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Taxonomy of the bean goose–pink-footed goose

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ABSTRACT

The bean goose *Anser fabalis* and the pink-footed goose *A. brachyrhynchus* breed in the tundra and taiga zones of Eurasia and eastern Greenland, and the taxonomy of the group based on morphology has been controversial. We investigated the phylogenetic relationships within the bean goose–the pink-footed goose complex using mitochondrial control region sequences of 199 individuals collected from the breeding areas in the Palaearctic and Eastern Nearctic. We found three mitochondrial clades geographically distributed to (1) Greenland, Iceland and Svalbard (*A. brachyrhynchus*), (2) the eastern taiga zone (former subspecies *A. fabalis middendorffii*), and (3) the western taiga and the tundra zone (subspecies *A. fabalis rossicus*, *serrirostris* and *fabalis*). MtDNA phylogeny suggests that morphological affinities between the taxa, e.g. in the bill structure, result from convergent evolution due to adaptation to similar habitats. Although a latitudinal cline in morphology was observed, clear phylogenetic discontinuities exist in the taiga and tundra zones supporting a species status for *brachyrhynchus* and *middendorffii*.

1. Introduction

The bean goose *Anser fabalis* (Latham, 1787) and the pink-footed goose *A. brachyrhynchus* Baillon, 1833 breed in the tundra and taiga zones of Eurasia and eastern Greenland (van den Bergh, 1999; Madsen et al., 1999; Mitchell et al., 1999; Nilsson et al., 1999) (Fig. 1). The taxonomy of the bean goose–pink-footed goose species complex is controversial, and evolutionary relationships among morphologically defined species and subspecies have not been resolved. The number of species described has varied from one to four, including up to seven subspecies (Naumann, 1842; Alpheraky, 1905; Hartert, 1914; Buturlin, 1935; Coombes, 1951; Delacour, 1951; Bauer, 1968; Cramp and Simmons, 1977; Sangster and Oreel, 1996; Mooij and Zöckler, 1999). The group shows great geographical variation in morphology, and traits such as bill colour pattern, size and shape of the head, bill and body, and colour of the plumage and feet, have been used for taxonomic purposes. Confusingly, individual variation exists in all these morphological traits also within the taxa, and often there is considerable overlap among the alleged subspecies or species. In earlier years this was believed to indicate that intermediate forms exist (Tugarinov, 1941; Delacour, 1951), i.e., that the subspecies were at least locally interbreeding. More recently, attention has been paid to differences in breeding ranges, vocalizations, behaviour, physiology, habitat use, and diet among the taxa (Mathiasson, 1963; van Impe, 1980; Yokota et al., 1982; Miyabayashi et al., 1994; Burgers et al., 1991; see also Sangster and Oreel, 1996, for a review).

Early taxonomists regarded bean geese (here including also the pink-footed goose) breeding in tundra or taiga as separate species (e.g., Naumann, 1842; Alpheraky, 1905; Buturlin, 1935; Berry, 1938; Coombes, 1951) and additionally, many colour-forms were described as species or subspecies (e.g., Alpheraky, 1905; Hartert, 1914; Lönnberg, 1923; Buturlin, 1935). Later, (Dementyev, 1936), (Tugarinov, 1941), and (Delacour, 1951) lumped the taxa into one species, *A. fabalis*, with different numbers of subspecies.

Most researchers have recognized two subspecies groups within the bean goose (including pink-footed goose), distinguished by the habitat types of the breeding areas and morphology. The taiga-breeding subspecies are characterized by elongate shape of the body with long and slender bill, whereas the tundra-breeding subspecies are small and stocky in shape and have a shorter bill that is relatively high near the base. According to Delacour (1951) the taiga subspecies included *A. fabalis fabalis* (Latham, 1787), breeding in the wooded parts of Fennoscandia and northern Russia east to the Ural mountains, and *A. fabalis middendorffii* Severtzov, 1872, breeding in forests of eastern Siberia. The third subspecies included into this group by Delacour (1951), *A. fabalis johanseni* was allegedly breeding in the forested region of western Siberia and intergrading with *fabalis* and *middendorffii*. The validity of *johanseni* and the existence of intergradation zones have been questioned by subsequent authors (Roselaar, 1977; Burgers et al., 1991; Sangster and Oreel, 1996; Mooij and Zöckler, 1999). Delacour (1951) listed into the tundra-breeding subspecies

