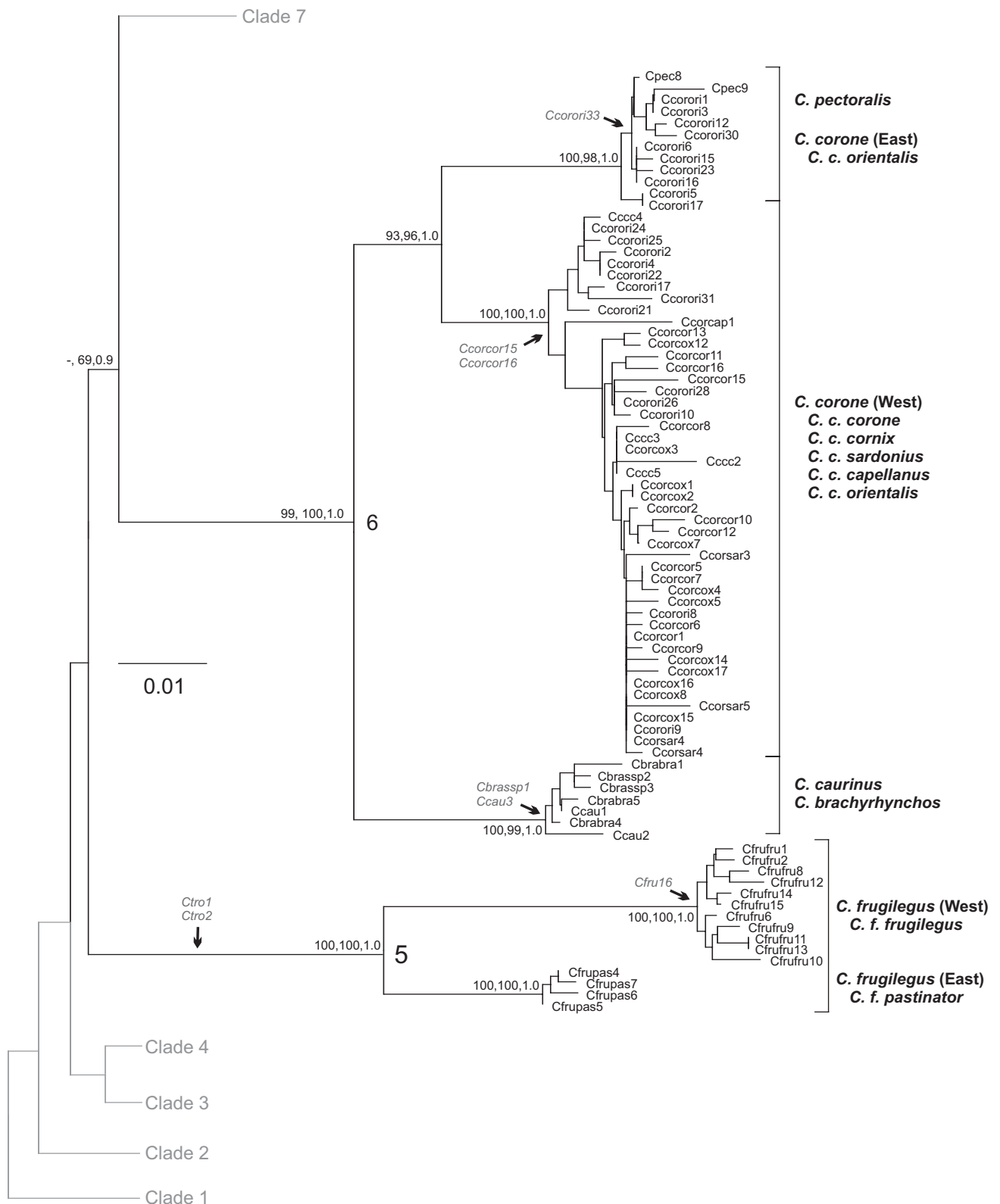


Fig. 3. Detailed view of clades 5 and 6. Node support values are given for NJ, MP, BI analyses at the major nodes (up to species level). Bootstrap values < 50% and BI values < 0.9 are not indicated. Individuals assigned to lineages according to short sequences are indicated with labcodes in italics and arrows

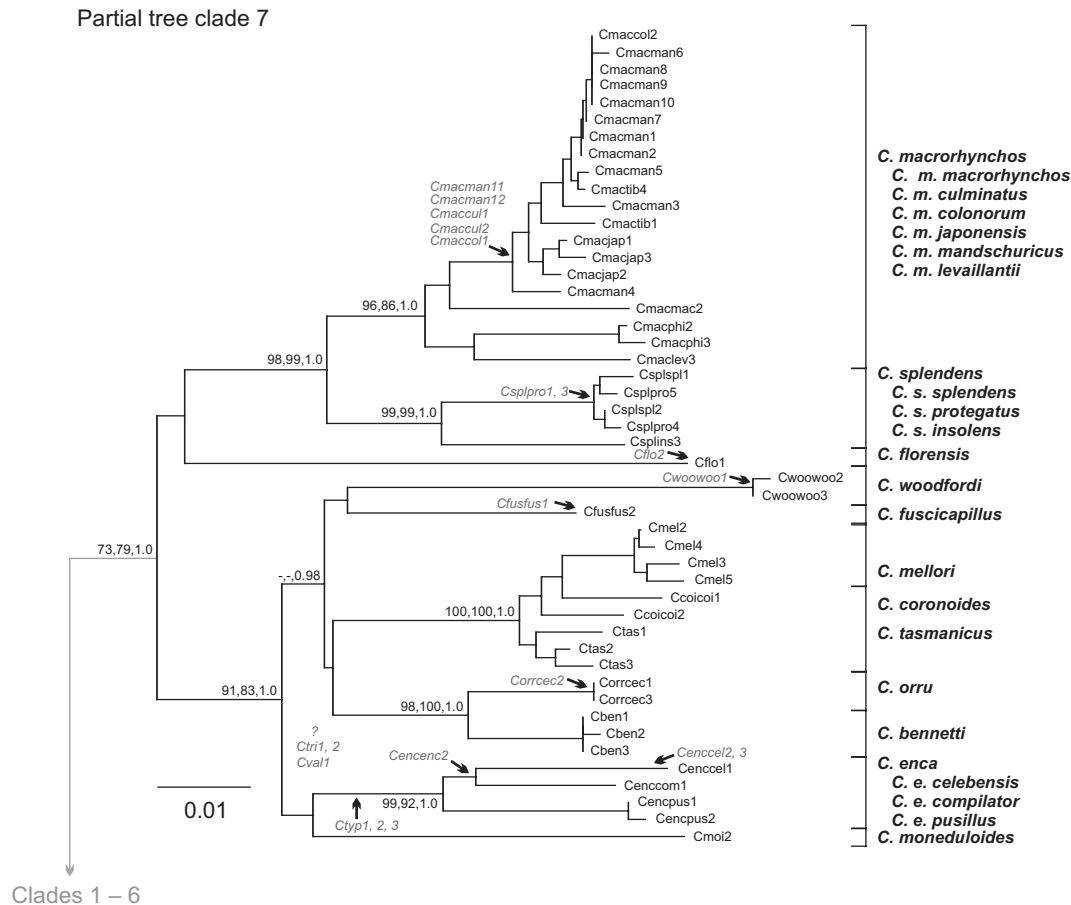


Fig. 4. Detailed view of clade 7. Node support values are given for NJ, MP, BI analyses at the major nodes (up to species level). Bootstrap values < 50% and BI values < 0.9 are not indicated. Individuals assigned to lineages according to short sequences are indicated with labels in italics and arrows

accordance with their geographical origin. Tentatively, *C. validus* and *C. tristis* appear related to the *C. enca/C. moneduloides* clade, while *C. typicus* appears even more closely related to *C. enca*.

Genetic distances

As becomes evident from the tree, ranges of distances between sister species and ranges of intraspecific pairwise distances are widely overlapping. The mean p distances between all species and the mean distances within species are listed in Table S1. (for *C. corone* and *C. frugilegus* distances were calculated separately for the groups West and East). For example, two of the clades are composed of two sister taxa: clade 1 with *C. monedula* and *C. dauuricus*, and clade 5 with the two taxa of *C. frugilegus*. The average pairwise distances between the two species *C. monedula* and *C. dauuricus* (5.8%) are in the same range as those between the two subspecies of *C. frugilegus* (4.8%). In contrast, the seven species in clade 4 are separated by average pairwise distances from 3.4% to 6.9% (with intraspecific distances ranging from 0.2% to 2.0%). Clade 7 is rather heterogeneous with very low interspecific distances, such as 1.7% (mean *C. coronoides/C. tasmanicus*) or 2% (mean *C. coronoides/C. mellori*), as well as very distantly related species (10.1% mean *C. moneduloides/C. splendens*). On the other hand, in some species the intraspecific distances are quite high, for example, up to 4.6% in *C. enca* (mean

3.0%), 4.1% in *C. macrorhynchos* (mean 1.4%) and 3.4% in *C. splendens* (mean 1.6%). Clade 6, finally, reveals discrepancies between taxonomy and genetic relationships. One subclade separated from the rest by approximately 5% contains *C. caurinus* and *C. brachyrhynchos* which are not differentiated in this mt sequence. In contrast, the two remaining subclades (separated by 4.0%) represent the western and eastern clades of *C. corone*, with the eastern one including also *C. pectoralis*. This species is not clearly differentiated from the Far Eastern *C. c. orientalis* individuals in this subclade. Thus, in this clade – due to the discrepancies between systematics and genetic affiliations – distance values ranging from 0.2% to 5.0% are found between as well as within species.

