Genetic Differentiation and Phylogenetic Relationships of an Avian Family, Alcidae (Auks)

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Abstract Electrophoresis was used in the analysis of 24 protein loci to clarify the genetic differentiation and phylogenetic relationships among 12 species of 10 alcid genera. The intraspecific genetic variation, expressed as the average heterozygosity, was 0.019, a little lower than the avian average. The genetic distances between the Alcidae, however, were somewhat higher than the avian average: 0.151 for species and 0.442 for genera. This gives genetic support to the current classification of the Alcidae. By comparative analysis of genetic differentiation among alcid species, this family can be divided into two main groups, Alcinae and Fraterculinae. The results of this study of genetic relationships generally support current classification based on morpho-anatomical and ecological studies. However, two points still remain for further analysis: one is genetic similarity between *Uria lomvia* and *Cepphus carbo*, and the other is genetic affinity between *Aethia cristatella* and *Cyclorhynchus psittacula*.

Introduction

A small group belonging to the Charadriiformes, the auks (Alcidae) are small- to medium-sized diving sea birds, which are predominantly arctic in breeding distribution and spend the winter season in coastal or offshore areas. Most genera of Alcidae are recorded and some breed in the ocean area around Japan. The 23 species of the Alcidae are split into 13 genera (Morony *et al.* 1975). There have been several taxonomic studies from the morphological, ecological and electrophoretic viewpoints (Kuroda 1954, 1955, Kozlova 1957, Sibley & Ahlquist 1972). Morpho-ecologically, many genera have been recognized within the relatively small family Alcidae, but their genetic differentiation and relationships have not been analyzed.

Recently, electrophoretic techniques have been applied in ornithology and, as genetic data on birds have accumulated, comparative studies of protein polymorphism among avian groups have become available. For example, Avise *et al.* (1982) reported that vireos, a passerine group, showed a larger degree of genetic differentiation than did other bird groups. The data on protein variations have made it possible to analyze genetic relationships among avian species quantitatively.

In the present paper, the affinities among alcid species are analyzed based on electrophoretic variation. Kakizawa *et al.* (1982) suggested that this family should be divided into two groups, based on their study of mitochondrial malate dehydrogenase (MDH)

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variation. In the present study, the proteins encoded by 24 loci were examined to provide a more detailed analysis of the relationships between the taxa in this family.

Materials and Methods

Specimens of the Alcidae were collected primarily from the Hokkaido coast in 1982: some had drowned in fish nets in the northwest Pacific. They were preserved at -30°C until being sent to our laboratory. They included: 1) Brunnich's Guillemot (*Uria lomvia*), 2) Common Guillemot (*Uria aalge*), 3) Spectacled Guillemot (*Cepphus carbo*), 4) Marbled Murrelet (*Brachyramphus marmoratus*), 5) Ancient Auk (*Synthliboramphus antiquus*), 6) Cassin's Auklet (*Ptychoramphus aleuticus*), 7) Parakeet Auklet (*Cyclorhynchus psittacula*), 8) Crested Auklet (*Aethia cristatella*), 9) Least Auklet (*Aethia pusilla*), 10) Horn-billed Puffin (*Cerorhinca monocerata*), 11) Horned Puffin (*Fratercula corniculata*), and 12) Tufted Puffin (*Lunda cirrhata*). Each bird was defrosted to remove samples of liver and muscle, which were minced for experimental use and preserved at -80°C until electrophoresis. The extracts from liver and muscle were subjected to starch gel electrophoresis to determine the allelic composition at each protein locus. Combinations of tissues and buffer systems for detection of the enzymes are shown in Table 1. The staining methods for enzymes were essentially the same as those described by Shaw & Prasad (1970), Selander *et al.* (1970) and Bell *et al.* (1982). The nomenclature of the alleles and the methods for data analysis are those mentioned in Numachi *et al.* (1983).

Results

Genetic variability and differentiation

No genetic variation was found among 24 loci examined in five out of 12 alcid species.

