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Phylogeny of magpies (genus *Pica*) inferred from mtDNA data

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Abstract

We investigated the phylogenetic relationships of species and subspecies of the cosmopolitan genus *Pica* using 813 bp of the mitochondrial genome (including portions of 16s rDNA, tRNA-Leu, and ND1). The phylogenetic relationships within the genus *Pica* revealed in our molecular analyses can be summarized as follows: (1) the Korean magpie (*Pica pica sericea*) appears basal within the genus *Pica*; (2) the European magpie (*Pica pica pica*) shows a close relationship to the Kamchatkan magpie (*Pica pica camtschatica*); (3) two North American species (*Pica hudsonia* and *Pica nuttalli*) shows a sister-group relationship; (4) most importantly, the European + Kamchatkan clade appears more closely related to the North American clade than to Korean magpies. Based on these results and genetic distance data, it is possible that members of an ancestral magpie lineage in East Asia initially moved north to form Kamchatkan magpies and then crossed the Bering land bridge to found North American taxa. At a later date, a group might have split off from Kamchatkan magpies and migrated west to form the Eurasian subspecies. The divergence between the two North American taxa appears to have happened no later than the divergence of Eurasian subspecies and both processes appear to have been relatively rapid. Rather than the formation of *P. hudsonia* by re-colonization from an Asian magpie ancestor, as suggested by Voous (1960), our data suggest a shared ancestry between *P. hudsonia* and *P. nuttalli*. Based on the above findings, including phylogenetic placement of *P. hudsonia* and *P. nuttalli* as nested within the larger *Pica pica* clade, and the lack of evidence suggesting reproductive isolation within the genus *Pica*, we believe that the current classification may be inaccurate. A more conservative classification would recognize one monophyletic species (i.e., *P. pica*) and treat *P. nuttalli* and *P. hudsonia* as subspecies (i.e., *P. p. nuttalli* and *P. p. hudsonia*). More extensive studies on the population genetics and biogeography of magpies should be conducted to better inform any taxonomic decisions.

1. Introduction

Magpies are members of the crow tribe, Corvini (Corvidae), which is composed of 113 species of medium to very large oscine passerines (Madge and Burn, 1994). Magpies are very adaptable and successful birds found in the northern hemisphere, ranging from northeastern Asia to Europe and North America (Fig. 1). Three species of the magpies were recognized in the most recent classification of the genus *Pica* (American Ornithologists' Union, 2000): (i) *Pica pica*, Eurasian black-billed magpie, (ii) *Pica hudsonia*, American black-billed magpie, and (iii) *Pica nuttalli*, yellow-billed magpie. *P. nuttalli* has distinct morphological characters including a yellow bill and small yellow patches around eyes (Birkhead, 1991; Goodwin, 1986; Sibley, 2000), and their distribution is restricted to a small region of California. *P. hudsonia*, which resides in the western parts of North America, has recently been split from Palearctic *P. pica* and raised to species level based on a number of morphological, behavioral (including vocal), and genetic characters (American Ornithologists' Union, 2000). *P. pica* is ubiquitous in temperate regions of the Eurasian continent and 12 subspecies (or races) are recognized (excluding *P. hudsonia* from the classification of Vaurie (1959) and Goodwin (1986)). These geographical races of *P. pica* were identified on the basis of morphological characteristics such as body size, relative tail length, color of gloss of wing and tail, size of black tips on white primaries and amount of white, gray, or black on rump; however, defining races is notoriously difficult because of clinal variation (Birkhead, 1991; Snow and Perrins, 1998).