Discussion

The present investigation is the first attempt to establish a comprehensive view on genetic variation and phylogenetic relationships in the genus *Corvus*. We provide the first DNA-based tree that includes most of the currently described species (34 of 40). Although it still has to be considered as preliminary (because it is based on only one rather short mt marker sequence), it allows some cautious interpretations. The tree is in accordance with several formerly postulated hypotheses concerning the radiation and interrelationships in this group of birds, which were based on morphological, ecological and biogeographical considerations.

The monophyly of *Corvus* is more or less undisputed (Amadon 1944; Ericson et al. 2005), although it was not supported in the *cytochrome b* tree presented by Cibois and Pasquet (1999). This might have been due to substitutional saturation as most splits are probably too old to be well resolved by that marker sequence. Furthermore, the study of Cibois and Pasquet (1999) was intended to elucidate the intergeneric relationships within the family Corvidae and included only three members of the genus *Corvus*. The same is true for other previously performed molecular studies (e.g. Kryukov and Odati 2000; Kryukov and Suzuki 2000; Ericson et al. 2005). In our tree the genus *Corvus* is well represented and appears as a highly supported monophyletic group. However, it has to be admitted that the outgroup consists of only seven species (5 genera). Thus, a final conclusion about monophyly cannot yet be drawn.

Interestingly, the grouping within the genus *Corvus* as suggested by Jollie (1978), who combined morphological, ecological and parasitological data, corresponds quite well with the clades in our tree, although within the clades the taxon composition differs to some extent. Also the basal split of *C. monedula*/*C. dauuricus* within the genus *Corvus* has been postulated already by Goodwin (1976) and Jollie (1978) and is found with good bootstrap support in the tree of Ericson et al. (2005), although in that study the genus is represented by four species only.

Origin and radiation of the genus *Corvus*

The corvid family has its origin on the Australian continent (Sibley and Ahlquist 1990). When the climate gradually cooled after the mid-Miocene Climatic Optimum, this change in temperature was accompanied by aridification especially of all southern continents. It can be assumed that in this period the forest living ancestors of the corvids presumably started to adapt to drier habitats and spread over Southeast Asia where the first radiation may have occurred (Ericson et al. 2005). This adaptation continued after the corvids successively colonized the world resulting in the current almost ubiquitous distribution of this family.

In our tree (Fig. 1) the first major splits within *Corvus* define clades with Palearctic, African, Holarctic and Nearctic representatives. The taxa of the Orientalis and Australis are united in clade 7 and separated more recently from the Holarctic clade 6. This suggests that the genus *Corvus* originated in the Palearctic which is in accordance with Ericson et al. (2005), whereas clade 7 probably resulted from the invasion of a single lineage to the Orientalis and Australis regions. The radiation of this group obviously was accompanied in some lineages by adaptation to the humid conditions of rain forests. In contrast, the New World has most probably been colonized repeatedly as the Nearctic taxa appear as several separated branches in distinct clades. *Corvus palmarum*, *C. ossifragus* as well as *C. cryptoleucus* are located on quite separated branches in the tree (clades 3 and 4). The former two species (clade 3) are very distinct lineages, but their clustering is not well supported. Thus, the data available do not allow any conclusions whether these species arose from independent colonization events. The fact that *C. jamaicensis* (from which only a partial sequence of 282 bp could be analysed) clusters with the two species would favour a single invasion early in the *Corvus* radiation. For *C. cryptoleucus* it can be assumed that its ancestor arrived much later on the North American continent, and *C. corax*

probably has expanded its distribution range to the Nearctic quite recently, as the only Nearctic subspecies *C. c. principalis* falls within the intraspecific diversity of all subspecies. Another independent colonization of the Nearctic is that of the *C. caurinus*/*C. brachyrhynchus* lineage that forms the sister group of the Palearctic *C. corone*. Hybridization between *C. caurinus* and *C. brachyrhynchus* has led to the discussions whether the former is merely a subspecies of the other. Land conversion by humans has facilitated the westward spread of *C. brachyrhynchus* and increased the incidence of the hybridization with *C. caurinus* to that point that today genetically distinct *C. caurinus* do not exist (Marzluff and Angell 2005). Although our sample size was small, our results support these reports. *Corvus brachyrhynchus* in the field appears similar to *C. ossifragus*, *C. sinaloae* and *C. imperatus*, but the four species (of which we could analyse only two) can be distinguished easily by their voices (Marzluff and Angell 2005). In our tree *C. brachyrhynchus* and *C. ossifragus* belong to very distant clades and thus must originate from different colonization events.

The African continent has been colonized at least two times independently as indicated by the separated lineages of *C. capensis* and the species united in clade 4. Most probably, several offshoots of the stem species of clade 4 colonized Africa.

The assumption of a Palearctic origin of the genus *Corvus* might seem to be in conflict with the Bayes-DIVA tree published by Jönsson et al. (2011; Fig. 1). In this tree, the possible origins and their probabilities are given for the common ancestor of the genera *Corvus*, *Aphelocoma* and *Gymnorhinus*: America (<50%), Australia + New Guinea + New Zealand + Asia (>50%). However, an American origin is rather unlikely given the fact that in the tree of Jönsson et al. (2011) the next ancestral node of the three genera as well as the whole clade, in which they are embedded, is assigned exclusively to Australis or Asia. Anyway, the biogeographical scenario outlined here is still hypothetical and the Palearctic origin of the genus *Corvus* remains to be tested with longer (and nc) marker sequences.

Composition of main clades – biogeographical and taxonomic considerations

In the tree based on the complete sequences (Fig. 1) several distinct lineages not closely related to other taxa of the genus became apparent. They represent open habitat species that did not experience much diversification: clade 1 consists of the sister species *C. monedula*/*C. dauuricus*, 'clade 2' is formed by *C. capensis*, clade 3 (which is in fact a poorly supported clade and possibly represents two separate lineages) is composed of two species (*C. palmarum*, *C. ossifragus*) and clade 5 consists of a single species (*C. frugilegus*). The isolated positions of *C. monedula* and *C. frugilegus* have been postulated previously by Goodwin (1976). The distant lineages of *C. capensis*, *C. palmarum* and *C. ossifragus* suggest that the first colonizations of the Nearctic and the Aethiopia started already early in the radiation of the genus *Corvus*. The closer relationship of *C. hawaiiensis* and *C. frugilegus* as suggested by the short CR sequences has to be considered with caution. A preliminary genetic analysis by Fleischer and MacIntosh (dos Anjos et al. 2009) suggests that the former species might be more closely related to *C. corax* than to other *Corvus* species. However, in their study they included only a few species, thus these

relationships are rather vague. The isolated geographical range of *C. hawaiiensis* does not allow any assumption based on biogeographical considerations. Due to the short sequence length analysed the current results can only be taken as a weak hypothesis that should be further investigated. If this relationship is confirmed by further sequence data, this would provide a nice opportunity to calibrate a rough molecular clock based on the age of the Hawaiian archipelago.

Clades 1 and 5 are further subdivided into subclades separated by similar genetic distances that represent western and eastern populations, respectively. The two subclades represent either subspecies (*C. f. frugilegus/C. f. pastinator*) or sister species (*C. monedula/dauuricus*). These clades are examples of a phylogeographical pattern described in detail by Haring et al. (2007), characterized by two distinct mitochondrial lineages separated by genetic distances between approximately 4% and 6%. Such a pattern has also been found in *C. corone* (clade 4) as well as in some widely distributed Palearctic corvids (e.g. *P. pica*, used here as outgroup). Whether there is gene flow between the western and eastern groups in these taxa remains to be investigated. *Corvus corone* is of special interest as it has been a textbook example for populations with strikingly different plumage types that are separated by quite stable hybrid zones (Fig. 5). It has a continuous Palearctic distribution from western Europe to eastern Asia. The hybrid zone between the grey-black *C. c. cornix* (eastern Europe to Central Siberia) and the black *C. c. orientalis* (eastern Siberia) extends between the rivers Ob and Yenisey in western Siberia and is about 150 km in width (Kryukov and Blinov 1989; Blinov and Kryukov 1992). The European hybrid zone between the black *C. c. corone* (western Europe) and *C. c. cornix* (width between 30 and 100 km) extends from the Ligurian Apennines through the southern edge of the Alps and through central Europe north to Jutland as well as to southern Scotland (Meise 1928; Mayr 1942, 1963). Several studies indicate that this zone has been remarkably stable over the last century (Picozzi 1975; Oeser 1986; Brtek 1987; Saino and Vila 1992; Haas and Brodin 2005) or has moved only rather slowly and locally (Cook 1975; Picozzi 1975; Haas and Brodin 2005). Despite field observations indicating extensive hybridization within both zones, species status for *C. c. corone* and *C. c. cornix* was proposed (Knox

et al. 2002; Parkin et al. 2003; dos Anjos et al. 2009). Furthermore, Knox et al. (2002) considered to treat the eastern form as a separate species (*C. orientalis*). Stepanyan (2003) regarded them as two semispecies (*C. corone* with the two subspecies *corone* and *orientalis* and *C. cornix*). Arguments were mainly based on plumage colour, fitness estimations for juveniles and pair composition in the hybrid zone. Most checklists, however, still treat *C. corone* as a single species with up to six subspecies (Mayr and Greenway 1962; Cramp and Perrins 1994; Dickinson 2003): *C. c. corone*, *C. c. orientalis*, *C. c. cornix*, *C. c. sardonius*, *C. c. sharpii* and *C. c. capellanus*. The latter subspecies has also been considered as a separate species (Madge and Burn 1993).