Table 1. Combinations of tissues and buffer systems for detection of the enzymes

Protein	Abbr.	Tissues	Buffers*
Alcohol dehydrogenase	ADH	Liver	Tris-Citrate
Creatine kinase	CK	Muscle	Tris-HCl
Diaphorase	DIA	Liver	Tris-HCl
Esterase	EST	Liver	Poulik
Glutamate dehydrogenase	GDH	Muscle	Tris-HCl
α -Glycerophosphate dehydrogenase	α GPDH	Muscle	Amine-Citrate
Isocitrate dehydrogenase	IDH	Liver	Amine-Citrate
Lactate dehydrogenase	LDH	Liver	Amine-Citrate
Malate dehydrogenase	MDH	Liver	Amine-Citrate
Peptidase	PEP	Muscle	Tris-HCl
6-Phosphate dehydrogenase	6PGD	Liver	Amine-Citrate
Phosphoglucomutase	PGM	Liver	Amine-Citrate
General protein	PT	Muscle, Liver	Tris-HCl, Poulik
Sorbitol dehydrogenase	SDH	Liver	Tris-Citrate
Superoxide dismutase	SOD	Liver	Amine-Citrate
Xylulose reductase	XR	Liver	Amine-Citrate

* Tris-HCl, Poulik: Selander *et al.* (1971), Amine-Citrate: Kuroda *et al.* (1982), Tris-Citrate: Numachi *et al.* (1983)

Table 2. Proportion of polymorphic loci and average heterozygosity (Observed and Estimated) for each species studied

Species	Sample size	Proportion of polymorphic loci	Average heterozygosity	
			Observed	Estimated
1) <i>Uria lomvia</i>	4	0.125	0.031	0.043
2) <i>Uria aalge</i>	1	0.083	0.083	0.042
3) <i>Cepphus carbo</i>	5	0.083	0.025	0.021
4) <i>Brachyramphus marmoratus</i>	5	0.083	0.025	0.028
5) <i>Synthliboramphus antiquus</i>	11	0.083	0.027	0.026
6) <i>Ptychoramphus aleuticus</i>	1	0	0	0
7) <i>Cyclorhynchus psittacula</i>	2	0.042	0.021	0.016
8) <i>Aethia cristatella</i>	10	0.042	0.017	0.029
9) <i>Aethia pusilla</i>	2	0	0	0
10) <i>Cerorhinca monocerata</i>	8	0	0	0
11) <i>Fratercula corniculata</i>	5	0	0	0
12) <i>Lunda cirrhata</i>	7	0	0	0
Mean		0.045	0.019	0.017

The sample sizes and genetic variability of all 12 species are shown in Table 2. The average proportion of polymorphic loci was 0.045: the highest value was 0.125, for *Uria lomvia*. The average heterozygosities also showed similarly low observed (0.019) and estimated (0.017) values. The sample sizes examined were relatively small, ranging from one (*Uria aalge* and *Ptychoramphus aleuticus*) to eleven (*Synthliboramphus antiquus*), but there were no correlations between genetic variability and sample size. Of the 12 alcid species examined, six (*U. lomvia*, *U. aalge*, *C. carbo*, *S. antiquus*, *C. psittacula* and *A. cristatella*) showed intraspecific variation at the EST-2 locus, four (*U. lomvia*, *U. aalge*, *B. marmoratus* and *S. antiquus*) at 6PGD, two (*U. lomvia* and *B. marmoratus*) at α -GPD and only one (*C. carbo*) at PGM-1. Intrageneric variation was found at seven loci (ADH, EST-1, EST-2, and α -GPD for *Uria* and ADH, PGM-2, PT-3 and SOD for *Aethia*) of the 24 loci.