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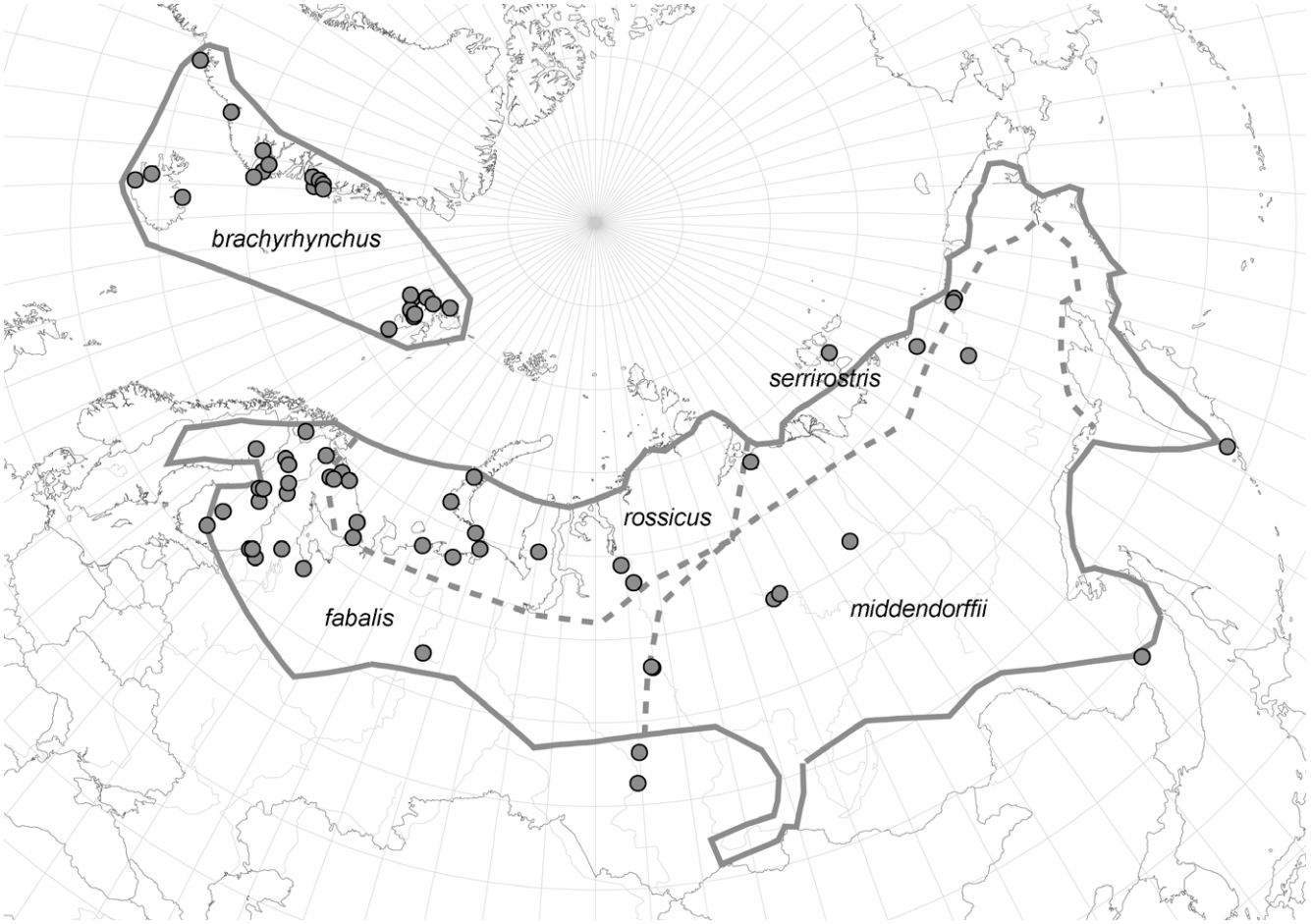

Fig. 1. Map showing the sampling localities. Approximate breeding areas of the taxa are circled.

A. fabalis serrirostris Swinhoe, 1871, breeding in the northeastern parts of Siberia, *A. fabalis rossicus* Buturlin, 1933, breeding in the northwestern Russia, and *A. fabalis brachyrhynchus* Baillon, 1833, breeding in eastern Greenland, Iceland, and Svalbard. According to Delacour (1951), the taiga- and tundra-breeding bean geese intermingle in northern Russia between the Kanin Peninsula and the Khatanga River. Delacour's classification has been largely followed until recently, with the exception of the pink-footed goose, *A. brachyrhynchus*, which has been given a species status by many recent authors (e.g., Cramp and Simmons, 1977). Also, for a long time *A. fabalis rossicus* was not recognised as a subspecies in the Russian literature (Dementyev and Gladkov, 1967; Stepanyan, 1978), even up to recent years (Stepanyan, 2003). Sangster et al. (1999) recently suggested that the bean goose should be split again into two monotypic species. They lumped the subspecies *fabalis*, *johanseni* and *middendorffii* into monotypic *A. fabalis*, the taiga bean goose, and subspecies *rossicus* and *serrirostris* into *A. serrirostris*, the tundra bean goose (Sangster et al., 1999). On the contrary, Mooij and Zöckler (1999) have suggested distinguishing four subspecies of *A. fabalis* belonging to one species.

Most of the earlier studies on the bean goose–pink-footed goose complex, putatively confounded with problems in subspecies identification and opposing views about the existence of intermediate individuals, have been based on individuals captured or observed in the non-breeding areas. In geese, pair-formation primarily takes place during the winter and early spring (Cooke et al., 1975) and, therefore, gene flow on breeding grounds is low and connectedness of the populations during the non-breeding season is also relevant. Western breeding *fabalis* and *rossicus* winter in Europe with partially overlapping ranges (Nilsson et al., 1999; van den Bergh, 1999; Heinicke et al., 2005). A large number of bean geese of both these subspecies, identified based on shape and structure of the bill and head, were captured and marked in The Netherlands. Based on morphological measurements, the two groups were shown to deviate from a random sample of a normally distributed population (Burgers et al., 1991), suggesting that two identifiable taxa exist. Further, *fabalis* and *rossicus* birds were recovered from different breeding areas (Burgers et al., 1991). The breeding population of the pink-footed goose *A. brachyrhynchus* winters in western Europe (Madsen et al., 1999; Mitchell et al., 1999) partially overlapping with *rossicus* and *fabalis*, but it is not known to form mixed pairs with the latter two taxa. The eastern breeding *serrirostris* and *middendorffii* winter in Asia, but differ from each other with respect to habitat preferences and vocalizations (Cramp and Simmons, 1977; Yokota et al., 1982; Miyabayashi et al., 1994). Because of mostly separate breeding and wintering areas, comparisons between the western and eastern subspecies have been scanty, except for morphological measurements.