So far, neither genetic nor morphometric analyses indicated a significant difference between *C. c. corone* and *C. c. cornix* (Glutz von Blotzheim and Bauer 1993; Kryukov and Suzuki 2000; Haring et al. 2007; Wolf et al. 2010). In an extensive analysis of nuclear introns Wolf et al. (2010) found no differentiation between *C. c. corone* and *C. c. cornix* at the DNA sequence level, confirming our results with mtDNA (Haring et al. 2007). Thus there is no indication for past isolation of *C. c. corone*, *C. c. cornix* or *C. c. orientalis*. Moreover, the mtDNA data showed that the division into mt clades is neither concordant with subspecific division nor with the plumage colour, the most conspicuous character of these birds. However, the two mt lineages show a clear geographic pattern. To illustrate this complicated pattern we show the distribution of subspecies (colour morphs) and haplogroups in Fig. 5. In this study for the first time specimens of *C. pectoralis* were included in a phylogenetic analysis. Interestingly, they cluster within the eastern clade of *C. c. corone*. Already Meinertzhagen (1926) suggested to consider the inclusion of *C. pectoralis* into *C. corone* (Goodwin 1976; Jollie 1978). The position of *C. pectoralis* in the tree has two consequences: (1) a taxonomic one, as *C. corone* is now paraphyletic, and (2) an interesting biological phenomenon: the occurrence of two colour morphs within one mt clade is now not only true for the western but also for the eastern clade. Given the fact that the two colour morphs do not correlate at all with mt clades and therefore do not provide any phylogenetic information, this trait should not be considered for species delimitation. Which interpretations are possible for this interesting pattern? A plausible explana-

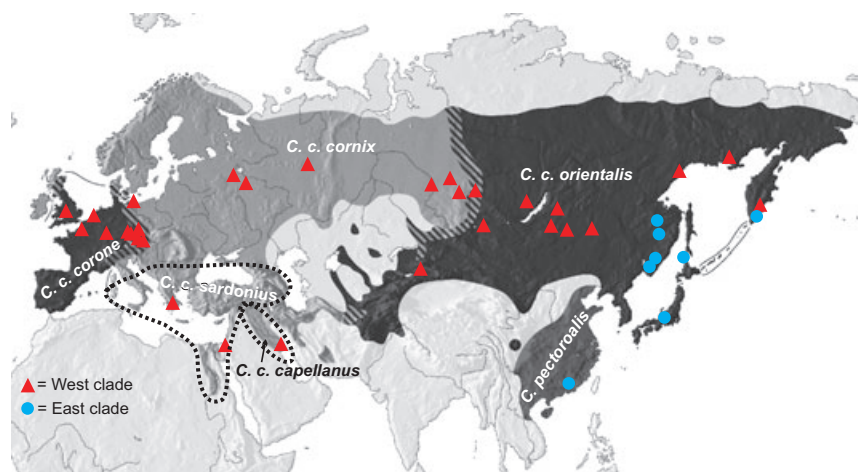


Fig. 5. Distribution ranges of the subspecies of *C. corone* and *C. pectoralis*. Ranges of additional subspecies recognized by Mayr and Greenway (1962) are indicated by dashed lines. Sample localities (present study and Haring et al. 2007) illustrate the distribution of haplogroups

tion is that the eastern clade in fact represents the original haplogroup of *C. pectoralis* which was captured by *C. c. orientalis* populations in the Russian Far East. It appears reasonable that these populations went through severe bottlenecks during glacial periods and possibly shifted their range even more to the south, where they could have come into contact with *C. pectoralis*. To clarify this question *C. pectoralis* should be analysed throughout its distribution range and both taxa should be compared with nuclear and mt markers. Whether similar explanations could serve for the enigmatic pattern of colour morphs in the rest of the distribution range of *C. corone* remains to be investigated, although for these subspecies the scenarios appear even more complicated. Anyway, despite the fact that hybrid zones have been investigated intensively in the past, the results raise the question (analogous to *C. frugilegus* and *C. monedula/C. dauricus*) whether representatives of the two clades interbreed, which could only be investigated in their contact zones, for example, on Sakhalin Island.

The weakly supported clade 3 consists of the Nearctic species *C. palmarum* and *C. ossifragus*, two quite distinct lineages that cluster with clade 4 but only with low support. The composition of clade 4, which includes all African taxa except *C. capensis*, is interesting from a biogeographical point of view. It includes also the Nearctic *C. cryptoleucus*, a relationship that was already found by Omland et al. (2000). The Holarctic *C. corax* appears as a younger branch of a clade composed of African and Nearctic species. Our finding that the various subspecies of *C. corax* do not cluster according to their taxonomy is in accordance with assumptions of Vaurie (1958) based on morphological data, although it has to be considered, that the sequences used in our study are quite short. Omland et al. (2000) reported that *C. corax* is paraphyletic as individuals from California (Californian clade) form the sister group of *C. cryptoleucus*. Moreover, in the tree presented by Feldman and Omland (2005) *C. albus* is even closer to the main (Holarctic) clade of *C. corax*. A possible explanation besides ancient hybridization resulting in mitochondrial capture is incomplete lineage sorting (Omland et al. 2006). Another possibility is that the Californian *C. corax* may represent a cryptic species. Because we have no samples from this region our data cannot contribute to this question. But the close relationship between *C. cryptoleucus* and the Californian *C. corax* fits well into a plausible phylogeographical scenario for this group: A widely distributed Palearctic stem species (like *C. corax* today) repeatedly colonized the Aethiopia and Nearctic in the past, where the various species subsequently split off and evolved triggered by isolation and adaptation. Another interesting finding is that in the tree of Baker and Omland (2006) *C. corax tingitanus* (= *C. corax canariensis* after Dickinson 2003) appears as a distinct haplogroup. However, in our study, individuals of *C. c. canariensis* from the same island (Fuerteventura) cluster close to the Holarctic clade. Further research is needed to clarify the relationships of this taxon.

Clade 7 (Australasia) is the second species-rich group in the tree. One highly supported group within clade 7 comprises *C. macrorhynchos* and *C. splendens* (*macrorhynchos*-complex). *Corvus macrorhynchos* is, like *C. corone*, a widely distributed species ranging from the Russian Far East to the Indonesian Islands and from the Himalayas to Japan. Not surprisingly, it has been subdivided into 11 subspecies (after Dickinson 2003; Dickinson et al. 2004). The higher intraspecific differentiation revealed by RAPD-PCR within *C. macrorhynchos* (Spiridonov

et al. 2003) does not appear in our data. It can be assumed that *C. macrorhynchos* originated in the rainforests of the south-east Asian tropics. Compared to a species adapted to semi-open habitats like *C. corone* the habitat requirements of *C. macrorhynchos* might favour the intraspecific differentiation. In the subspecies *C. m. levaillantii* and *C. m. japonensis* from the southern slopes of the Himalayas acoustic differences with taxonomic relevance indicate that they represent in fact distinct biospecies (*C. levaillantii* and *C. japonensis*). Discriminant analysis of call structure completely separated them, a finding consistent with morphological, ecological and parasitological data (Klockenhoff 1969; Martens et al. 2000). More detailed discussions of the intraspecific taxonomy including all subspecies are found in Dickinson et al. (2004), who gives a detailed review of up to seven proposed species, including further potential splits as proposed by various authors (Martens et al. 2000; Rasmussen and Anderton 2005; Brazil 2009; BirdLife International 2011).

Implementing all suggested species splits would result in the following species besides *C. macrorhynchos* (monotypic): *C. japonensis* (monotypic), *C. osai* (including *connectens*), *C. intermedius* (including *mandschuricus*, *colonorum*, *tibetosinensis*), *C. culminatus* (monotypic), *C. levaillantii* (monotypic) and *C. philippinus* (monotypic).

Among the subspecies included in our tree *C. m. philippinus* and *C. m. macrorhynchos* appear as separated lineages, while *C. m. japonensis* nests in a subclade comprising *C. m. mandschuricus*, *C. m. colonorum* and *C. m. tibetosinensis* (and according to the SF1 sequence also *C. m. culminatus*). From the three individuals of *C. m. levaillantii* available for extraction only one yielded a PCR product (Cmaclev-3). The separated position of this haplotype might support the proposed species status of *C. levaillantii*. Altogether the current data from the eight subspecies included suggest a rough geographical differentiation in (1) Indian subcontinent (*C. m. levaillantii*), (2) Malayan Peninsula and Lesser Sunda Islands (*C. m. macrorhynchos*), (3) the Philippines (*C. m. philippinus*) and (4) the region north of these three ranges (*C. m. japonensis*, *C. m. mandschuricus*, *C. m. colonorum*, *C. m. tibetosinensis* and *C. m. culminatus*).