All taxa were monomorphic for the same allele at eight loci (CK-1, DIA, GDH, IDH-2, MDH-1, PEP, PT-1 and PT-2). The other 16 loci showed interspecific genetic variation. The following three patterns of variation were recognized: 1) many different alleles (EST-2, α -GPD, 6PGD, PGM-2 and SOD), 2) alleles forming two or three main groups (CK-2, EST-1, LDH, MDH-2, PT-3, PT-4 and SDH), 3) a few common alleles shared by most species, but unique alleles for some species (ADH, IDH-1, PGM-1 and XR). *C. monocerata*, *F. corniculata* and *L. cirrhata* had the same alleles at α -GPD and SOD, although these two loci were highly polymorphic relative to the other loci examined. The twelve species of the Alcidae were divided into two groups based upon CK-2, EST-1, LDH, MDH-1 and SDH, with a few exceptions. One group was comprised of guillemots and murrelets, and the other consisted of an auk, auklets and puffins. This grouping had also been demonstrated in mitochondrial MDH (MDH-2) by Kakizawa *et al.* (1982). *U. aalge*, *B. marmoratus* and *A. cristatella* had species-specific alleles at the ADH locus. *S. antiquus* had species-restricted alleles at α -GPD, IDH-1 and XR. At the XR locus, *C. carbo* also had a species-specific allele.

Interspecific genetic distance and identity were calculated from Table 3 using Nei's

Table 3. Alleles and their frequencies at variable loci for 12 species of the Alcidae.

Species	ADH	CK-2	EST-1	EST-1	J-GPD	IDH-1	LDH	MDH-2	6PGD	PGM-1	PGM-2	PT-3	PT-4	SDH	SOD	XR
1) <i>U. lomvia</i>	a	a	a	a=.125 c=.375 d=.500	c=.875 d=.125	b	a	a	b=.125 c=.875	b	c	a	a	c	d	b
2) <i>U. aalge</i>	b	a	b	c=.500 d=.500	c	b	a	a	b=.500 c=.500	b	c	a	a	c	d	b
3) <i>C. carbo</i>	a	a	a	c=.800 d=.200	c	b	a	a	b	a=.100 b=.900	c	a	a	c	d	c
4) <i>B. marmoratus</i>	d	b	a	d	b=.400 c=.600	b	b	a	c=.100 d=.900	b	b	a	a	c	d	b
5) <i>S. antiquus</i>	a	a	a	d=.864 f=.136	e	a	a	a	a=.273 b=.727	b	d	c	a	a	d	a
6) <i>P. aleuticus</i>	a	b	c	c	b	b	b	b	d	b	d	b	a	b	c	b
7) <i>C. psittacula</i>	a	b	c	c=.250 d=.750	c	b	b	b	d	b	d	b	b	a	a	b
8) <i>A. cristatella</i>	c	b	c	b=.050 c=.300 d=.200 e=.400 f=.050	c	b	b	b	d	b	d	b	b	a	d	b
9) <i>A. pusilla</i>	a	b	c	c	c	b	b	b	d	b	c	c	b	a	a	b
10) <i>C. monocerata</i>	a	b	c	b	a	b	b	b	c	b	b	c	b	a	b	b
11) <i>F. corniculata</i>	a	b	c	b	a	b	b	b	c	b	a	c	a	a	b	b
12) <i>L. cirrhata</i>	a	b	c	c	a	b	b	b	c	b	b	c	a	a	b	b

Table 4. Matrix of genetic distance (below diagonal) and genetic identity (above diagonal) for 12 species of Alcidae, based on allele frequencies at 24 loci and calculated by Nei's (1972) formula