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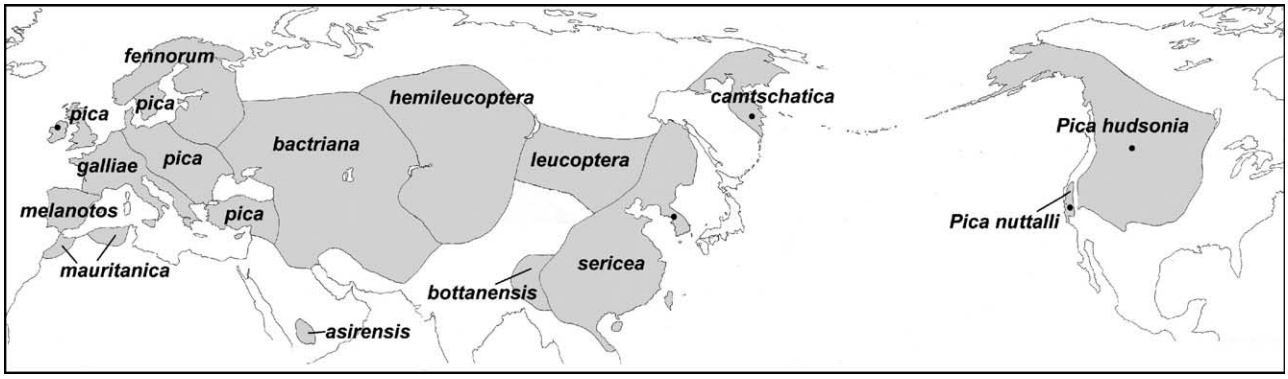

Fig. 1. Distribution of the species and subspecies within genus *Pica* showing their approximate range (based on Birkhead, 1991; Bährmann, 1995; Gee et al., 1927; Goodwin, 1986; Lee et al., 2000; Sibley, 2000; Vaurie, 1959). The range of Palearctic black-billed magpie *P. pica* is given with their subspecific name. Circles indicate locations from which samples were collected.

The taxonomic status of *P. nuttalli* and its relationship with *P. hudsonia*, the American black-billed magpie, remain controversial. Under previous classifications, *P. hudsonia* was included in the nominate species *P. pica* (i.e., as *P. p. hudsonia*). However, paraphyly was thought to be present within the genus because DNA hybridization and ecological evidence suggested a close relationship between *P. nuttalli* and *P. p. hudsonia* (Birkhead, 1991; Madge and Burn, 1994; Sibley and Ahlquist, 1990). Since the existence of paraphyly had not been tested and the phylogenetic relationships among the various suprageneric taxa within *Pica* are not clearly known, the new specific status of *P. hudsonia* could cause additional confusion.

In view of the lack of a systematic biochemical study on the genus *Pica*, we sequenced and analyzed mitochondrial DNA of five species and subspecies which are the representatives of each continental region. This is the first in a series of studies examining the phylogenetic relationships, patterns of diversification, and historical biogeography of the magpies. This study aims at: (1) resolving relationships between New World and Old World magpie populations and (2) clarifying taxonomic status of New World magpie taxa based on a mitochondrial sequence analysis.

2. Materials and methods

2.1. Sampling of taxa

Mitochondrial DNA sequences of partial 16s rDNA, complete tRNA-Leu and partial NADH dehydrogenase subunit 1 (ND1) regions were used in our analysis. We used 19 samples of 11 taxa (Table 1; collection sites are marked in Fig. 1). Ingroups were chosen as the representatives of major continental regions so that the direction of invasions on each continents can be inferred (following Zink et al.'s (1995) suggestion), and consist of Korean (*Pica pica sericea*), Kamchatkan (*P. p. camtschatica*), European (*P. p. pica*), American black-billed magpies (*P. hudsonia*), and yellow-billed magpies (*P. nuttalli*). For ingroup taxa, additional samples were included in the analysis as a partial check for the exemplar effect (e.g., Zink et al., 1998). Outgroups represent possible sister taxa and proximal outgroups to the genus *Pica* (*Cyanopica* and *Urocissa*) as well as slightly more distant ones (*Platylophus* and *Corvus*) within the Tribe Corvini (Goodwin, 1986; Hope, 1989). We also included published nucleotide sequence of *Corvus frugilegus* in our analyses (GenBank Accession No. Y18522; Harlid and Arnason, 1999). Multiple outgroups were included because sister taxa for the genus *Pica* are not clearly known (Hope, 1989).