The sister clade of *C. macrorhynchos* is *C. splendens*, which is subdivided into two lineages separated by a genetic distance (3.4%) similar to that found between the most distant lineages within *C. macrorhynchos* (3.0–4.1%). One lineage represents *C. s. insolens* (Csplins-3 from Myanmar), while the nominate form *C. s. splendens* (Singapore, probably introduced from India) and *C. s. protegatus* (Sri Lanka) are not genetically differentiated. Considering the rather small sample size and the fact that two subspecies (*C. s. zugmayeri*, *C. s. maledivicus*) are not represented in our data set a taxonomic evaluation is not possible. Interestingly, the clades of *C. macrorhynchos* and *C. splendens* share roughly the same coalescences time. Moreover, it seems that the two clades separated in the period when major radiations took place in several other clades. Lacking a reliable calibration a molecular clock analysis is not reasonable. Nevertheless, genetic distances of approximately 6% suggest that these radiations are quite old. Presumably they date to the Pliocene climate change that finally led to the Pleistocene glaciations.

In our tree *C. florensis* forms a quite distinct lineage not closely related to any of the two subclades of clade 7. Its clustering with the *macrorhynchos* complex is not well supported and the branching topology must be considered as a trichotomy, but the tentative association of this species

confirms earlier assumptions of several authors who postulated *C. florensis* as an ancient derivative of the *C. enca*-complex or as a close relative of *C. typicus* and *C. unicolor* (Stresemann 1940; Vaurie 1958; Goodwin 1976; Jollie 1978; dos Anjos et al. 2009). In our material we had no samples of *C. unicolor*, but the short sequences of three individuals of *C. typicus* appear more closely related to *C. enca*.

The second highly supported subclade of clade 7 comprises the Southeast Asian *C. enca* as well as taxa from the Australian region. Although we could include only four of the eight subspecies of *C. enca*, the picture is similar to that found in *C. macrorhynchos*. The three subspecies *C. e. celebensis* (Sulawesi), *C. e. compilator* (Malaysia and Greater Sundas) and *C. e. pusillus* (Philippines) are clearly differentiated. Based on morphological differences some subspecies have been raised to species status in the past (*C. pusillus*: Stresemann 1943; *C. violaceus*, not included in the present study: Oortwijn 1987). The nominate form *C. e. enca* is represented by one short sequence only which clusters closely with the other subspecies. The information content of this short section is, however, too low to draw further conclusions about intraspecific relationships. Obviously a high cryptic genetic diversity exists in these widespread southeast Asian crows, as has been reported from other species in this region indicating that avian endemism is gravely underestimated (Lohmann et al. 2010).

The Australian crows are a difficult group disputed among lumpers (Vaurie 1958) and splitters (Dickinson 2003; dos Anjos et al. 2009). Among the seven species from the Australian region included in our study almost all (*C. woodfordi*, *C. fuscicapillus*, *C. mellori*, *C. orru*, *C. bennetti* and *C. moneduloides*) represent distinct clades. *Corvus coronoides* and *C. tasmanicus* are not clearly differentiated which questions their species status. Thus, our data support the earlier assumption (Vaurie 1954) that these taxa may be conspecific. A close similarity in vocalization and reproductive biology has been observed in these two taxa by Secomb (2005). Moreover, *C. coronoides* is paraphyletic as *C. mellori* is nested within this clade, but this position may be a consequence of the short marker sequence. Anyway, the data confirm the postulated close relationships among these species (R. Schodde in Sibley and Ahlquist 1990).

Corvus moneduloides from New Caledonia, famous for its tool-using abilities, appears as a separated branch in the clade. Except this species (the relationships of *C. moneduloides* are not clearly resolved) the Australian taxa form one clade, which is in accordance with the assumption of a single colonization of the region. *Corvus moneduloides* could represent an early offshoot of this radiation, although it might also stem from an independent colonization. Still these considerations are preliminary as for some species of the Australian regions data are still missing or insufficient. According to the short sequence *C. validus* and *C. tristis* stand close to the lineage *C. moneduloides/C. enca*, while *C. typicus* shows even more similarity with *C. enca*. Again, these results have to be taken with severe caution, as the information content of this short sequence is quite low. *Corvus validus* is restricted to the northern Moluccas, where it overlaps with *C. orru*, the only Australian species that is distributed also outside Australia. This is in concordance with the assumptions of Meinertzhagen (1926) and Vaurie (1954). The pale eyes of *C. validus* suggest an affinity with the Australian white-eyed crows and ravens. Another assumption is that it is more closely related to *C. enca* (dos Anjos et al. 2009), which is not supported by our preliminary

data. The phylogenetic position of the island endemic *C. kubaryi* (not included in this study), which might be expected within the Australasian clade, remains an open question. The species was included in the tree published by Omland et al. (2000). In that study it formed the sister group of *C. brachyrhynchos*, but the two species appeared only distantly related and the tree contained only a very limited set of taxa. Unfortunately, the 310 bp section of the CR used in that study does not overlap with the marker sequence used in the present analysis, and therefore this sequence cannot be included into our data set.

Considering the genetic diversity observed in the various clades, it is interesting to compare the taxonomic state of lineages, for example, within clade 7 there is a group of seven closely related Australian species. Their interspecific distances (1.3–7.0%) are in the same range as the maximum values within some single species in other clades (*C. macrorhynchos*: 4.1%, *C. enca*: 4.6%, *C. splendens*: 5.9%, *C. corone*: 5.1%). Furthermore, some of the described species are hardly or not at all genetically differentiated (in our marker sequence): *C. mellori/C. coronoides/C. tasmanicus*, *C. caurinus/C. brachyrhynchos*, *C. c. orientalis/C. pectoralis*. These results underline the fact that the variation occurring between species and subspecies may overlap considerably. As Fregin et al. (2012) emphasized, there is no clear threshold at a certain genetic distance that could be used to delimitate species. Besides these considerations about genetic distances plumage colouration may influence taxonomic decisions. Bicoloured forms are in general more likely to be accepted as distinct species separated from their black relatives. Within the genus *Corvus* this was certainly the case. Among the seven species of the genus *Corvus* that formerly had been assigned to other genera – *C. monedula*, *C. dauuricus* formerly assigned to the genus *Coloelus*, *C. florensis* and *C. typicus* to *Nesocorax*, *C. albicollis* and *C. crassirostris* to *Corvultur*, and *C. rhipidurus* to *Rhinocorax* (Amadon 1944) – only two are black: *C. florensis* and *C. rhipidurus*.

Colour traits

Most clades in the tree of the genus *Corvus* contain both black and bicoloured representatives (Fig. 1). In North America and Australia no species with bicoloured plumage occur, whereas almost all African species south of the Sahara show a bicoloured pattern. In 10 (*C. monedula*, *C. dauuricus*, *C. splendens*, *C. tristis*, *C. typicus*, *C. corone*, *C. pectoralis*, *C. albus*, *C. albicollis* and *C. crassirostris*) of 40 species bicoloured plumage occurs, two of them (*C. albicollis*, *C. crassirostris*) possess also a white-tipped beak. In addition, two unicoloured species have white areas on their beaks (*C. woodfordi* and *C. fuscicapillus*).

Besides the visible part of the plumage, the proximal parts of the feathers are brightened in some species. While in some cases the colour traits reflect phylogenetic relationships, there are several examples of parallelism, for example, in the three closely related black species (*C. coronoides*, *C. mellori* and *C. tasmanicus*) the proximal part of the feather is grey, and in the black sister species *C. orru* and *C. bennetti* it is white. Among the Nearctic species *C. palmarum* and *C. jamaicensis* possess grey proximal feather parts but in *C. nasicus*, *C. leucognaphalus* and *C. cryptoleucus* they are white.

While the majority of the species has black eyes, 10 species possess more or less white eyes (*C. monedula*, *C. validus*, *C. woodfordi*, *C. fuscicapillus*, *C. tristis*, *C. insularis*, *C. orru*,

C. bennetti, *C. coronoides* and *C. mellori*). Ten of them constitute the Australian clade suggesting that this trait may have arisen in their common ancestor. However, variation in eye colour is already present in the *C. monedula*/*C. dauuricus* clade. The same is true for bicoloured plumage, but this trait obviously arose many times independently in the genus *Corvus*, even in closely related taxa.

Conclusion

The first insights into the phylogenetic relationships of the genus *Corvus* presented here, although preliminary and still leaving several open questions, can be interpreted quite reasonably from a biogeographical point of view. We favour a scenario assuming that the genus *Corvus* originated in the Palearctic from where various lineages radiated to the other continents. The spread to the Nearctic and Aethiopia probably occurred several times independently, while the south-east Asian region and the Australis most probably were colonized only once, which to some extent might have been accompanied by adaptation to tropical rain forests. Concerning colour traits in the genus *Corvus* the distribution of bicoloured forms among taxa suggests that these traits should be used as phylogenetic characters only with great caution. Especially plumage colour and pattern could be misleading if it is employed for tracing relationships.

