

Status of the form *barabensis* within the '*Larus argentatus-* *cachinnans-fuscus* complex'

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ABSTRACT Between 19th July and 1st August 1997, at the Chany Lakes in southwestern Siberia, data were collected on phenotype features and behaviour of the local populations of gulls *Larus* belonging to the taxonomically vague form *barabensis*. These were compared with data from the literature and museum material on the morphological, oological and behavioural characters of *L. c. cachinnans* and *L. (fuscus?) heuglini*, as well as those of some other related gull forms. In size, proportions and coloration, *barabensis* most closely resembles *heuglini*, while also showing

some admixture of *cachinnans* characters. The authors conclude that *barabensis* is a well-defined taxon that has arisen as a result of introgression by *cachinnans* genes into *heuglini* populations as the latter expanded their range southwards. They suggest that *barabensis* be treated as a subspecies of *L. heuglini* unless the latter's status as specifically distinct from Lesser Black-backed Gull *L. fuscus* is proven to be unwarranted.

The various forms of large gull *Larus* that breed in Europe and, particularly, Asia have for some time been a source of much confusion among taxonomists. Traditionally, they have been treated as subspecies of the Herring Gull *L. argentatus* or the Lesser Black-backed Gull *L. fuscus*, although the populations breeding in south Europe and southwest Asia have often been regarded as representing a third species, the Yellow-legged Gull *L. cachinnans* (see e.g. Garner & Quinn 1997). As a group, all these populations are generally referred to as the '*Larus argentatus-cachinnans-fuscus* complex'. For the sake of clarity, the different populations are here referred to by their scientific names.

The large white-headed gulls inhabiting lakes of the Ishim, Barabinsk and Kulunda steppes, between 52° and 58°N in the Omsk region of southwest Siberia (fig. 1), are among the least well-studied Palearctic representatives of this complex. This is manifested, in particular, by the wide variation in opinion regarding their systematic position. They have been placed by various authors in different species, either Herring Gull or Yellow-legged Gull, being regarded either as a local population within a particular subspecies (namely, '*L. argentatus taimyrensis*') or as another, separate subspecies (*L. cachinnans barabensis*) (Dement'ev 1951; Johansen 1960). A further view is that these gulls are closely related to the northern form *heuglini* (Filchagov 1993), apparently of European origin, which, in turn, is regarded either as an independent species, commonly referred to as 'Siberian Gull' or 'Heuglin's Gull' (Stepanyan 1990), or as a subspecies of Lesser Black-backed Gull (Cramp & Simmons 1983). The probable genealogical relationship between *barabensis* and the Armenian Gull *L. (cachinnans?) armenicus* has also been discussed (e.g. Filchagov 1993). In

recent reviews of the Russian avifauna, *barabensis* is not accepted as a valid race, on the grounds that it is not sufficiently distinct from such taxa as *taimyrensis* or nominate *cachinnans* (Stepanyan 1975; Yudin & Firsova 1988).

Significantly, all these discussions have taken place in the almost complete absence of reliable data on the morphological features, field characters and natural history of the gulls in question (Garner & Quinn 1997). The aim of the present study is to fill, at least partly, the gap in our knowledge of these 'enigmatic' birds.

The range of *barabensis* extends westwards to, probably, the eastern foothills of the southern Urals, some 600 km west of the well-documented breeding colonies on Tenis Lake (locality 2 in fig. 1); in addition, a few *barabensis*-type gulls (which cannot be distinguished with certainty from *heuglini* types) occur farther west, at the Volga-Kama confluence and in Nizhniy Novgorod region (5 & 6 in fig. 1). This gull very probably breeds also in the Kulunda steppe (locality 3 in fig. 1). In northeast Kazakhstan, individuals with *cachinnans*-type features but with wingtip pattern approaching that of *barabensis* are rather common, and may be hybrids between those two forms.

From 19th July to 1st August 1997, we conducted field studies in two localities about 80 km apart within the breeding range of *barabensis*. On the Malye Chany Lake (54°40'N, 78°E), we captured gulls, and made tape recordings in a non-breeding flock consisting of about 20-30 individuals. On the Bol'shie Chany Lake (54°40'N, 77°E), similar studies were carried out in a nesting colony on Uzkoredkiy Island during the period when most of the chicks had already left the nest. Altogether, 12 adults (six males and six females) were captured, and from these, as well as from ten chicks, blood samples were



Fig. 1. Breeding areas of *L. heuglini* and *L. cachinnans*. Note areas of *L. heuglini* and *L. cachinnans*.

obtained for comparison with those of the collection of the Moscow State University series of *cachinnans* and *taimyrensis*.