2.2. Laboratory procedures

MtDNA was extracted from the heart and pectoral muscle using QIAamp Tissue Kits (Qiagen) and from feather quills by the addition of dithiothreitol to the QIAamp protocol. These tissues contain relatively high mtDNA compared with blood, which enables us to minimize the possibility of isolating nuclear pseudogenes (Quinn, 1997; Sorenson and Fleischer, 1996). L3827-H4644 primer pair (Sorenson et al., 1999) was used in subsequent amplification. Amplifications were performed in 50 μl reaction volumes using *Taq* DNA polymearse and 10× reaction buffer (500 mM KCl, 100 mM Tris–HCl, 1.0% Triton X-100, and 25 mM $MgCl_2$) from Viogene. PCRs were performed in a PTC100 (MJ Research) thermocycler under the following profile: hot start at 94 °C for 2 min, 35 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 20 s, elongation at 72 °C for 1 min 20 s, and a final elongation at 72 °C for 7 min. PCR products were then purified from the 2% agarose gels stained with ethidium bromide using QIAquick Gel Extraction Kits (Qiagen). Sequencing was done in both directions with the ABI

Table 1
Specimens used in present study

Taxon	Locality	Source	GenBank No.
Pica pica sericea	Korea: Seoul	This study	AY129259
P. p. sericea	Korea: Seoul	This study	AY129260
P. p. sericea	Korea: Seoul	This study	AY129261
P. p. camtschatica	Russia: Kamchatskaya Oblast	Burke Museum SAR 6220	AY129262
P. p. camtschatica	Russia: Kamchatskaya Oblast	Burke Museum SAR 6223	AY129263
P. p. camtschatica	Russia: Kamchatskaya Oblast	Burke Museum SAR 6224	AY129264
P. p. pica	Ireland: Rathcormac	LSUVM B-21965	AY129265
P. p. pica	Ireland: Ballymacoda	LSUVM B-21966	AY129266
P. nuttalli	USA: Carmel Valley, CA	G. Bolen, W. Koenig	AY129267
P. nuttalli	USA: Chico, CA	Burke Museum JMB 750	AY129268
P. hudsonia	USA: Idaho	UMMZ	AY129269
P. hudsonia	USA: Idaho	C. Trost	AY129270
P. hudsonia	USA: Idaho	C. Trost	AY129271
Platylophus galericulatus	USA: Houston Zoo	LSUVM B-20752	AY129272
Cyanopica cyana	Russia: Primorskiy Kray	Burke Museum DAB 289	AY129273
Urocissa erythrorhynchos	USA: Houston Zoo	LSUVM B-8678	AY129274
Corvus brachyrhynchos	USA: Ann Arbor, MI	UMMZ T-777	AY129275
Corvus macrorhynchos	Japan	T. Yuri, 96-077	AY129276
Corvus frugilegus		Harlid and Arnason (1999)	Y18522

377 automated sequencer at the KAIST BioMedical Research Center, Korea.

2.3. Phylogenetic analyses

All sequences were aligned using ClustalW (Thompson et al., 1994) and checked by eye. To evaluate the levels of saturation, we plotted uncorrected p distance versus the proportions of substitutions. Phylogenetic trees were sought with both maximum parsimony (MP) using PAUP ver 4.0b1 (Swofford, 1998) and neighbor-joining (NJ) using MEGA (Kumar et al., 1993). NJ searches were performed to assess the influence of alternative phylogenetic algorithms on the tree topology. For finding the shortest (MP) tree, a branch-and-bound search was performed with an unknown initial upper bound and 'furthest' taxa addition sequence. Exhaustive searches with selected taxa were also conducted. For the NJ search, we used Kimura 2-parameter distance. Relative support for nodes in resulting trees (both by MP and NJ) was evaluated using 1000 bootstrap replicates.

3. Results

3.1. Base composition and sequence divergence

Aligned mtDNA sequences totaled 813 bp in length with 4 gaps, corresponding to the *C. frugilegus* mitochondrial genome position 2584–3395 (Harlid and Arnason, 1999). The first 135 bp correspond to the part of 16s rDNA, 75 bp to tRNA-Leu, followed by 7–9 bp spacers and 593 bp of the partial ND1 gene. Mean base proportions were 25.54% T, 29.36% C, 30.16% A, and 14.94% G. A total of 253 (31.1%) characters were variable and 161 (19.8%) characters were taxonomically informative. Within the protein coding region of the partial ND1 gene, substitutions were strongly skewed toward third codon positions (146 of 253, or 57.7% of variable sites).