Taxonomical knowledge of the bean goose–pink-footed goose complex is essential for population management and conservation purposes. The total population of the bean goose is not regarded as threatened, but local decreases have been reported in recent years, especially for eastern subpopulations (e.g. Yokota et al., 1982; Rogacheva, 1992; Andreev, 1997; Mooij and Zöckler, 1999; Emelyanov, 2000; Gärdenfors, 2000; Melnikov, 2001; Rassi et al., 2001; Bakken et al., 2003; Heinicke et al., 2005). Here, we use mtDNA control

region sequences to construct a molecular phylogeny in order to examine the evolutionary and taxonomic relationships of the bean goose–pink-footed goose complex. Contrary to many previous studies (listed in Sangster and Oreel, 1996) carried out in the non-breeding areas, material for this study was collected from the breeding areas of the species. We will examine whether the bean geese breeding in taiga and tundra habitats represent distinct species, or whether the observed morphological variation represents polymorphism within a species. A further aim is to clarify the taxonomical status of the pink-footed goose.

2. Materials and methods

The total sample comprises of 199 individuals from 14 geographical areas (Fig. 1, Table 1, Supplementary Table 1). All material was collected from breeding areas during ringing projects (blood), from hunters (muscle), or from museums (feathers). Feather samples were obtained from zoological and natural history museums in Amsterdam (ZMA), Copenhagen (ZMUC), Gothenburg (MNHG), Helsinki (FMNH), Iceland (IINH), Moscow (ZMMU), Oslo (ZMUO), Stockholm (NMR), Tomsk (ZMTSU) and Tring (BMNH). The sequences of the pink-footed goose have been published earlier (Ruokonen et al., 2005).

Total DNA was isolated using proteinase-K digestion followed by phenol–chloroform extraction (blood, muscle) and ethanol precipitation, or proteinase-K digestion followed directly by ethanol precipitation (feathers) (Sambrook and Russell, 2001). MtDNA control region and flanking areas were amplified in two fragments as in Ruokonen et al. (2000a) from eight individuals representing six different haplotypes. The sequences obtained cover tRNAglu and almost the complete control region (C stretch in the 5' end and 11 bp from the 3' end were excluded). Additional mtDNA control region sequences were obtained from GenBank (Accession Nos. AF159951 (ROS2b), AF159952 (BRA1) and AF159953 (BRA3)). From the remaining 191 individuals, the 5' region of the control region (CRI) was amplified and sequenced. Standard PCR reactions were carried out using PCR conditions and primers L16642 and H411-AL (other tissues than feathers) and L180 and H466 (feathers) as described elsewhere (Ruokonen et al., 2000a, 2000b). Precautions taken to avoid amplification of nuclear copies of mtDNA (numts) have been published earlier (Ruokonen et al., 2000a). Additionally, 43% of the material for DNA isolation was feathers, which should be less prone to problems with numts (Sorenson and Quinn, 1998). Double-stranded sequencing of PCR products was carried out by using BigDye 3.0 or 3.1 and ABI PRISM 377 according to the manufacturer's instructions. PCR primers were used for sequencing. Haplotype sequences have been submitted to GenBank with Accession Nos. EU186805–EU186812 and EU186813–EU186828.

Sequences were aligned manually, and Modeltest 3.06 (Posada and Crandall, 1998) was used to choose the DNA substitution model. HKY model (Hasegawa et al., 1985) was used to estimate genetic distances of both the complete control region and the CRI in PAUP*4.0b10 (Swofford, 2003). Maximum parsimony analysis was carried out with PAUP* using TBR branch swapping and random addition of taxa. Transitions and transversions were weighted equally and gaps were excluded. A consensus tree was constructed based on a heuristic search of 1000 bootstrap replicates. Branches with zero lengths or less than 50% support were collapsed. Bayesian analysis was performed with MrBayes v3.0 (Huelsenbeck and Ronquist, 2001). The search was run with four incrementally heated MCMC chains for 106 generations using a GTR + gamma model of substitution and default priors. Sampling frequency was set to 100, and the first 1000 trees were discarded as burn-in, yielding a total of 9001 trees for constructing the consensus tree. Mitochondrial control region sequencies of the greylag goose *A. anser* (GenBank Accession No. AF159961) and the white-fronted goose *A. albifrons* (GenBank Accession No. AF159958) were included as outgroups. A parsimony network for the shorter mtDNA control region sequences was constructed using program TCS 1.21 (Clement et al., 2000). In addition, bayesian analysis was carried out with an alignment including both short and long sequences (data not shown). Compared to the Fig. 2, the same clades were retained in this analysis with good support (posterior probabilities: *brachyrhynchus* 1.0, middendorffii 0.8 and *fabalis–rossicus–serrirostris* 0.7).

Mantel test was performed in TFPGA (Miller, 1997) separately for birds breeding in tundra and taiga using geographical distances (difference between two populations in longitudes) and the number of nucleotide differences among the sampling areas corrected for within-population polymorphism (equation 9.22 in Nei, 1987). Sampling areas with less than five individuals were excluded from the analysis. Statistical significance was tested by permutation as implemented in TFPGA (Miller, 1997).