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Zusammenfassung

Genetische Divergenz und innerartliche Variation in Corviden der Gattung Corvus – eine erste Bestandsaufnahme auf Basis von Museumsexemplaren

Der erste umfassende Überblick über die inner- und zwischenartliche Variation innerhalb der Gattung *Corvus* sowie erste Einblicke in die phylogenetischen Verwandtschaftsbeziehungen der Arten werden präsentiert. DNA Sequenzen der mitochondrialen Kontrollregion wurden von 34 der 40 beschriebenen Arten (unter Einbeziehung der Unterarten: 56 Taxa) extrahiert. Da in der Arbeit hauptsächlich Museumsmaterial verwendet wurde, konnte von einigen Exemplaren die Markersequenz nicht in voller Länge erhalten werden. In diesen

Fällen konnte nur eine kurze Teilsequenz der Kontrollregion analysiert werden. Nichtsdestotrotz konnten auch diese Individuen zumindest ungefähr den Clades zugeordnet werden, die sich auf Basis der kompletten Markersequenz ergaben. Die Einbeziehung von Sequenzen anderer Corviden-Gattungen aus der GenBank bestätigten die Monophylie der Gattung *Corvus*. Innerhalb des *Corvus*-Clades sind mehrere differenzierte Subclades erkennbar. Manche repräsentieren Stammlinien einzelner Arten oder Artenpaare, während andere Clades mehrere Arten umfassen. Generell spiegelt die Zusammensetzung der Clades die geografische Zusammengehörigkeit wider und bestätigt frühere Vermutungen über einen paläarktischen Ursprung der Gattung *Corvus* mit mehreren unabhängigen Kolonisationen der Nearktis und der Äthiopis. Die australasiatische Radiation scheint hingegen von einer einzigen Linie abzustammen. Die Verteilung der Gefiederfärbung im phylogenetischen Stammbaum deutet darauf hin, dass die hellen Markierungen mehrmals unabhängig entstanden sind. Das weiß/graue Muster im Gefieder – welches auch in anderen Gattungen der Familie der Corviden zu finden ist – tritt bereits in dem Artenpaar auf, welches die erste Aufspaltung innerhalb der Gattung *Corvus* (*Corvus monedula*, *Corvus dauuricus*) repräsentiert. Somit scheint eine Merkmalsumkehr zur komplett schwarzen Färbung ebenfalls stattgefunden zu haben. Die Verwendung von Farbmerkmalen als phylogenetischer Marker in der Gattung *Corvus* sollte daher mit großem Vorbehalt betrachtet werden.

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Supporting Information

Additional supporting Information may be found in the online version of this article:

Table S1. P distances of CR sequences (LF) between species/clades. coW, *C. corone* West; coE, *C. corone* East; br/ca, *C. brachyrhynchus/C. caurinus*; mac, *C. macrorhynchus*; spl, *C. splendens*; flo, *C. florensis*; woo, *C. woodfordi*; fus, *C. fuscicapillus*; mel, *C. mellori*; coi, *C. coronoides*; tas, *C. tasmanicus*; orr, *C. orru*; ben, *C. bennetti*; enc, *C. enca*; moi,

C. moneduloides; frW, *C. frugilegus* West; frE, *C. frugilegus* East; cry, *C. cryptoleucus*; coa, *C. corax*; rhi, *C. rhipidurus*; alb, *C. albus*; rfc, *C. ruficollis*; aco, *C. albicollis*; cra, *C. crassirostris*; cap, *C. capensis*; oss, *C. ossifragus*; pal, *C. palmarum*; mon, *C. monedula*; dau, *C. dauuricus*.

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Appendix: Specimens included in the analysis

Taxon/Code	Geographical origin	Coll./Vouch. No.	T	S	Acc. No.
<i>Corvus albicollis</i> Latham, 1790					
Caco-1	Captivity	NMW 88.581	p	LF	JQ900712
Caco-2	Captivity	NMW 88.582	p	LF	JQ900713
Caco-4	DR Congo, Kivu	NMW FC 904	f	LF	JQ900714
<i>Corvus albus</i> Statius Müller, 1776					
Calb-2	Kenya, Nairobi		f	LF	JQ900708
Calb-3	Gulf of Guinea	NMW 35.440	p	SF1	JQ900725
Calb-4	Uganda	NMW 34.937	p	LF	JQ900709
Calb-6	DR Congo	NMW FC 395	f	LF	JQ900710
<i>Corvus bennetti</i> North, 1901					
Cben-1	Australia, NT, Alice Springs	NMW 75.232	p	LF	JQ900691
Cben-2	Australia, NT, Alice Springs	NMW 75.231	p	LF	JQ900692
Cben-3	Australia, NSW, White Cliffs	NMW, FC 201	f	LF	JQ900693
<i>Corvus brachyrhynchus brachyrhynchus</i> C. L. Brehm, 1822					
Cbrabra-1	USA, ID, Rush County	NMW 72.870	p	LF	JQ900644
Cbrabra-4	USA, KS, Overland Park	KU 4389	m	LF	JQ900645
Cbrabra-5	USA, KS, Leawood	KU 4391	m	LF	JQ900646
<i>Corvus brachyrhynchus ssp.</i> C. L. Brehm, 1822					
Cbrassp-1	North America	NMW 70.392	p	SF1	JQ900726
Cbrassp-2	USA, MO, St. Louis		f	LF	JQ900647
Cbrassp-3	USA, MO, St. Louis		f	LF	JQ900648
<i>Corvus capensis capensis</i> M. H. C. Lichtenstein, 1823					
Ccapcap-1	South Africa, Transvaal	NMW 77.795	p	LF	JQ900716
Ccapcap-2	South Africa, Natal, Ladysmith	NMW 77.796	p	LF	JQ900717
<i>Corvus caurinus</i> S. F. Baird, 1858					
Ccau-1	USA, WA, Seattle	ZMMU RYA082	l	LF	JQ900649
Ccau-2	USA, WA, Seattle	ZMMU RYA083	l	LF	JQ900650
Ccau-3	Canada, Vancouver I., Kildonan	NMW 76.119	p	SF1	JQ900727
<i>Corvus crassirostris</i> Rüppell, 1836					
Ccra-1	Ethiopia	NMW 167	p	SF1	JQ900728
Ccra-2	Ethiopia, Ambo	Phyl. Mus. Jena 7561	p	LF	JQ900715
<i>Corvus corax corax</i> Linnaeus, 1758					
Ccoarax-1	Russia, Khabarovsk reg., Ayan	AK 0276	m	LF	EU070825
Ccoarax-2	Russia, Smolensk reg.	ZMMU LVE55	m	LF	EU070826
Ccoarax-3	Russia, Moscow reg.	ZMMU LVE59	m	LF	EU070827
Ccoarax-4	Russia, Kirov	ZMMU SVD2400	m	LF	EU070828
Ccoarax-5	Russia, Chita reg.		m	LF	EU070829
Ccoarax-6	Spain, Mallorca		f	LF	EU070830
Ccoarax-7	Austria, Steyr	NMW 87.417	p	LF	EU070831
Ccoarax-8	Romania, Rastolita	NMW 76.484	p	SF1	EU070764
Ccoarax-9	Estonia, SW Tartu		f	LF	EU070832
Ccoarax-10	Spain, Linares	Phyl. Mus. Jena 7556	p	SF1	EU070765
Ccoarax-11	Sweden, Östersund	Phyl. Mus. Jena 7558	p	LF	EU070833
Ccoarax-12	Belarus, Beloozersk		m	LF	EU070834
Ccoarax-13	Austria, Rax Mt.		f	LF	JQ900702
Ccoarax-14	Austria, Rax Mt.		f	LF	JQ900703
Ccoarax-15	Austria, Großglockner Mt.		f	LF	JQ900704
<i>Corvus corax canariensis</i> E. O. J. Hartert & O. Kleinschmidt, 1901					
Ccoacan-1	Spain, Canary Is., Fuerteventura	NMW 63.837	p	SF1	EU070766
Ccoacan-2	Spain, Canary Is., Fuerteventura		f	LF	EU070837

Appendix: (Continued)