Uncorrected pairwise sequence divergence (p) is given in Table 2. Excluding sites with gaps, the mean observed pairwise percent divergence for comparisons involving the genus *Pica* was 2.35%, ranged from 1.23% (within *P. hudsonia*) to 4.31% (*P. p. sericea* vs *P. nuttalli*: Table 2). Notably, genetic divergences between Palearctic subspecies and *P. hudsonia* and *P. nuttalli* are not distinct from those within Palearctic subspecies. For example, mean sequence divergences between *P. hudsonia* and *P. nuttalli* to *P. p. camtschatica* were 2.59 and 1.13%, respectively, while mean sequence divergence within Palearctic subspecies is 2.55%.

3.2. Sequence saturation

Plotting the proportion of substitutions against sequence difference (Fig. 2a) reveals that neither transitions nor transversions were saturated. Even in the third codon position in ND1 region, evidence of transition saturation is weak, at least in the comparisons within the genus *Pica* (Fig. 2b). While transitions increase almost linearly with sequence divergence, transversions show concave increase. Thus, the plateau found in the plot of transitions against transversions (Fig. 2c) is likely to result from this difference in the rate of increase between transition and transversion rather than from saturation of transition substitutions. Fig. 2c also shows that transitions are more meaningful than transversions in sequence comparisons with low-level divergence, which suggests that phylogenetic relationship within the genus

Table 2
Summarized data on sequence divergence represented as uncorrected *p* distance and level of substitution for pairwise comparisons of mitochondrial DNA sequences

	Mean values			
	p Distance	Ti	Tv	Ti:Tv
Within *Pica* subspecies/species				
Pica pica sericea	0.010	7.33	0.67	9.5
P. p. camtschatica	0.005	4.67	0.67	4.5
P. p. pica	0.002	0	2	0
P. nuttalli	0.009	4	3	1.33
P. hudsonia	0.003	1.33	1	0.75
Between *Pica* subspecies/species				
P. p. sericea × *P. p. camtschatica*	0.032	23.78	2	13.18
P. p. sericea × *P. p. pica*	0.033	24	2.67	9.05
P. p. sericea × *P. nuttalli*	0.037	27	3.17	8.69
P. p. sericea × *P. hudsonia*	0.035	27.11	2.33	13.49
P. p. camtschatica × *P. p. pica*	0.009	6	1	5.7
P. p. camtschatica × *P. nuttalli*	0.025	19	1.5	12.63
P. p. camtschatica × *P. hudsonia*	0.026	20	1	12.9
P. p. pica × *P. nuttalli*	0.024	18	2	7.05
P. p. pica × *P. hudsonia*	0.024	18	1.67	14.44
P. nuttalli × *P. hudsonia*	0.011	7	2.167	4.33
Pica vs outgroups				
P. pica × *Platylophus*	0.164	97	36.25	2.68
P. pica × *Urocissa*	0.125	81.13	20.25	4.01
P. pica × *Cyanopica*	0.138	82.13	30	2.74
P. pica × *Corvus*	0.127	81.33	21.42	3.84
P. nuttalli × *Platylophus*	0.166	97	37.5	2.59
P. nuttalli × *Urocissa*	0.128	82.5	21.5	3.84
P. nuttalli × *Cyanopica*	0.144	87	29.5	2.95
P. nuttalli × *Corvus*	0.128	81.67	24.5	3.70
P. hudsonia × *Platylophus*	0.165	97.33	36.67	2.66
P. hudsonia × *Urocissa*	0.128	83.67	20.67	4.06
P. hudsonia × *Cyanopica*	0.142	85	29.67	2.87
P. hudsonia × *Corvus*	0.125	80	21.33	3.80

Pica would be mostly explained by transitions. The average pairwise transition to transversion ratio for all comparisons was 6.1 and for ingroup taxa was 9.74.

3.3. Phylogenetic analyses

A branch-and-bound search with equally weighted data produced a single tree (Fig. 3), where three major clades were evident: (i) a North American clade (consisting of *P. nuttalli* and *P. hudsonia*), (ii) a Palearctic clade (*P. p. pica* and *P. p. camtschatica*), and (iii) a basal Korean clade (*P. p. sericea*). Bootstrap values obtained from 1000 replication ranged from 51 to 100, and all of the ingroup nodes had values above 60%. The topology was robust to changes in branch-swapping method and taxa addition sequence. In addition, exhaustive searches with selected ingroup taxa produced trees with congruent topology. Additional analyses with down-weighting on transition over transversion were not conducted, because the saturation plots do not show clear evidence of transition saturation and much information on the phylogenetic relationships within the genus *Pica* would be lost by such down-weighting.