Table 1
Sampling areas and numbers of sampled individuals ($N = 199$)

Sampling area	N
Greenland	17
Iceland	13
Svalbard	23
Norway, Finnmark	2
Sweden, Lapland	3
Finland, North Ostrobothnia	15
Finland, Lapland	15
Russia, Kola Peninsula	8
Russia, European Russia	27
Russia, Novaya Zemlya	6
Russia, West Siberia	12
Russia, Enisey	7
Russia, Yakutia	20
Russia, Kamchatka	19
Russia, Amur	12

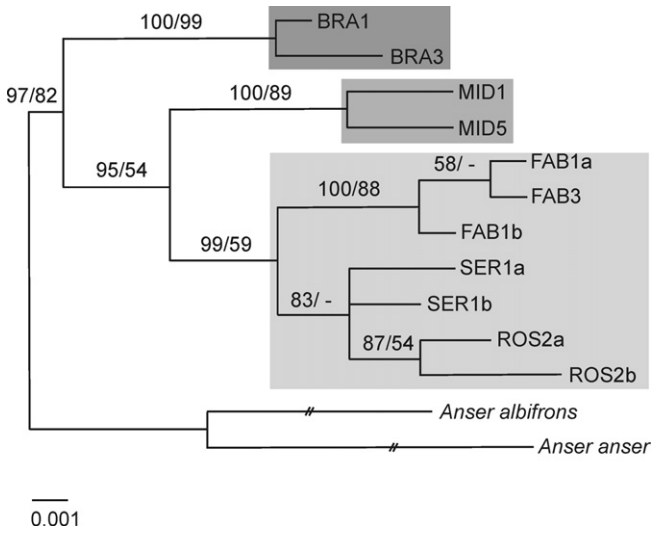

Fig. 2. A consensus tree of the mtDNA control region sequences (1164 bp). Branches with less than 50% support were collapsed. Support exceeding 50% in Bayesian and maximum parsimony replicates, respectively, are shown in each branch. Branch lengths are given according to Bayesian analysis. The three major clades found are shown with coloured boxes. Letters a and b in haplotype names indicate haplotypes which are identical for 221 bp sequences but differ for 1164 bp sequences.

Of the total sample of 199 individuals, morphological measurements were obtained for 84 birds (26 *brachyrhynchus*, 20 *fabalis*, 14 *middendorffii*, 10 *rossicus* and 14 *serrirostris*). All measurements were taken by the same person (T. Aarvak). Age from the original label was followed, unless if it was determined wrong based on colour pattern of the bill and barring of feathers in the body flanks (Madge and Burn, 1988). Only adult individuals were included in the morphological analyses. Minimum wing length (not flattened cord) was measured to the nearest mm using a stopped ruler, but had to be excluded as a proxy for body size because in 32% of the individuals the wings were not fully grown after moult. Bill length, bill height, bill nail length and colour height (the height of the yellowish/pink area, measured from bottom of the upper beak and upwards, behind the nostril), were measured to the nearest 0.1 mm with vernier callipers. Grinning patch was not measured *in situ*, but from digital pictures with ImageJ 1.33u. Except for colour height for *middendorffii* and *serrirostris* ($p < 0.001$), the other variables (bill length, bill height and bill nail length) were not significantly different from a normal distribution (Kolmogorov–Smirnov test, $p > 0.1$). Colour height was therefore excluded from further analyses. Statistical analyses were carried out with SPSS 15.0 for Windows.

Grouping of the individuals for morphological analyses was done primarily based on the original taxon identities. However, in some cases the original identification of individuals was not congruent with the genetical analysis (see Sections 3 and 4). An independent re-classification of those individuals was carried out by an expert familiar with all the taxa involved. The blind test was based on photos and morphological measurement data (without information about the sampling location or the original taxonomical assignment).

3. Results

3.1. Sequence variation

The alignment included tRNAglu and almost the complete mitochondrial control region (Table 2), excluding the hairpin-loop region (Quinn and Wilson, 1993) and the 3' end. The length of the alignment was 1164 bp of which 1091 nucleotide positions were constant. Of the 73 variable nucleotide positions, 25 were parsimony-informative. When the outgroup sequences were excluded, the number of variable nucleotide positions decreased to 30, and 18 of them were parsimony-informative. Transitions were observed in 24 and transversions in four nucleotide positions. In one nucleotide position multiple changes were observed and another contained a deletion.

In the shorter fragment of the control region (CRI, 221 bp) sequenced from all 199 individuals, 20 variable sites were found and 11 of them were parsimony-informative (Table 3). Thus, this short fragment encompasses 67% of the total variation in the larger fragment of the control region in the bean goose and the pink-footed goose. Variation observed included 16 transitions, one transversion, one deletion, and two nucleotide positions each had three different nucleotides.

3.2. Phylogenetic trees

Bayesian and maximum parsimony methods converged to the same tree topology (Fig. 2). In maximum parsimony analysis the length of the best tree was 84 steps (consistency index = 0.845, rescaled consistency index = 0.717). Three well-supported clades were found within the ingroup: (1) *brachyrhynchus*, (2) *middendorffii*, and (3) *rossicus*, *serrirostris*, *fabalis*. Additionally, *fabalis* individuals formed a group of closely related haplotypes. Whereas the posterior probabilities of the Bayesian analysis gave a good support for the tree topology (1.00–0.83), bootstrap support in maximum parsimony analysis was moderate (59 and 54%) for two interior nodes. Because Bayesian phylogenetic analyses are based on likelihood function and an explicit model of nucleotide changes (with a better correction for unequal nucleotide frequencies, rate variation across sites and saturation; Huelsenbeck et al., 2002), the posterior probabilities of the Bayesian analysis were relied on.

Based on variation in the shorter mtDNA fragment (CRI), 22 different haplotypes in three main groups identical to the ones mentioned above were found (Fig. 3). One of the haplotypes (SER1, Fig. 3) was shared by *rossicus* and *serrirostris*.