Taxon/Code	Geographical origin	Coll./Vouch. No.	T	S	Acc. No.
<i>Corvus corax principalis</i> Ridgway, 1887					
Ccorpri-1	Canada, Ontario, Moosonee	NMW 73.200	p	LF	EU070835
<i>Corvus corax tibetanus</i> Hodgson, 1849					
Ccoatib-1	China, Tibet, Ladakh	ZFMK F.VII.3.g8.b	p	LF	EU070839
<i>Corvus corax varius</i> Brünnich, 1764					
Ccoavar-1	Iceland, Kjós	NMW 88.372	p	LF	EU070836
Ccoavar-2	Faroe Is., Nólsoy	ZFMK 53.7	p	LF	EU070837
<i>Corvus corone corone</i> Linnaeus, 1758					
Ccorcor-1	Austria, Gars/Kamp		m	LF	EU070774
Ccorcor-2	France, Paris	AK 3356	l	LF	EU070775
Ccorcor-5	Austria, Unterwolfen	NMW 82.612	f	LF	EU070776
Ccorcor-6	France, Paris	AK 3354	m	LF	EU070777
Ccorcor-7	the Netherlands, Leiden		f	LF	EU070778
Ccorcor-8	the Netherlands, Leiden		f	LF	EU070779
Ccorcor-9	the Netherlands, Leiden		f	LF	EU070773
Ccorcor-10	Austria, Öblarn		f	LF	EU070780
Ccorcor-11	Austria, Öblarn		f	LF	EU070781
Ccorcor-12	Germany, Rostock		f	LF	EU070782
Ccorcor-13	Great Britain, Glastonbury		f	LF	EU070783
Ccorcor-14	France, Strasbourg		f	LF	EU070784
Ccorcor-15	Austria, Mühlbach-Garsten	NMW 74.245	s	LF	JQ900637
Ccorcor-16	Belgium, Tervuren		f	LF	JQ900638
<i>Corvus corone capellanus</i> P. L. Sclater, 1877					
Ccorcap-1	Iraq, N Amara	ZFMK 65.1203	p	LF	EU070818
<i>Corvus corone cornix</i> Linnaeus, 1758					
Ccorcox-1	Russia, Moscow	AK 0101	l	LF	EU070785
Ccorcox-2	Russia, Novosibirsk	AK 327	l	LF	EU070786
Ccorcox-3	Russia, Kirov	AK 0164	l	LF	EU070787
Ccorcox-4	Austria, Schönherrn		m	LF	EU070788
Ccorcox-5	Russia, Moscow	AK 0304	m	LF	EU070789
Ccorcox-6	Russia, Moscow	AK 0308	m	LF	EU070790
Ccorcox-7	Russia, Moscow	AK 0312	m	LF	EU070791
Ccorcox-8	Russia, Ivanovo reg.	AK 0213	l	LF	EU070792
Ccorcox-12	Russia, Moscow	AK 715	m	LF	EU070793
Ccorcox-15	Russia, Novosibirsk	AK 303	l	LF	EU070794
Ccorcox-16	Austria, Vienna		f	LF	JQ900640
Ccorcox-17	Austria, Hallein	NMW 63.851	p	LF	JQ900641
Hybrid <i>Corvus corone corone</i> x <i>Corvus corone cornix</i>					
Cccc-2	Austria, Vienna, Hadersdorf		f	LF	JQ900639
Cccc-5	Austria, Vienna, Hadersdorf		f	LF	EU070822
Ccco-3	Russia, Kemerovo reg.	AK 307	d	LF	EU070823
Ccco-4	Russia, Kemerovo reg.	AK 312	d	LF	EU070824
<i>Corvus corone orientalis</i> Eversmann, 1841					
Ccorori-1	Russia, Kamchatka, Pinachevo	AK 0154	m	LF	EU070795
Ccorori-2	Russia, Kamchatka, Pinachevo	AK 0155	m	LF	EU070796
Ccorori-3	Russia, Kamchatka, Pinachevo	AK 0156	m	LF	EU070797
Ccorori-4	Russia, N Sakhalin, Oha	AK 732	m	LF	EU070798
Ccorori-5	Russia, Primorje reg.	AK 602	m	LF	EU070799
Ccorori-6	Russia, S Sakhalin	AK 811	m	LF	EU070800
Ccorori-7	Russia, Krasnojarsk	AK 325	m	LF	EU070801
Ccorori-8	Russia, Tuva	AK 0103	m	LF	EU070802
Ccorori-9	Russia, Chongeo-Nur		f	LF	EU070803
Ccorori-10	Russia, Chongeo-Nur		f	LF	EU070804
Ccorori-12	Russia, Khabarovsk reg., Solnechny	AK 0288	m	LF	EU070805
Ccorori-15	Russia, Khabarovsk reg., Evoron L.	AK 0244	m	LF	EU070806
Ccorori-16	Russia, Khabarovsk reg., Evoron L.	AK 0245	m	LF	EU070807
Ccorori-17	Russia, Primorye region	AK 601	m	LF	EU070808
Ccorori-21	Kyrgyzstan, Issyk Kul L.	MAR1852, AK 922	b	LF	EU070809
Ccorori-22	Russia, Magadan	AK 0417	m	LF	EU070810
Ccorori-23	Russia, S Sakhalin	ZMMU, RYA1050	m	LF	EU070811
Ccorori-24	Russia, Russia, Chita reg.		m	LF	EU070812
Ccorori-25	Russia, Baikal Lake, Olkhon I.		f	LF	EU070813
Ccorori-26	Russia, Chita region, Kira		f	LF	EU070814
Ccorori-28	Russia, Chita region, Kira		f	LF	EU070815
Ccorori-30	Japan, Tokyo		m	LF	EU070816
Ccorori-31	Russia, Buriatia, W Chorinsk		m	LF	EU070817

Appendix: (Continued)

Taxon/Code	Geographical origin	Coll./Vouch. No.	T	S	Acc. No.
Ccorori-33	North Korea, Prov. S Phjongan	ZMB, not catalogued	p	SF1	JQ900729
<i>Corvus corone sardonius</i>	Kleinschmidt, 1903				
Ccorsar-3	Greece, Pilion, Ag. Ioannis		f	LF	EU070819
Ccorsar-4	Israel, Haifa	NMW 76681	p	LF	EU070820
Ccorsar-5	Greece, Volos		f	LF	EU070821
<i>Corvus coronoides coronoides</i>	Vigors & Horsfield, 1827				
Ccoicoi-1	Australia, ACT, Canberra	NMW 75.236	p	LF	JQ900684
Ccoicoi-2	Australia, ACT	NMW 75.237	p	LF	JQ900685
<i>Corvus cryptoleucus</i>	Coch, 1854				
Ccry-1	USA, NM, Hobbs	AMNH PRS 1528	m	LF	JQ900699
Ccry-2	USA, TX, Laredo	LSU B-37376	m	LF	JQ900700
Ccry-3	USA, TX, Laredo	LSU B-37377	m	LF	JQ900701
<i>Corvus dauuricus</i>	Pallas, 1776				
Cdau-1	Russia, Dauria, Koonkoo		m	LF	EU070867
Cdau-2	Russia, Primorye reg.	AK 917	l	LF	EU070868
Cdau-3	Russia, Primorye reg., Gaivoron	ZMMU EAK 034	l	LF	EU070869
Cdau-4	Russia, Primorye reg., Gaivoron	ZMMU EAK 039	l	LF	EU070870
Cdau-5	China, Gansu, Hoi-Syan Mt.	ZMMU 90686	p	LF	EU070871
Cdau-6	Russia, Chita, Batakan		m	LF	EU070872
Cdau-7	Russia, Charamodun		m	LF	EU070873
Cdau-8	Russia, Baikal Lake, Olkhon I.		f	LF	EU070874
Cdau-9	Russia, Baikal Lake, Olkhon I.		f	LF	EU070875
<i>Corvus enca enca</i>	(Horsfield, 1821)				
Cencenc-2	Indonesia, Java, Cheribon	ZMB 28.365	p	SF1	JQ900730
<i>Corvus enca celebensis</i>	Stresemann, 1936				
Cenccel-1	Indonesia, Sulawesi	NMW 35.465	p	LF	JQ900694
Cenccel-2	Indonesia, Sulawesi, Makassar	ZMB 33.1086	p	SF1	JQ900731
Cenccel-3	Indonesia, Sulawesi, Makassar	ZMB 33.1088	p	SF1	JQ900732
<i>Corvus enca compiler</i>	Richmond, 1903				
Cenccom-1	Indonesia, Sumatra, Bukittinggi	RMNH 101690	p	LF	JQ900695
<i>Corvus enca pusillus</i>	Tweeddale, 1878				
Cencpus-1	Philippines, Palawan, Quezen	NMW 90.108	p	LF	JQ900696
Cencpus-2	Philippines, Palawan, Quezen	NMW 90.107	p	LF	JQ900697
<i>Corvus florensis</i>	Büttikofer, 1894				
Cflo-1	Indonesia, Flores, Sesok	RMNH 85140-1	p	LF	JQ900676
Cflo-2	Indonesia, Flores, Sesok	RMNH 85140-2	p	SF1	JQ900733
<i>Corvus frugilegus frugilegus</i>	Linnaeus, 1758				
Cfrufu-1	Russia, Ivanovo reg.	AK 0102	l	LF	EU070840
Cfrufu-2	Russia, Kirov reg.	AK 0166	l	LF	EU070841
Cfrufu-6	Russia, Smolensk	AK 0217	m	LF	EU070842
Cfrufu-8	Great Britain, Barnard Castle		f	LF	EU070843
Cfrufu-9	Great Britain, Barnard Castle		f	LF	EU070844
Cfrufu-10	Great Britain, Alnwick		f	LF	EU070845
Cfrufu-11	Great Britain, Leeds		f	LF	EU070846
Cfrufu-12	Great Britain, Easby Abbey		f	LF	EU070847
Cfrufu-13	Great Britain, Richmond		f	LF	EU070848
Cfrufu-14	Serbia, Belgrade		f	LF	EU070849
Cfrufu-15	Austria, Graz	NMW 88/05	m	LF	EU070850
Cfrufu-16	Kyrgyzstan, Issyk Kul L.	NMW 63.816	p	SF1	EU070767
<i>Corvus frugilegus pastinator</i>	Gould, 1845				
Cfrupas-4	Russia, Primorye reg., Gaivoron	ZMMU EAK037	m	LF	EU070851
Cfrupas-5	Russia, Primorye reg., Gaivoron	ZMMU EAK036	m	LF	EU070852
Cfrupas-6	Russia, Primorye reg., Lipovsty	AK 911	m	LF	EU070853
Cfrupas-7	Russia, Primorye reg., Gaivoron	ZMMU EAK 042	m	LF	EU070854
<i>Corvus fuscicapillus fuscicapillus</i>	G. R. Gray, 1859				
Cfusfus-1	Indonesia, Aru Is.	NMW 52.686	p	SF1	JQ900734
Cfusfus-2	Indonesia, Aru Is.	SNS C7406	p	LF	JQ900679
<i>Corvus hawaiiensis</i>	Peale, 1848				
Ctro-1	USA, Hawaii	RMNH 100699	p	SF1	JQ900735
Ctro-2	USA, Hawaii, Kona	RMNH 100700	p	SF1	JQ900736
<i>Corvus jamaicensis</i>	J. F. Gmelin, 1788				
Cjam-1	Jamaica	NMW 31.864	p	SF2	JQ900636
<i>Corvus macrorhynchos macrorhynchos</i>	Wagler, 1827				
Cmacmac-2	Indonesia, Flores, Rahong	RMNH 85141	p	LF	JQ900655
<i>Corvus macrorhynchos colonorum</i>	Swinhoe, 1864				
Cmaccol-1	Taiwan, Wanta	RMNH 53153	p	SF1	JQ900737