NJ method found a single tree of the same branching pattern as the tree found by maximum parsimony (Fig. 4). We used Kimura 2-parameter distance, although analyses with different types of distances yielded the same tree. Phylogenetic analyses by MP and NJ methods produced essentially the same tree topology. In general, bootstrap values for the neighbor-joining tree showed stronger support for nodes than in the of MP tree. Ingroup topology was highly robust to different tree-searching options and ingroup nodes above subspecies level were supported with high bootstrap values (>90%). Contrary to the well-resolved ingroup topology, closer relationship between the magpie clade and any of the selected outgroup taxa is not well supported (<70% bootstrap supports).

4. Discussion

4.1. Phylogenetic relationship and biogeography

Phylogenetic analyses on the mitochondrial nucleotide data identified three major clades: (i) Kamchat-

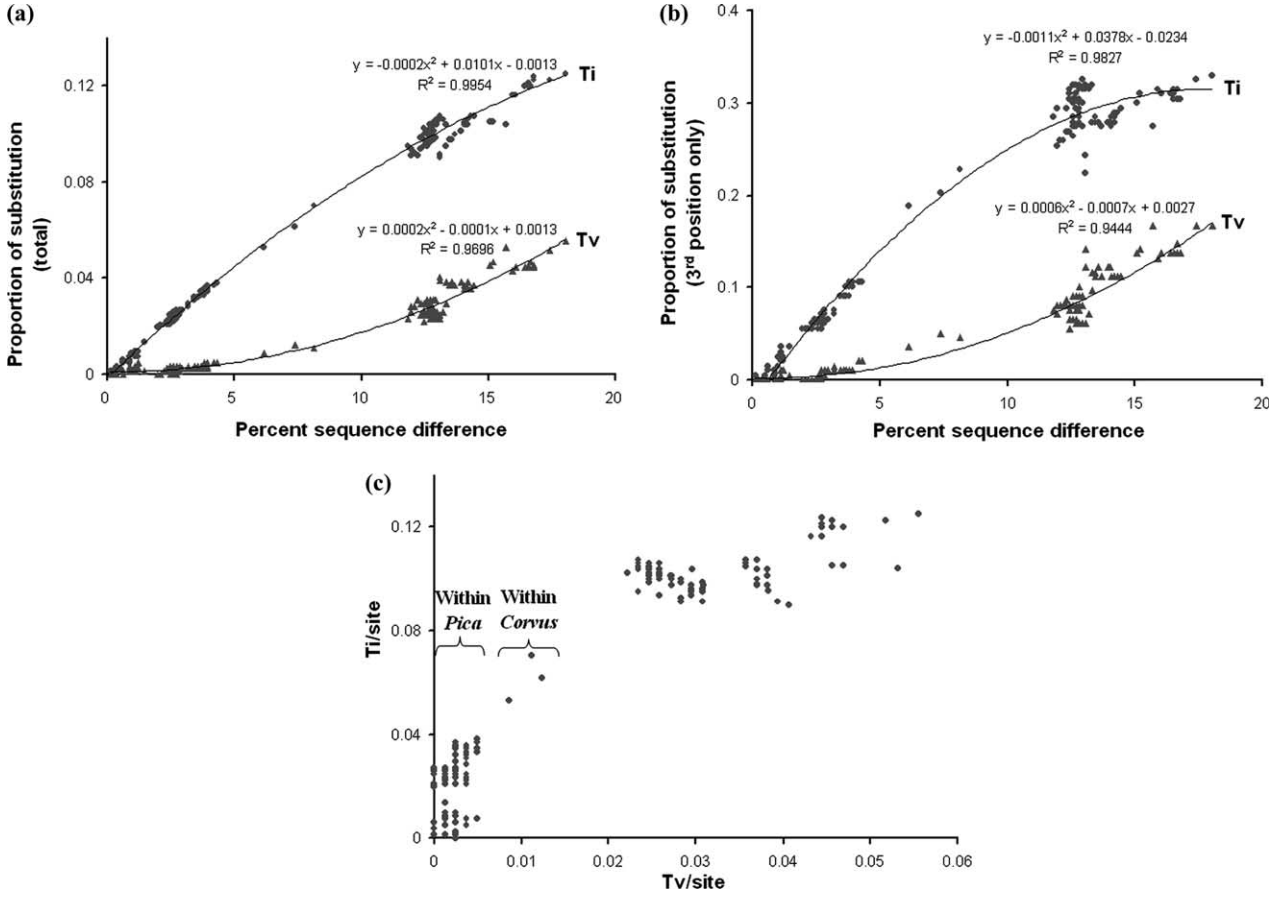

Fig. 2. Saturation plots of transition and transversion calculated through pairwise sequence comparisons. (a) Percent sequence difference versus total proportion of substitution; (b) percent sequence difference versus substitutions in third codon position of ND1; (c) transition plotted against transversion.

kan + European magpies, (ii) two North American species, and (iii) Korean magpies which form a basal group to clade (i) and (ii). In other words, the North American taxa were closer to the Kamchatkan + European clade than to the basal Korean magpies. Although it may be premature to speculate on the divergence route of *Pica* without including data from intervening subspecies in the analysis, it is possible that magpie ancestors in East Asia initially moved north giving rise to Kamchatkan magpie populations and then crossed the Bering land bridge