3.3. Genetic distances

In the long fragment of the control region the average genetic distance of *brachyrhynchus* to *fabalis–rossicus–serrirostris* and

Table 2
Variable nucleotide positions in the mtDNA tRNAglu (nucleotides 1–68) and the control region (69–1164)

	1111
	1111111111111222222222222222222222233333333333346667777889999000 1
	1177789224455566777802222334456667788889999011124445579314834552705783452
	0226804360312734035294789050151373802680147856780251227142213279288309010
BRA1	CGCAACGTAAAATTAGTTCGTATACGGTCTTCCCACCCTGTCCACCTTCCTCTCGCTCGTTCGCTCGACTGCA
BRA3	.....T.....A.....
MID1	T.A..T.....G....C.....CT.TG.....T.....C...C.....G.....
MID5	TAA..T.....G....C.....CT.TG.....-.T.....C.....G.....
SER1a	..A.....G.....G....C.....C...C.....C.....C.....AG.....
SER1b	..A..T....G.....G....C.....C...C.....C..A.....C.....G.....
ROS2a	..A..T....G..C....G....C.....C...C.....C.....C...C..G.....
ROS2b	.....T....G..C....G....C.....C...C.....C.....C..T...G....G
FAB1a	..A.GT....G.....G....C.....C...C.T.....T.....A.....C.....G.....
FAB1b	..A..T....G.....G....C.....C...C.T.....T.....A.....C.....G.....
FAB3	..A.GT....G.....G....C.....C...C.T.....A.....C.....G.....
A. albifrons	...G.TA.....AC.G....C.....T...T..CACAT....C.T.....A...CC..T...G..A..
A. anser	.....T.CGT.GC.GA.CGACGCCTAACTCC.....T..CA.GTT.C.TCTC....T..CTA..T..---TG

Table 3
Variable nucleotide positions in CRI (221 bp)

	1111122222222222333 4456724666677788911 3574581137803802056
BRA1	ATTGCACTCCCCCACCGCCT
BRA2	..................T.
BRA3	.........T..........
BRA4	..............T.....
BRA6	...A................
BRA7	.C................T.
MID1	....GC.CT...TG......
MID2	....GT.CT...TG...T..
MID3	G...GC.CT...TG......
MID4	....GC.CT...TG..A...
MID5	....GC.CT...TG.....-
MID6	....GT.CT...TG......
SER1	G...GC.C.....C......
SER2	G...GC.C.....C....T.
SER3	G...GC.CT..T.C.T....
SER4	....GC.C.....C......
ROS2	G.C.GC.C.....C......
ROS3	G.C.GC.C.T...C......
ROS4	G.C.GCTC..T..C......
FAB1	G...GC.C.....C.T..T.
FAB3	G...GC.C.....C.T....
FAB6	G...GT.C.....C.T..T.

Numbering follows that in Table 2.

middendorffii haplotypes was 1.1%. The two bean goose clades were slightly more closely related with a genetic distance of 0.9%. The genetic distances to outgroups, the greater white-fronted goose and the greylag goose, were 2.0% and 3.7%, respectively. Based on the CRI sequences, genetic distances within the clades were 0.9% for *brachyrhynchus*, 0.7% for *middendorffii* and 1.3% for *fabalis–rossicus–serrirostris*. Again, the average genetic distance of *brachyrhynchus* clade to *fabalis–rossicus–serrirostris* and *middendorffii* clades (3.4%) was greater than between the latter two (2.7%).

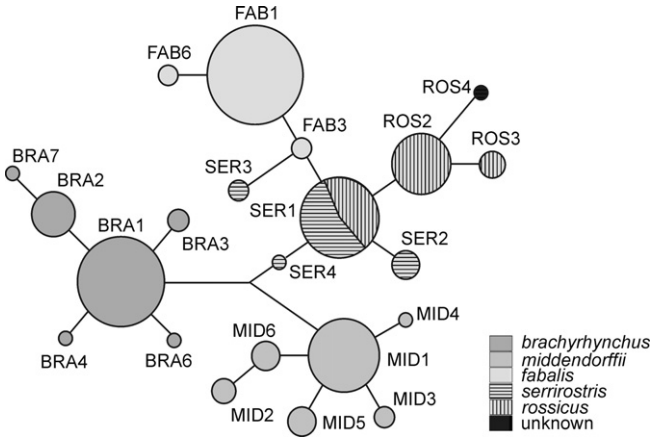

Fig. 3. Minimum spanning network based on CRI of mtDNA in 199 individuals studied. The size of each circle is proportional to the number of individuals having the haplotype. Haplotype names correspond to those in Fig. 2.

3.4. Morphology

Clinal variation in morphology was studied by using bill length as a proxy for body size, which was shown to increase from west to east ($r^2 = 0.5237$, $p < 0.0001$, $y = 51.4679 + 0.1123^{*}x$) (Fig. 4). The ANOVA test showed that there were significant differences between *brachyrhynchus*, *fabalis*, *rossicus*, *serrirostris* and *middendorffii* for the body size variables bill length ($F = 119.6$, df = 4, $p < 0.001$), bill height ($F = 64.1$, df = 4, $p < 0.001$), nail length ($F = 49.1$, df = 4, $p < 0.001$) and grinning patch height ($F = 33.0$, df = 4, $p < 0.001$) (Table 4). In pairwise comparisons of the groups significant differences were found for all measurements (Post-hoc Scheffe, $p < 0.001$, 0.05, 0.01, and 0.01, respectively). One group, *brachyrhynchus* differed significantly from the other groups with respect of all four measurements ($p < 0.001$–0.05). Also, *middendorffii* differed from all groups with respect of bill length ($p < 0.001$–0.001) and from *fabalis* in the three other measurements too ($p < 0.001$–0.001). Two of the groups, *fabalis* and *rossicus*, did only differ in the measurement of grinning patch height ($p < 0.05$). The groups *rossicus* and *serrirostris* differed with respect of bill length and bill height ($p < 0.01$–0.05).