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) <i>Uria lomvia</i>	—	.906	.917	.782	.713	.570	.573	.566	.607	.548	.591	.607
(2) <i>Uria aalge</i>	.099	—	.856	.740	.638	.532	.536	.572	.575	.489	.532	.553
(3) <i>Cephus carbo</i>	.087	.156	—	.713	.717	.535	.520	.521	.577	.459	.501	.535
(4) <i>Brachyramphus marmoratus</i>	.246	.301	.338	—	.594	.646	.649	.673	.613	.596	.596	.638
(5) <i>Synthliboramphus antiquus</i>	.338	.449	.333	.521	—	.507	.538	.522	.507	.507	.549	.549
(6) <i>Ptychoramphus aleuticus</i>	.563	.631	.626	.436	.680	—	.808	.774	.750	.667	.708	.750
(7) <i>Cyclorrhynchus psittacula</i>	.557	.623	.654	.432	.619	.213	—	.905	.892	.756	.714	.724
(8) <i>Aethia cristatella</i>	.569	.558	.653	.396	.650	.256	.100	—	.816	.721	.679	.689
(9) <i>Aethia pusilla</i>	.499	.554	.550	.490	.680	.288	.114	.203	—	.792	.750	.792
(10) <i>Cerorhinca monocerata</i>	.601	.714	.779	.518	.680	.405	.280	.327	.234	—	.917	.917
(11) <i>Fratercula corniculata</i>	.526	.631	.691	.518	.600	.345	.337	.387	.288	.087	—	.917
(12) <i>Lunda cirrhata</i>	.499	.592	.626	.449	.600	.288	.322	.372	.237	.087	.087	—

formula (1972). The matrix of genetic differences and identities between alcid species is shown in Table 4. The genetic distances between two congeneric species pairs were 0.099 (*Uria lomvia* and *U. aalge*) and 0.203 (*Aethia cristatella* and *A. pusilla*); the average was 0.151. This mean value is higher than the avian mean genetic distance between congeneric species (0.044, Barrowclough 1980). Unexpectedly, the intergenetic distances between the species pairs *Uria lomvia* and *Cephus carbo* ($D=0.087$); *Cyclorrhynchus psittacula* and *Aethia cristatella* (0.100); and *C. psittacula* and *A. pusilla* (0.114), had values

Fig. 1. Dendrogram of 12 species of the Alcidae based on Nei's genetic distances at 24 loci derived by the UPGMA method.

even lower than those of intrageneric species pairs. Genetic distances among the three puffins (*Cerorhinca monocerata*, *Fraterucula corniculata* and *Lunda cirrhata*) were as low as 0.087, in spite of morphological differences. The mean genetic distance of the Alcidae was 0.442 at the genus level, higher than the avian mean (0.214, Barrowclough 1980).

Phylogenetic relationships of the Alcidae

A phenogram of 12 species of the Alcidae was constructed, using genetic distances and the UPGMA method of Sneath & Sokal (1973). The phenogram (Fig. 1) shows that these 12 species are split into two distinct groups. One group is comprised of the guillemots and murrelets and the other includes an auk, auklets and puffins. Among guillemots, *Cephus carbo* and *Uria lomvia* have a genetic distance smaller than that between *U. lomvia* and *U. aalge*. Similarly, *Cyclorhynchus* and *Aethia psittacula* are closer to each other than the latter is to *Aethia pusilla*. The three puffins (*Cerorhinca*, *Fratercula* and *Lunda*), are separated by a genetic distance of 0.087. The positions of *Brachyramphus*, *Synthliboramphus* and *Ptychoramphus* are somewhat further removed from other genera as shown in Fig. 1. *B. marmoratus* is split from the *Uria-Cephus* cluster at a distance of 0.295. *S. antiquus* is separated from the above cluster of *Uria*, *Cephus* and *Brachyramphus* at 0.411. *P. aleuticus* is segregated from the *Cyclorhynchus-Aethia* cluster at a distance of 0.252.

Discussion

Genetic variation and differentiation

The genetic variability of the Alcidae was rather lower than that of birds in general. The proportion of polymorphic loci was 0.045, and the mean observed and expected heterozygosities were 0.019 and 0.017, respectively. The avian mean heterozygosity of 0.053 (Barrowclough 1983) is about 2.5 times larger than that of the Alcidae. No significant correlation was observed between sample size and heterozygosity among the 12 alcid species we have studied, which constitute about half of the Alcidae of the world. Therefore, the low level of genetic variability among the Alcidae is probably not due to small sample size, although the possibility cannot be ruled out.