Genetic studies

On the lakes to 105 m above sea level, at least two or three most often situated on the very dense, a Nests are placed on flattened rocks carried ashore, they are somewhat like a mound, never more than 0.5-1.5 m in diameter, 30-1

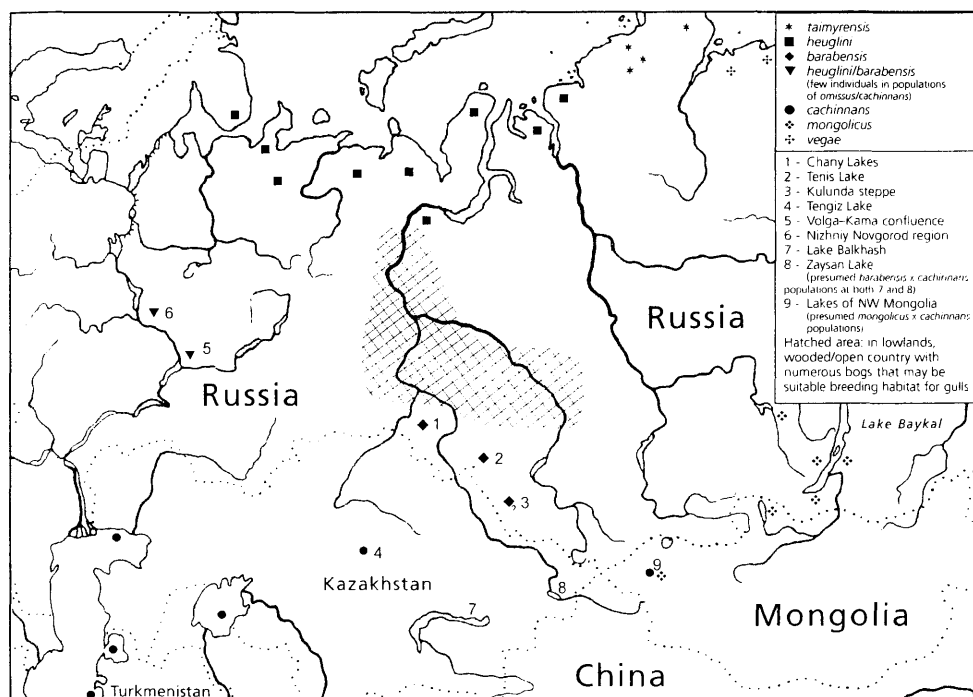


Fig. 1. Breeding areas of different populations of the '*Larus argentatus-cachinnans-fuscus* complex'. Note areas of hybridisation. Western populations of *taimyrensis* appear almost indistinguishable from *heuglini* and eastern ones from *vegae*.

obtained for subsequent genetic analysis. We compared the characteristics of these gulls with those of the few (12) others held in the collection of the Museum of Zoology (Moscow State University), as well as with series of *cachinnans* specimens from the Caspian Sea, and of *heuglini* and *taimyrensis*.

General features of breeding biology

On the lakes of the Barabinsk lowlands (up to 105 m above sea level), the gulls breed in at least two different habitats. Colonies are most often situated at shallow lake margins, bounded on the shore side by a broad belt of very dense, almost impenetrable reedbeds. Nests are placed either on a layer of dead, flattened reeds or on a carpet of jetsam carried ashore by the action of the waves; they are sometimes built on the abandoned lodge of a Muskrat *Ondatra zibethicus*, but never more than 3-5 m from open water that is 0.5-1.5 m deep. The nest itself is a bulky structure, 30-120 cm across and up to 30 cm

in height, constructed of dead reed stalks and leaves. According to Khodkov (1981), the largest colonies are found mainly in this habitat type. They comprise up to 200 pairs and occupy an area of up to 10 ha, with minimum distance between nests averaging 8.8 m (range 3-25 m), although most reedbed colonies are rather small, consisting of 10-40 breeding pairs. Some nests are apparently used for many years (Khodkov 1981).

A second habitat type consists of small, dry islands partly covered with woods of tall, mature birch *Betula*. There, the gulls use level and open sandy-clay areas on the central, highest part of the island, as well as low earth bluffs along its shores, nesting among low, generally sparse grassy vegetation. Nests in such habitat are usually far less bulky than those in reedbeds; not infrequently, the nest looks simply like a shallow depression in the ground, carelessly lined with a thin layer of dry grass. In contrast to reedbed colonies, the nests on small islands are widely dispersed, being separated by distances of about 20 m and more. It was in

Table 1. Mean size (in mm) of *barabensis* eggs compared with corresponding data on some other representatives of the '*Larus argentatus-cachinnans-fuscus* complex'. Figures show means with (in parentheses) S.D. and range where available.