A discriminant function analysis (Stepwise, Wilks' Lambda, Fig. 5) showed that 90.7% of the individuals can be correctly classified to their mtDNA haplotype groups. The final model generated two canonical functions using measurements for bill length, bill nail length and grinning patch height (covariance matrices were not significantly different, Box's $M = 29.269$, $p = 0.356$), but excluded bill height. The percentage of correctly classified individuals was 100.0% for *brachyrhynchus*, 88.2% for *fabalis*, 100.0% for *middendorffii*, 88.9% for *rossicus* and 71.4% for *serrirostris*. When *rossicus* and *serrirostris* were lumped as one group they were classified correctly in 87.0% of the cases.

3.5. Spatial pattern of genetic variation

Based on morphological characters, it has been suggested that bean geese show clinal variation in morphology (Tugarinov, 1941; Cramp and Simmons, 1977), e.g. in both tundra and taiga the sizes of the body and the bill increase from west to east, as was also shown here. As arbitrary sections of a cline should not be regarded as evolutionarily distinct entities (Cracraft, 1983) Sangster and Oreel (1996) did not recognise any subspecies. A gradual change in morphology is considered to indicate that sub-

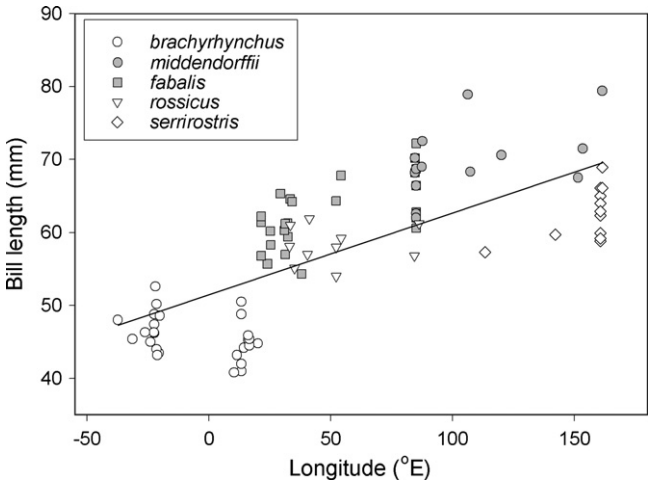

Fig. 4. Bill length as a function of the longitude of the sampling locality. The regression is statistically significant ($r^2 = 0.5237$, $p < 0.0001$, $y = 51.4679 + 0.1123^{*}x$).

Table 4
Morphological measurements of the taxa

Group	Bill length (mm)			Bill height (mm)			Nail length (mm)			Grinning patch height (mm)		
	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*	Mean	SD	*N*
brachyrhynchus	45.8	2.92	26	25.5	1.77	26	12.8	1.17	25	4.7	0.99	26
rossicus	57.8	2.42	10	30.7	1.52	10	16.5	0.84	9	7.29	1.01	10
serrirostris	62.9	3.00	14	33.8	1.52	14	18.2	1.84	14	7.7	1.12	14
fabalis	61.5	4.24	20	30.5	1.89	20	15.3	1.11	20	5.8	1.18	17
middendorffii	69.7	4.98	14	34.1	2.80	14	17.5	1.46	14	8.4	1.04	10

stantial gene flow among the neighbouring populations is taking place. Thus, genetic and geographic distances should show a positive correlation in accordance with the isolation by distance model (Wright, 1978; Slatkin, 1993). Whereas, a sharp boundary in genetic differentiation between the areas shows that the populations do not interbreed and that they should be considered as separate taxa. Consequently, we examined if the patterns of genetic variation show phylogenetic discontinuities or isolation by distance along the west–east gradient.

The spatial pattern of genetic variation within the bean goose–pink-footed goose complex was analysed separately for the birds breeding in tundra and taiga based on genetic distances between the sampling localities. For tundra-breeding *brachyrhynchus*, *rossicus* and *serrirostris* no statistically significant association was found between genetic and geographic distances among all sampling areas (Mantel test, $r = 0.41$, $p > 0.05$) (Fig. 6). Association was non-significant also when *brachyrhynchus* was excluded ($r = 0.65$, $p > 0.10$). A clear phylogenetic discontinuity was found between *brachyrhynchus* vs. *rossicus* and *serrirostris*: the sampling localities in the groups differed by Nei's dA 4.98–5.64, whereas, *rossicus* and *serrirostris* sampling localities differed only by Nei's dA 0.24–0.64. Within *brachyrhynchus*, *rossicus* and *serrirostris* the levels of genetic divergence were small (Nei's dA 0.01–0.10, 0.00 and 0.25, respectively).

In the taiga group, *fabalis* and *middendorffii*, a significant positive correlation was observed when all sampling localities were included ($r = 0.93$, $p < 0.05$)(Fig. 6). However, this significant correlation emerged because of a mixture of *fabalis* and *middendorffii* individuals in the West Siberian sample, and when excluded, the estimate became non-significant despite the high correlation ($r = 0.96$, $p > 0.05$). In fact, the three individuals with *fabalis* type mtDNA in the West Siberian sample were collected in early May, suggesting that they were still on migration towards the breeding areas (see below). Thus, a probable phylogenetic discontinuity was found also between *fabalis* and *middendorffii* with Nei's dA of 5.82–6.16 between them. Within *fabalis* and *middendorffii* no genetic divergence was found between sampling localities (Nei's dA 0 for both groups).