to found North American taxa. At a later date, a group might have split off from Kamchatkan magpies and migrated west to form the Eurasian subspecies. The divergence between the two North American taxa appears to have happened no later than the divergence of Eurasian subspecies and both processes appear to have been relatively rapid (see also '*Tempo and Timing of Divergence*' section).

This postulation on the direction of invasions into major continental areas is consistent with Sibley and Ahlquist's hypothesis (1986) on the origin and emigration of corvids. They proposed that an Australian ancestor of corvids emigrated to southeast Asia, where it underwent radiation and emigration to North America, Europe, and Africa. Shared ancestry between North American and Palearctic taxa (except the Korean subspecies) found in our phylogenetic tree suggests that magpies have undergone the typical emigration route of corvids.

Considering the geographic range of Palearctic magpies and the isolation of the Kamchatkan subspecies, it is noteworthy that Kamchatkan magpies appear more closely related to European rather than Korean magpies. This close relationship between the two marginal subspecies might indicate a small overall genetic divergence among most Palearctic subspecies due to high gene flow, as Goodwin (1976) predicted from the magpie's propensity to wander. Additional sampling of the geographically intervening subspecies, such as *Pica pica galliae*, *P. p. bactriana*, *P. p. hemileucoptera*, and *P. p. leucoptera*, would reveal more of the interesting evolutionary history of Palearctic magpie populations. The close relationship of Kamchatkan with European subspecies rather than with North American species might also be attributed to the latter's isolation due to the disappearance of the Bering land bridge.