The Alcidae is a small family consisting of 23 species, split into 13 genera, with an average of 1.8 species per genus. This value is remarkably small: the avian mean species number per genus is 4.4 (Bock & Farrand 1980). Genetic distances of the Alcidae were 0.151 at the species level and 0.442 at the genus level. These values are rather larger than the respective avian mean distances. These results support the bi-group classification of the Alcidae. At the same time, they indicate the ancient origin of species divergence in this family.

Phylogenetic relationships of the Alcidae

Although not all alcid genera were treated, two main groups were recognized in this study. This division of the Alcidae has been proposed by Kakizawa *et al.* (1982) based on an electrophoretic study of mitochondrial MDH (MDH-2 in this study), and is con-

firmed by the present work on 24 protein loci. In addition to the MDH-2 locus, EST-1, CK-2 and LDH were the key enzyme loci responsible for this two-group division. This bi-group classification originated from Ogilvie-Grant (1898), whose basic division was between Alcinae and Fraterculinae. In the Alcinae, the lores are covered with feathers from the edges of the eyes to the external nostril, which is naked or covered with feathers. On the other hand, Fraterculinae have lore feathers which cover from the edges of the eyes to the base of the bill, but which do not reach the external nostril, which is covered with keratinized scales. The two subfamilies proposed by Ogilvie-Grant have not been used until now. However, bi-group classification based upon protein variations in the Alcidae agrees completely with that of Ogilvie-Grant. In addition, Alcinae and Fraterculinae are separated by a genetic distance of 0.582, which corresponds to the genetic distance (0.592) between families of the Emberizidae and the Fringilidae (Awise *et al.* 1980). We conclude that the use of Alcinae and Fraterculinae as subfamilies of the Alcidae is worthwhile.

Three groupings of genetically related species of the Alcidae emerged from this study. The first group consists of *Uria* and *Cepphus*, which have a similar genetic constitution. Among the three species of *Uria* and *Cepphus*, *Uria aalge* had two species-specific alleles at ADH and EST-1, and *Cepphus carbo* had one species-specific allele at XR. *Uria lomvia* had two (EST-2 and α -GPD), and *Cepphus carbo* had one (PGM-1) species-specific allele at low frequency. There were no other unique alleles among the three species at the 24 loci studied. *Uria* and *Cepphus* had been united (e.g. Ogilvie-Grant 1898, Hand-List of Japanese Birds 1932, 1942), until the anatomical divergence of *Cepphus* was reported (Storer 1946, Kuroda 1954). We suggest, based on the present genetic study, that *Cepphus* should be included in *Uria* because of the small genetic divergence between the two species.

Uria lomvia and *U. aalge* form a species pair of a similar eco-morphological type with slight differences in structural proportions and tongue shape. *U. lomvia* has a similar tongue shape to that of *Cepphus* and the puffins. On the other hand, *U. aalge* has a corneous and slender tongue such as *Brachyramphus* and *Synthliboramphus* have, reflecting its food preference (Kuroda 1954, Spring 1971). Species of *Uria* are offshore deep-sea feeders, while *Cepphus* is a coastal and bottom feeder with a large gizzard and a long caeca, which are unique among alcid species (Kuroda l.c.). Osteological wing-sternum and leg-pelvis proportions of *Cepphus* are different from those of *Uria*, and similar to those of Fraterculinae (Storer 1946, Kuroda 1954). These eco-morphological deviations of *Cepphus* from *Uria* seem to be relatively recent events since their genetic relationship was proved to be very close in the present study. On the other hand, Strauch (1985) deduces an entirely different phylogenetic position for *Cepphus*. He forms the tribe Cepphini, including *Synthliboramphus* and *Endomychura*. However, the only key factor uniting them is a clutch size of two eggs, all other taxa having a clutch size of one egg. Strauch himself described the need to obtain biochemical evidence which would suggest genetic relationships of *Cepphus* to other alcid species.