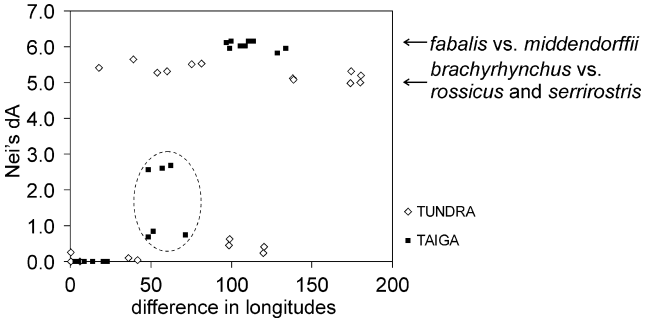

Fig. 6. The geographical distance between the sampling areas (difference in longitudes) plotted against Nei's genetic distance. Circled squares are comparisons between the West Siberia and other sampling areas (see Section 3 for a detailed explanation).

3.6. Disagreements between morphological identification and genetical results

Altogether 15 (7.5%) of the original morphological assignments of individuals (i.e. in the field or museum at the time when the birds were sampled) were conflicting with mtDNA results. Eight individuals from Western Russia were originally determined as *A. fabalis fabalis*, whereas based on mtDNA they belonged to the tundra-breeding group. Seven of them were re-classified as *rossicus* based on independent re-identification (see Section 2) and/or discriminant function analysis of morphological data, but the taxonomical position of one individual remained uncertain. This individual was a subadult and therefore morphological measurement data were not fully informative for identification purposes. A difference in taxonomical practices explains the existence of many misclassified *rossicus* individuals. In some Russian literature the bean geese breeding in western Russia were considered to form one subspecies, *A. fabalis fabalis*, and subspecies *A. fabalis rossicus* was not recognised (Dementyev and Gladkov, 1967).

One nesting female from Novaya Zemlya was originally identified as *brachyrhynchus*, because of an untypical rose bill stripe (Kalyakin, 2001). Based on mtDNA, discriminant function analysis and independent re-identification it clearly belonged to the tundra-breeding group and was re-classified as *rossicus*.

Re-examination of photos and morphological data revealed that three individuals were originally misclassified as *serrirostris*, whereas, and also based on mtDNA, they belonged to *middendorffii*. Three individuals originally assumed to be *middendorffii* were

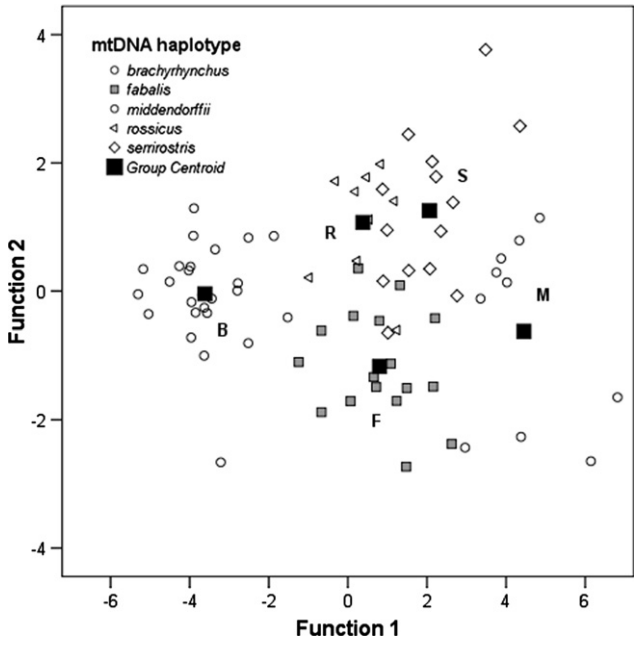

Fig. 5. Discriminant function analysis of morphological measurements.

found to have mtDNA haplotype typical for *fabalis*, which was supported also by discriminant function analysis for two of them. Four of these birds were sampled in early May and were most likely still on migration towards the breeding areas, and two of them in a moulting area, in both cases within the breeding area of another taxon. As a conclusion, it seems that the area from which the birds were sampled is important in taxon assignment in the field: identification is often based on knowledge about the breeding distribution of the taxa rather than on morphological characteristics.

Additionally, one individual, to which no subspecies was originally assigned, remained unclear. Independent re-identification and discriminant function analysis supported either taiga subspecies (*fabalis* or *middendorffii*) or *serrirostris*, but based on mtDNA this bird was placed into the *rossicus* group (the sole carrier of ROS4 haplotype in Fig. 3).

4. Discussion

Classification of the bean goose–pink-footed goose complex has been previously based on morphological and ecological traits, but our molecular data suggest that taxonomical changes are warranted. Distinct lineages in the phylogenetic trees (Figs. 2 and 3) support the existence of three species: (1) the pink-footed goose *A. brachyrhynchus* Baillon, 1833, breeding in Greenland, Iceland and Svalbard, (2) the Middendorff's goose *A. middendorffii* Severtzov, 1872 (former subspecies *A. fabalis middendorffii*), breeding in the eastern taiga zone, and (3) the bean goose *A. fabalis* Latham 1787, breeding in the western parts of the taiga zone and in the tundra zone of the Palearctic. Because mtDNA is inherited maternally only, data from biparentally inherited nuclear markers would be useful to corroborate the interpretation, although also morphometrics supported the distinctiveness of both *brachyrhynchus* and *middendorffii*.