Appendix: (Continued)

Taxon/Code	Geographical origin	Coll./Vouch. No.	T	S	Acc. No.
Cmaccol-2	Taiwan, Wanta	RMNH 53511	p	LF	JQ900651
<i>Corvus macrorhynchos culminatus</i> Sykes, 1832					
Cmaccul-1	Sri Lanka, Tannikitiya	RMNH 5037	p	SF1	JQ900738
Cmaccul-2	Sri Lanka, Trincomalee		f	SF1	JQ900739
<i>Corvus macrorhynchos japonensis</i>					
Cmacjap-1	Russia, S Sakhalin	AK 0814	l	LF	JQ900652
Cmacjap-2	Russia, S Sakhalin	AK 815	l	LF	JQ900653
Cmacjap-3	Japan, Tokyo	Ferdinandeam, not cat.	m	LF	JQ900654
<i>Corvus macrorhynchos leuallantii</i> Lesson, 1831					
Cmaclev-3	Nepal, Malde	AMNH JGG 1028	m	LF	JQ900656
<i>Corvus macrorhynchos mandshuricus</i> Buturlin, 1813					
Cmacman-1	Russia, Vladivostok	AK 705	m	LF	JQ900657
Cmacman-2	Russia, N Sakhalin, Okha	AK 731	m	LF	JQ900658
Cmacman-3	Russia, Primorye reg.	AK 004	m	LF	JQ900659
Cmacman-4	Russia, Primorye reg.	AK 817	m	LF	JQ900660
Cmacman-5	Russia, Khabarovsk reg., Solnechny	AK 0284	m	LF	JQ900661
Cmacman-6	Russia, Khabarovsk reg., Solnechny	AK 0283	m	LF	JQ900662
Cmacman-7	Russia, Primorye reg.	ZMMU RYA640	m	LF	JQ900663
Cmacman-8	Russia, Primorye reg.	ZMMU RYA713	m	LF	JQ900664
Cmacman-9	Russia, Khabarovsk reg., Solnechny	AK 0282	m	LF	JQ900665
Cmacman-10	Russia, N Sakhalin, Okha	AK 735	l	LF	JQ900666
Cmacman-11	North Korea, Pyongyang	NMW FC 478	f	SF1	JQ900740
Cmacman-12	Russia, Chita, Urjupino		m	SF1	JQ900741
<i>Corvus macrorhynchos philippinus</i> (Bonaparte, 1853)					
Cmacphi-2	Philippines, Mindanao, Cotobato	NMW 90.199	p	LF	JQ900667
Cmacphi-3	Philippines, Mindanao, Cotobato	NMW 90.200	p	LF	JQ900668
<i>Corvus macrorhynchos tibetosinensis</i> O. Kleinschmidt & Weigold, 1922					
Cmactib-1	China, Gansu, Xiahe		f	LF	JQ900669
Cmactib-4	China, N Yunnan	AK 0722	f	LF	JQ900670
<i>Corvus mellori</i>					
Cmel-2	Australia, NSW, Narrandera	NMW 75.237	p	LF	JQ900680
Cmel-3	Australia, NSW, Finlay	NMW, FC 182	f	LF	JQ900681
Cmel-4	Australia, NSW, Barrington	NMW, FC 183	f	LF	JQ900682
Cmel-5	Australia, NSW, Barrington	NMW, FC 184	f	LF	JQ900683
<i>Corvus monedula monedula</i> Linnaeus, 1758					
Cmonmon-1	Russia, Kirov region	ZMMU SVD2405	l	LF	EU070861
Cmonmon-2	Russia, Moscow	AK 0303	m	LF	EU070862
Cmonmon-3	Russia, Smolensk region	ZMMU SKY007	m	LF	EU070863
Cmonmon-4	Russia, Ivanovo region	AK 0220	l	LF	EU070864
Cmonmon-5	Russia, Kirov region	AK 0222	l	LF	EU070865
<i>Corvus monedula soemmeringii</i> J. G. Fischer von Waldheim, 1811					
Cmonsoe-6	Greece, Kozani		f	LF	EU070866
<i>Corvus monedula spermologus</i>					
Cmonspe-1	Spain, Burguillos		f	LF	EU070855
Cmonspe-2	Spain, Burguillos		f	LF	EU070856
Cmonspe-7	Austria, Schloss Hubertendorf	NMW 94.222	f	LF	EU070857
Cmonspe-8	Austria, Schloss Hof		f	LF	EU070858
Cmonspe-9	Lithuania		f	LF	EU070859
Cmonspe-10	Great Britain, Stonehenge		f	LF	EU070860
<i>Corvus moneduloides</i> Lesson, 1831					
Cmoi-2	New Caledonia, Loyalty I., Maré I.	ZFMK 751305	p	LF	JQ900698
<i>Corvus orru ceciliae</i> Mathews, 1912					
Corrcec-1	Australia, NT, Undoolya	NMW 75.233	p	LF	JQ900689
Corrcec-2	Australia, QLD, Brisbane	RMNH 6398	p	SF1	JQ900742
Corrcec-3	Australia, NSW	NMW FC 167	f	LF	JQ900690
<i>Corvus ossifragus</i> A. Wilson, 1812					
Coss-1	USA, FL, Port Orange	RMNH 8967	p	SF1	JQ900743
Coss-2	USA, FL, Lake Placid	NMW 73.807	p	LF	JQ900718
Coss-3	USA, FL, Port Orange	NMW 73.808	p	LF	JQ900719
Coss-4	USA, NY, New York	AMNH JJW 094	m	LF	JQ900720
Coss-5	USA, NY, New York	AMNH JJW 095	m	LF	JQ900721
<i>Corvus palmarum palmarum</i> Paul von Württember, 1835					
Cpalpal-1	Dom. Republic, S. Baoruco NP	KU 6345	m	LF	JQ900722
Cpalpal-2	Dom. Republic, S. Baoruco NP	KU 6346	m	LF	JQ900723
<i>Corvus pectoralis</i> Gould, 1836					
Cpec-8	China, Guangdong	ZMB 31.4117	p	LF	JQ900642
Cpec-9	China, Guangdong	ZMB 31.4118	p	LF	JQ900643

Appendix: (Continued)

Taxon/Code	Geographical origin	Coll./Vouch. No.	T	S	Acc. No.
<i>Corvus rhipidurus rhipidurus</i> E. J. O. Hartert, 1918					
Crhirhi-1	Kenya, North Horr	ZFMK 76.050	p	LF	JQ900705
<i>Corvus rhipidurus stanleyi</i> Roselaar, 1993					
Crhista-1	Israel, Eilat	NMW 94.250	p	LF	JQ900706
Crhista-2	Israel, Sedom	NMW 94.249	p	LF	JQ900707
Crhista-3	Egypt	NMW FC 57	f	SF1	JQ900744
<i>Corvus ruficollis ruficollis</i> Lesson, 1831					
Crufruf-1	Jordan		m	LF	JQ900711
<i>Corvus splendens splendens</i> Vieillot, 1817					
Csplspl-1	Singapore	AMNH PRS 687	l	LF	JQ900671
Csplspl-2	Singapore	AMNH PRS 686	l	LF	JQ900672
<i>Corvus splendens insolens</i> Hume, 1874					
Csplins-3	Myanmar	ZFMK 39.107	p	LF	JQ900673
<i>Corvus splendens protegatus</i> Madarász, 1904					
Csplpro-1	Sri Lanka, Maradana	RMNH 4995	p	SF1	JQ900745
Csplpro-3	Sri Lanka, Maradana	RMNH 4962	p	SF1	JQ900746
Csplpro-4	Sri Lanka, Galle		f	LF	JQ900674
Csplpro-5	Sri Lanka, Galle		f	LF	JQ900675
<i>Corvus tasmanicus</i> Mathews, 1912					
Ctas-1	Australia, TAS, Derwent Bridge	NMW 75.240	p	LF	JQ900686
Ctas-2	Australia, TAS, Derwent Bridge	NMW 75.239	p	LF	JQ900687
Ctas-3	Australia, TAS	NMW FC 824	f	LF	JQ900688
<i>Corvus tristis</i> Lesson & Garnot, 1827					
Ctri-1	Indonesia, New Guinea, Irian Jaya	RMNH 22782	p	SF1	JQ900747
Ctri-2	Papua New Guinea, Potsdamhafen	NMW 36.678	p	SF1	JQ900748
<i>Corvus typicus</i> Bonaparte, 1853					
Ctyp-1	Indonesia, Sulawesi, Loka	RMNH 101686	p	SF1	JQ900749
Ctyp-2	Indonesia, Sulawesi	ZMB 33.1076	p	SF1	JQ900750
Ctyp-3	Indonesia, Sulawesi	ZMB 33.1074	p	SF1	JQ900751
<i>Corvus validus</i> Bonaparte, 1850					
Cval-1	Indonesia, Maluku Is., Batjan	NMW 35.466	p	SF1	JQ900752
<i>Corvus woodfordi woodfordi</i> Ogilvie-Grant, 1887					
Cwoowoo-1	Solomon Is., Guadalcanal	RMNH 101728	p	SF1	JQ900753
Cwoowoo-2	Solomon Is., Guadalcan., Babanakira	AMNH MKL 164	m	LF	JQ900677
Cwoowoo-3	Solomon Is., Guadalcan., Babanakira	AMNH MKL 165	m	LF	JQ900678
Outgroup taxa					
<i>Cyanocorax chrysops chrysops</i> (Vieillot, 1817)					
Cchrchr-1	Argentina, Colonia Mado, Misiones	NMW 84.144	p	LF	EU070898
<i>Cyanocorax cyanomelas</i> (Vieillot, 1818)					
Ccme-1	Brazil, Karumba, Mato Grosso	NMW 81.697	p	LF	EU070899
<i>Cyanopica cyanus cyanus</i> (Pallas, 1776)					
Ccyacya-24	Russia, Chita reg., Olowjannaja		m	LF	AY701138
<i>Cyanopica cyanus cooki</i> Bonaparte, 1850					
Ccyacoo-6	Spain, Badajoz		d	LF	AY701132
<i>Nucifraga caryocatactes caryocatactes</i> (Linnaeus, 1758)					
Nncarcar-1	Russia, Kirov reg.	AK 0171	l	LF	EU070786
<i>Perisoreus infaustus infaustus</i> (Linnaeus, 1758)					
Pinfinf-1	Russia, Karelia	AK 0315	m	LF	EU070876
<i>Pica pica bactriana</i> Bonaparte, 1850					
Ppicbac-7	Armenia		m	LF	JQ900724
<i>Pica pica jankowskii</i> Stegmann, 1928					
Ppicjan-5	Russia, Primorye reg., Nadezhdinskaya	AK 714	m	LF	AY701171