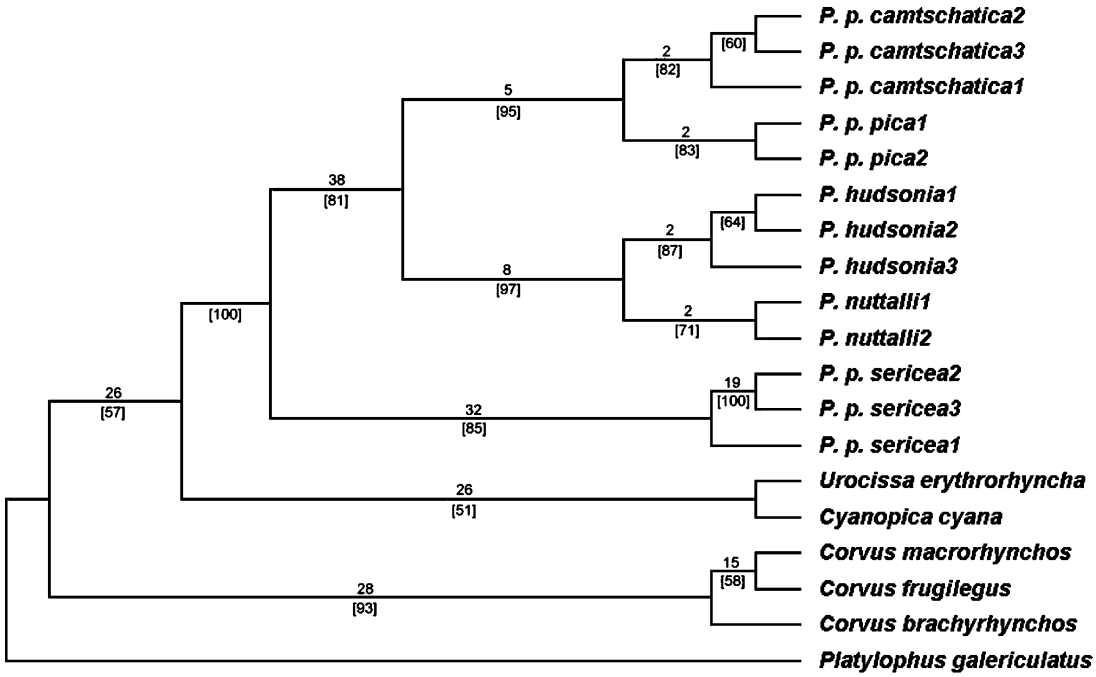

Fig. 3. The most parsimonious phylogenetic tree showing relationships among the species and subspecies of genus *Pica* (rooted to *Platylophus galericulatus*). Numbers above the nodes represent steps and the numbers in brackets denote bootstrap support based on 1000 replication with branch-and-bound search. Numbers after taxon names refer to different individuals sequenced (following the order of appearance in Table 1). Tree statistics are $L = 456$, $CI = 0.6689$, $RI = 0.6918$ excluding uninformative characters.

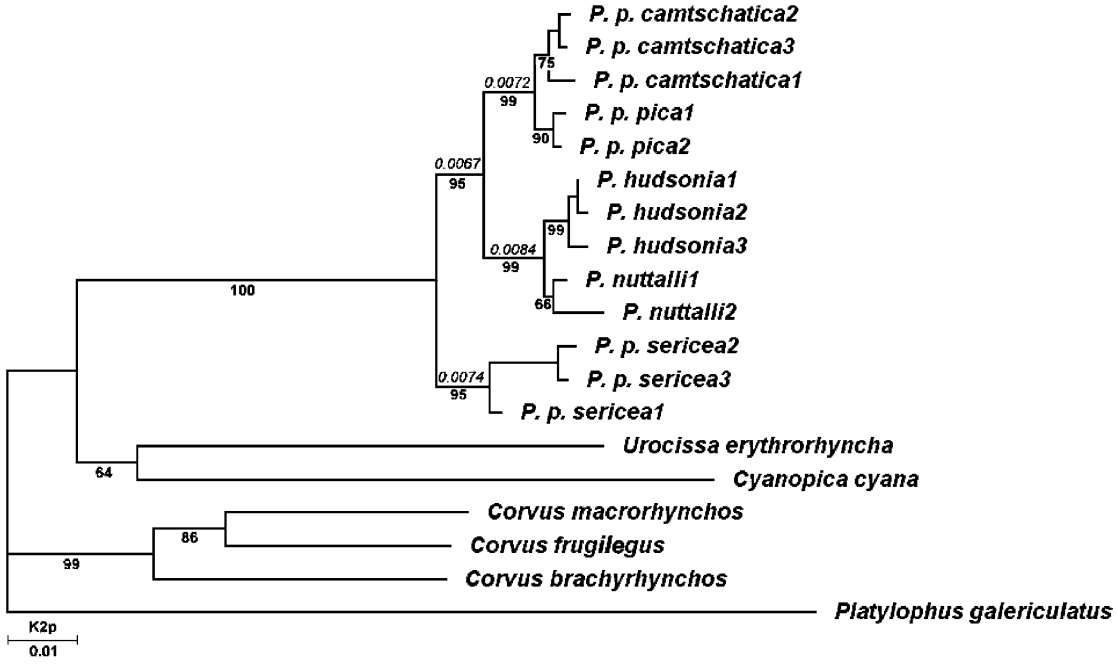

Fig. 4. Neighbor-joining tree on the relationships within *Pica*. Lengths of the branches which lead to the major ingroup clusters are given in italic. Numbers below the nodes represent bootstrap support values calculated from 1000 replications with neighbor-joining search.