The pink-footed and the Middendorff's goose can be considered monotypic species based on small amounts of intraspecific genetic and morphological variation, whereas, more variation is found within the bean goose. Based on the results of this study, we recognise three subspecies within *A. fabalis*: nominate *A. fabalis fabalis, A. fabalis rossicus* Buturlin, 1933 and *A. fabalis serrirostris* Swinhoe, 1871. The subspecies *fabalis* is almost monophyletic within the species, but a more thorough analysis is warranted for assigning a species status. A larger sample, including birds from the non-breeding areas, suggests that the situation is more complicated than based on breeding individuals only (own unpublished data). Although it is not possible to unambiguously differentiate between western and eastern birds within the tundra-breeding bean geese based on mtDNA haplotypes, separate breeding areas, migration routes and wintering areas suggest that *rossicus* and *serrirostris* should be treated as subspecies. Based on this study, one of the haplotypes (SER1 in Fig. 3) is found throughout the Russian tundra zone. This suggests that there may be gene flow between the western and eastern parts of the distributional area, or that *rossicus* and *serrirostris* have separated recently. A migratory divide exists in western Taimyr (Rogacheva, 1992): birds breeding west from Taimyr migrate to Europe for the winter, whereas eastern breeding birds overwinter in Asia. Because pair-formation takes place during the winter or early spring, when the western and eastern birds are segregated, it is probable that they presently interbreed rarely. Therefore, the most likely reason for the common haplotype SER1 in *rossicus* and *serrirostris* is a recent common ancestry of the subspecies. In West Siberia both *middendorffii* and *fabalis* haplotypes were found, and it was not possible to identify the species for all these individuals based on morphology. Whether this is because the species are utilizing the same habitat (a species border) or interbreeding (hybrid zone) in this area cannot be confirmed based on mtDNA only. No *fabalis* haplotypes were found east, or *middendorffii* haplotypes west, of this area.

Most of the previous authors have considered adaptation to the habitat type, tundra vs. taiga, significant in the evolutionary history and taxonomical classification of the bean goose–pink-footed goose complex (Naumann, 1842; Alpheraky, 1905; Buturlin, 1935; Berry, 1938; Coombes, 1951; Delacour, 1951; Ploeger, 1968; Sangster and Oreel, 1996). Many of the morphological characters separating the taiga- and tundra-breeding geese are shared by the taxa breeding in similar habitats and thus potentially indicate common ancestry for them. Accordingly, Ploeger (1968) suggested that the pink-footed goose as well as the bean geese breeding in tundra and taiga were differentiated to some extent already before the last glacial, whereas the subspecies developed through vicariant events during the last glacial. Instead of synapomorphies, morphological affinities of the taxa may be determined by symplesiomorphic character states or obscured by morphological convergence due to adaptations to similar habitats and food resources. In this study, we have shown that the phylogenetic relationships of the taxa do not follow the habitat types, as phylogenetic discontinuities were found both between and within habitat types. Therefore, similar morphological characteristics shared by the taxa studied are likely convergent changes due to habitat similarity (e.g., Grant and Grant, 1995; Zeffer et al., 2003; Irestedt et al., 2004).

The phylogenetic tree does not give a definite answer to whether the common ancestor of the taxa was breeding in the tundra or taiga. If the ancestral population inhabited tundra habitats, which were prevalent during the ice ages (Andersen and Borns, 1997), it means that adaptation to taiga habitat has taken place twice independently: first when *A. middendorffii* diverged and second when *A. fabalis fabalis* colonised the western taiga zone. An example of adaptation to foraging in similar habitats is the structure of the bill: in the bean and Middendorff's geese breeding in taiga, the bill is typically long and slender with a relatively low base of the bill, whereas in the bean and pink-footed geese breeding in tundra the bill is shorter, with a relatively higher base of the bill, irrespective of the phylogenetic history of the taxa.

A longitudinal cline with body size increasing from west to east has been found previously in, for example, the dunlin *Calidris alpina* (Wennerberg et al., 1999) and in the white-fronted goose *A. albifrons* (Ely et al., 2005) in addition to bean, Middendorff's and pink-footed goose (Cramp and Simmons, 1977; this study). We did not find patterns of isolation by distance in the genetic differentiation, suggesting that the cline is not formed by gene flow between neighboring areas. Longitude is not a biologically meaningful variable and the existence of the cline is probably related to a west–east gradient of decreasing temperature (Danilov, 1966). In the greater white-fronted goose the body size has been shown to correlate positively with temperature on the breeding grounds, breeding habitat, and migration distance (Ely et al., 2005).

Discriminant function analysis showed that it is possible to identify the taxa in 87% of the cases using three morphological measurements: bill length, bill nail length and grinning patch height. Bill height did not contribute significantly in discrimination of the groups. Nonetheless, most of the measurements were overlapping in *A. fabalis* and *A. middendorffii*, and *A. brachyrhynchus* was the only taxon with non-overlapping measurement ranges. Including sex as one of the variables would probably increase the proportion of correctly assigned individuals, as there is sexual dimorphism in geese (Cramp and Simmons, 1977; Ely et al., 2005). Obtaining morphological measurement data obviously requires that the individual is in hand. In our sample from the breeding areas, 7.5% (10.0% if *A. brachyrhynchus* is excluded) of the individuals were originally misidentified based on morphology and sampling locality. In order to be able to carry out census counts for population management and conservation purposes it should be possible to identify the taxa unambiguously. Our results suggest

that, in the absence of diagnostic morphological traits, morphological measurements (including also others not used here, see e.g., Burgers et al. 1991) or genetical analyses are needed for reliable identification of the taxa especially in their wintering areas.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ympev.2008.04.038.

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