Taxa are listed alphabetically (species names). Year, year of collection; Coll./Vouch. No., collection and voucher number (if available); not cat., not catalogued; T, type of tissue (d, extracted DNA; b, blood; f, feather; l, liver; m, muscle; p, foot pad, skin); S, section sequenced (LF, long fragment; SF1, SF2, short fragments); Acc. No., GenBank accession number. Collections: AMNH, American Museum of Natural History, New York, USA; AK, Tissue collection Alexey Kryukov, IBSS, Vladivostok, Russia; Ferdinandeum, Tiroler Landesmuseum, Innsbruck, Austria; KU, Kansas State University-Natural History Museum, Lawrence, USA; LSU, Louisiana State University, Baton Rouge, USA; MAR, Tissue collection J. Martens NMW, Museum of Natural History, Vienna, Austria; Phyl. Mus. Jena, Phyletical Museum Jena, University of Jena, Germany; RMNH, Naturalis, Leiden, the Netherlands; SNS, Senckenberg Naturhistorische Sammlungen, Dresden, Germany; ZFMK, Alexander Koenig Research Institute and Zoological Museum, Bonn, Germany; ZMB, Zoological Museum Berlin, Germany; ZMMU, Zoological Museum Moscow State University, Moscow, Russia.

Table S1. P distances of CR sequences (LF) between species / clades

	coW	coE	br/ca	mac	spl	flo	woo	fus	mel	coi	tas	orr	ben	enc	moi	frW	frE	cry	coa	rhi	alb	rfc	aco	cra	cap	oss	pal	mon	dau
coW	0,9																												
coE	4,0	0,4																											
br/ca	5,0	4,8	0,6																										
mac	10,1	10,3	9,7	1,4																									
spl	10,4	10,4	9,6	5,6	1,6																								
flo	10,9	11,7	10,3	8,1	9,2	—																							
woo	12,0	11,7	10,0	9,0	9,1	10,1	0,2																						
fus	10,1	10,1	8,9	8,6	8,6	9,8	6,0	—																					
mel	11,0	10,6	10,4	9,7	10,1	10,0	6,6	5,7	0,5																				
coi	10,7	10,2	10,0	9,7	9,9	9,8	7,0	5,5	2,0	1,8																			
tas	10,0	9,9	9,4	9,3	9,9	9,3	6,3	5,3	2,0	1,7	0,9																		
orr	10,4	10,1	9,1	8,1	8,8	8,6	6,3	4,6	5,4	4,9	5,1	0,0																	
ben	10,1	10,5	9,2	8,5	8,9	8,4	6,7	4,9	5,4	5,1	5,0	2,3	0,1																
enc	10,7	10,6	9,8	7,8	8,4	9,3	7,1	6,4	7,2	7,1	7,4	5,5	5,8	2,5															
moi	11,1	11,2	10,0	8,6	10,1	10,1	8,7	6,2	7,8	7,4	7,7	5,7	6,3	6,5	—														
frW	11,0	12,2	11,2	11,7	12,3	12,8	12,9	10,5	12,6	12,1	11,8	10,9	11,0	11,5	11,7	0,6													
frE	9,2	10,8	9,8	10,5	10,9	11,7	12,1	9,5	10,4	10,6	10,5	8,6	9,5	10,3	10,3	4,8	0,3												
cry	11,6	11,9	10,7	11,6	12,4	12,6	12,0	12,0	11,0	13,0	12,8	12,4	10,8	11,7	12,7	11,9	10,3	0,9											
coa	11,5	11,8	9,8	12,3	12,4	12,7	12,6	10,5	13,9	13,6	13,4	11,0	11,5	12,8	11,7	9,8	10,1	6,0	1,0										
rhi	11,9	12,6	10,7	11,8	12,5	12,5	12,8	10,7	13,0	12,8	12,4	11,1	11,2	12,3	11,0	10,7	10,1	5,4	4,3	1,2									
alb	11,5	12,1	10,9	12,5	13,5	13,2	12,6	11,2	13,1	12,9	12,6	11,2	12,2	13,0	11,9	11,0	10,5	4,9	4,2	3,4	0,4								
rfc	10,7	11,0	9,4	10,9	11,8	11,8	11,6	10,0	12,7	12,3	12,1	10,1	11,0	11,6	11,0	10,0	9,0	4,7	4,2	4,2	3,5	—							
aco	11,0	10,9	10,1	10,4	11,4	12,3	12,1	10,3	13,0	12,8	12,3	10,5	11,4	12,3	10,2	10,9	10,0	5,9	5,8	5,0	5,0	5,3	0,7						
cra	12,3	12,0	11,2	11,9	12,4	13,1	12,5	11,5	13,4	13,4	13,0	11,4	12,1	12,6	11,9	12,0	10,8	6,5	6,9	5,7	4,8	5,7	4,9	—					
cap	13,3	13,8	11,9	12,9	13,1	12,1	13,9	12,5	13,9	13,8	13,2	12,3	12,2	12,7	14,3	13,3	13,2	12,4	12,7	12,2	13,0	11,3	13,5	13,7	0,0				
oss	13,9	14,1	13,8	13,4	14,3	12,3	15,2	12,0	13,7	13,8	13,3	13,4	12,8	13,0	13,5	12,2	12,1	12,7	11,9	11,4	11,7	11,6	12,4	12,2	14,1	0,4			
pal	11,8	11,7	12,6	12,8	13,4	12,5	12,8	12,4	12,8	12,9	12,4	13,1	13,2	12,9	13,2	12,0	11,9	11,2	11,8	11,6	11,9	10,8	11,3	10,6	13,4	12,2	0,0		
mon	14,7	15,0	14,0	15,9	15,2	16,0	15,1	13,0	13,5	13,6	13,7	13,9	12,8	13,9	15,3	16,5	15,3	15,4	16,3	16,1	16,7	15,3	16,0	16,8	15,6	15,6	15,2	0,4	
dau	15,2	15,0	14,0	16,2	15,0	15,8	15,1	13,1	13,6	13,8	13,8	13,8	12,8	13,8	15,0	15,6	15,0	16,0	16,9	16,2	17,3	15,8	16,4	16,9	15,4	15,4	14,3	5,8	0,6

coW, *C. corone* West; coE, *C. corone* East, br/ca, *C. brachyrhynchus* / *C. caurinus*; mac, *C. macrorhynchus*; spl, *C. splendens*; flo, *C. florensis*; woo, *C. woodfordi*; fus, *C. fuscicapillus*; mel, *C. mellori*; coi, *C. coronoides*; tas, *C. tasmanicus*; orr, *C. orru*; ben, *C. bennetti*; enc, *C. enca*; moi, *C. moneduloides*; frW, *C. frugilegus* West; frE, *C. frugilegus* East; cry, *C. cryptoleucus*; coa, *C. corax*; rhi, *C. rhipidurus*; alb, *C. albus*; rfc, *C. ruficollis*; aco, *C. albicollis*; cra, *C. crassirostris*; cap, *C. capensis*; oss, *C. ossifragus*; pal, *C. palmarum*; mon, *C. monedula*; dau, *C. dauuricus*