Large genetic distances between Korean magpies and other *Pica* samples imply that the split is rather old (probably late Pliocene origin, if we follow the rate of 1.6% substitutions per million years; Fleischer et al., 1998; Omland et al., 2000; Tarr and Fleischer, 1993). Considering the wide distribution of *P. p. sericea* and

the location of the Korean Peninsula, it is possible that Korean magpies may represent a marginal population of the subspecies. Geological history suggests that there were frequent volcanic eruptions and plateau formation near the border of the Korean Peninsula and Manchuria during the late Oligocene–early Pleistocene (Jin, 1998). This geotectonic movement might have prevented gene flow between Korea and China, causing the isolation of the Korean population and enabling them to remain genetically distinct. Further biogeographic study within *P. p. sericea* would help address these issues; it would be interesting to include *P. p. bottanensis* in such a study.

4.2. Tempo and timing of divergence

Short terminal branches in our phylogenetic tree imply rapid and recent diversification of magpies. This conclusion is also supported by the lack of Ti saturation, low-level of Tv substitution and high value of Ti:Tv (Brown et al., 1982; Moore and DeFilippis, 1997) within *Pica* (average of 9.74). The timing of divergence is estimated to be around 375–625 ka between Kamchatkan and European subspecies and 625–750 ka between American species (based on 1.6% substitution rate per million years); thus, most diversification within the genus *Pica* would date to the middle Pleistocene. This estimate is consistent with the fossil records; the oldest magpie fossil found in Europe can be traced back as early as the Middle Pleistocene (Jánossy, 1974; Jánossy and Vörös, 1987).

4.3. Formation of new world taxa

Along with DNA hybridization and other ecological studies, our results support the close relationship between *P. nuttalli* and *P. hudsonia* and contradict the re-colonization hypotheses proposed by Voous (1960). In this scenario, magpies were originally distributed throughout the northern hemisphere, but during the Pleistocene period, they became extinct in North America except for a small population in California that became the present-day *P. nuttalli.* The current *P. hudsonia* was thought to have re-colonized from Asia after the last glaciation when there was a land bridge between the two continents (around 40,000 ya). However, our data suggest that the origin of American magpies resulted from a single dispersal event into North America. Rather than extinction and re-colonization of *P. hudsonia*, our results suggest that *P. nuttalli* and *P. hudsonia* share an ancestor and diverged from each other around the middle Pleistocene. The derived phenotypic features of *P. nuttalli* compared to *P. hudsonia* suggest their rapid differentiation. A founder event followed by genetic drift and geographic isolation might have played a role in rapid morphological differentiation in *P. nuttalli*, although the reason for their isolation in California is not clear.

4.4. Taxonomic considerations

Based on our data, *P. pica* does not appear to be monophyletic, with *P. hudsonia* and *P. nuttalli* representatives being phylogenetically placed within the *P. pica* group (Figs. 3 and 4). This observation and the low-level of genetic divergence among *P. pica*, *P. nuttalli*, and *P. hudsonia* (Table 2; c.f., subspecies divergence of $<7\%$ in *Poospiza*, Lougheed et al., 2000; average divergence of 5.1% for 35 songbird species pairs, Klicka and Zink, 1997) lead us to question the species status of New World magpies (both *P. nuttalli* and *P. hudsonia*). Currently, we do not have reliable evidence of either reproductive isolation or hybridization between New World and Old World magpies, or between the two New World magpies. Considering current distribution of magpie populations, there are geographic barriers that prevent interbreeding between New World and Old World magpies and between the New World magpies. However, it is possible that there has been a small level of gene flow between the two continents until recently via the Bering land bridge (closed at 11,000 ya; Elias et al., 1996). In addition, we do not know if such slight differences in morphology and behavior (e.g., vocalization) in magpie populations may have acted as barriers to interbreeding.

Thus, the current classification may be inaccurate in light of the criterion of reproductive isolation. A more conservative classification would recognize one monophyletic species (i.e., *P. pica*) and treat *P. nuttalli* and *P. hudsonia* as subspecies (i.e., *P. p. nuttalli* and *P. p. hudsonia*). Field observations on breeding behavior where two subspecies meet (in the Palearctic magpies) would be helpful for estimating the degree of reproductive isolation within the genus *Pica*. In addition, more extensive studies on the population genetics and biogeography of magpies should be conducted to better inform any taxonomic decisions.

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