The second group of closely related species is that including *Cyclorrhynchus* and *Aethia*, which showed a pattern similar to that of *Uria* and *Cepphus*. The genetic dis-

tance between *Cyclorrhynchus psittacula* and *Aethia cristatella* was smaller than that between *A. cristatella* and *A. pusilla*. In *Cyclorrhynchus* and *Aethia*, only *Aethia pusilla* had species-specific alleles at ADH and EST-2 among 12 species examined. On the other hand, SOD^a was an allele restricted to *Cyclorrhynchus* and *Aethia*. There was no allele which distinguished *Cyclorrhynchus* from *Aethia*. In morphological studies, the separation of *Cyclorrhynchus* as a single genus and species from *Aethia* has been proposed by Kuzlova (1957) based solely on its bill character. Bédard (1969) found a resemblance between the tongues of *Cyclorrhynchus* and *Aethia*, although the tongue of the former was narrow compared with that of the plankton-eating *Aethia*. Kuroda (1954, 1955) proposed, based on his osteological study that *Cyclorrhynchus* should be annexed to *Aethia*, because he saw no important difference between the two genera. Strauch (1985) also unites *Cyclorrhynchus* and *Aethia* in his compatibility analysis of 33 characters in these species.

The third group of closely related species contains the three puffins. *Cerorhinca*, *Fratercula* and *Lunda* are currently treated as generically distinct forms. In this study, however, each puffin had only one allele which was not shared by the other two species. Interestingly, α -GPD^a and SOD^b were found only in these three of the 12 alcid species. The genetic distances between these puffins were small ($D=0.087$), even lower than the mean genetic distance (0.151) at the species level of the Alcidae. Although each puffin is morphologically distinct, one morphological characteristic common to these three puffins is the dropping of bill appendages after the breeding season. *Cerorhinca monocerata* has a deciduous elevated horn at the base of the culmen and *Fratercula corniculata* has eyelids with deciduous horny appendages during the breeding season. Similarly, *F. corniculata* and *Lunda cirrhata* have a deciduous shield covering the base of the bill. These deciduous phenomena are, however, known in a few other alcids (*A. cristatella*, *Cyclorrhynchus* and *Alca*). In addition, Kuroda (1954, 1955) suggested osteologically close relatedness among the three puffins. It is likely that *Cerorhinca* and *Lunda* are included in *Fratercula*.

Based on the above genetic data, we divide the 12 alcid species into two subfamilies, Alcinae and Fraterculinae, each of which contains three groups of related species. Alcinae consists of *Uria* (including *Cephus*), *Brachyramphus* and *Synthliboramphus*. Fraterculinae consists of *Ptychoramphus*, *Aethia* (including *Cyclorrhynchus*) and *Fratercula* (including *Cerorhinca* and *Lunda*). The above six groups seem to have speciated in relatively ancient periods but species within each group are less diverged genetically in spite of their eco-morphological divergence. Although further study is needed, these results basically support the current morphological and ecological classification of the Alcidae.

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ウミスズメ科鳥類の遺伝的分化と類縁関係

ウミスズメ科 10 属 12 種のアイソザイム遺伝子座について電気泳動による分析を行ない、遺伝的変異や遺伝的分化の程度を調査し、さらに遺伝的距離に基づく系統樹を作成した。ウミスズメ科の遺伝的変異は

鳥類の平均と比較するとやや小さく、逆に遺伝的分化の程度はやや高かった。今回調査したウミスズメ科の類縁関係は一般的には従来の分類と一致しており、ウミガラス属、ケイマフリ属、ウミスズメ属とコウミスズメ属、ウトウ属、エトビリカ属の 2 つの大きなグループに分割された。しかしながらケイマフリがハシブトウミガラスと近縁になり、ウミオウムはコウミスズメ属に合一することなどが問題点として残り、これらについてはその原因について論議した。

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