TAXON/ POPULATION	LOCALITY	SAMPLE (NO.)	LENGTH	BREADTH	SOURCE
<i>armenicus</i>	Transcaucasia (Sevan Lake)	113	68.1 (2.3; 61.5-74.9)	48.1 (1.4; 45.1-51.0)	Filchagov 1993
<i>armenicus</i>	Transcaucasia (Sevan Lake)	153	68.3 (2.9; 59.4-75.9)	48.7 (1.6; 42.5-52.0)	Buzun 1993
<i>cachinnans</i>	Black Sea	185	72.8 (63.3-80.5)	50.4 (44.6-58.5)	Kostin 1983
<i>cachinnans</i>	E Azov region	311	70.9 (63.0-79.6)	50.4 (46.0-53.5)	Kazakov & Yazykova 1982
<i>cachinnans</i>	Volga delta	66	71.2 (65.7-81.5)	49.6 (44.4-52.8)	Lugovoy 1958
<i>cachinnans</i>	SW Caspian Sea	56	72.0 (61.0-79.0)	49.0 (40.0-52.0)	Dyunin 1948
<i>cachinnans</i>	SE Caspian Sea	126	70.1 (2.9; 63.0-78.2)	48.6 (1.6; 42.1-52.3)	Panov <i>et al.</i> 1990
<i>cachinnans</i>	N Turkmenistan (Lake Sarykamysh)	70	71.8 (2.7; 65.6-77.6)	50.0 (1.7; 47.4-53.2)	Filchagov 1993
<i>cachinnans</i>	Aral Sea	705	71.0 (64.0-84.0)	50.0 (44.0-55.0)	Ismagilov 1955
<i>cachinnans</i>	NE Kazakhstan	926	71.3 (3.2; 60.9-81.9)	49.7 (1.6; 40.6-60.0)	Zykova & Panov unpubl.
<i>cachinnans</i> / <i>barabensis</i> (?)	N Kazakhstan (Zharkol' Lake)	47	72.8 (67.0-82.0)	50.3 (45.0-57.0)	Samorodov 1970
<i>barabensis</i>	SW Siberia (Saltain Lake)	43	70.8 (2.5; 66.2-76.1)	48.9 (1.3; 46.4-51.9)	Filchagov 1993
<i>barabensis</i>	SW Siberia (Chany Lakes)	42	70.1 (1.8; 66.0-73.7)	48.1 (1.5; 44.5-51.3)	Khodkov 1981
<i>beuglini</i>	Barents Sea (Kanin Pen.)	91	70.0 (3.0; 63.0-76.8)	48.2 (1.6; 45.0-56.3)	Filchagov 1993
<i>beuglini</i>	Gulf of Ob ¹	44	69.0 (2.2; 65.1-76.3)	49.1 (1.3; 45.6-51.6)	Filchagov 1993
<i>beuglini</i>	NW Siberia (Yamal Pen.)	21	70.2 (64.4-75.2)	48.0 (46.1-49.8)	Danilov <i>et al.</i> 1984
<i>taimyrensis</i>	N Siberia (W Taimyr Pen.)	30	71.7 (2.7; 66.0-76.5)	50.8 (1.3; 48.5-53.5)	Filchagov <i>et al.</i> 1992
<i>taimyrensis</i>	N Siberia (E Taimyr Pen.)	46	73.4 (3.5; 66.8-82.0)	50.5 (1.2; 47.8-52.3)	Filchagov <i>et al.</i> 1992
<i>vegae</i>	E Siberia (Chukotka)	30	73.8 (2.8; 68.1-77.5)		Filchagov 1993

such a colony that we carried out our study on Uzkoredkiy Island.

The spring arrival of gulls in the Barabinsk lowlands begins in mid April, continuing up to mid June, and the main hatching period apparently commences in the last third of May. Nests inspected by Khodkov (1981) on 7th May held eggs containing

embryos about half the size of a newly hatched chick; on 10th-12th June, chicks three to 18 days old were present in a colony. In 1997, on Uzkoredkiy Island, despite the very early and warm spring, the majority of young were still not able to fly in late June, and in a few nests we found newly hatched chicks.

Being in *barabensis* than *nans*. In a population of Tengiz Lake in a locality closest to the breeding range, a few chicks in 1 May, while the others were observed on 14 May, that the whole of *barabensis* takes more than that of the other populations. For breeding data, *beuglini* are in a nest on the Yamal Peninsula on 27th June, hatching; and, on 29th June (Danilov Semashko 1987).

Table 1 compares the dimensions of *barabensis* populations of the region and Siberia. The tendency towards a decrease from south to north in the breeding range of *barabensis*. In egg width, it differs from that of the nearest *barabensis* of the Tengiz Lake. The difference in length between localities and *barabensis*, as well as between *cachinnans* and *barabensis* from the Yamal Peninsula, is not significant. The difference between those of *beuglini* and those of Chany is significantly narrower. The difference between *barabensis* (Siberia) and *beuglini* (Siberia) seems to be rather small.

In summary, it seems to be rather small populations from the Yamal Peninsula throughout *taimyrensis*, it is apparently a

¹ P<0.001.

² P<0.01; P<0.05.

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Being in general a late breeder, *barabensis* thus differs sharply from *cachinnans*. In a population of the latter inhabiting Tengiz Lake in northeast Kazakhstan, the locality closest to (about 1,000 km south of) the breeding range of *barabensis*, the first few chicks in 1978 appeared on 8th and 9th May, while the start of mass hatching was observed on 14th May. It would thus appear that the whole breeding process of *barabensis* takes place almost a month later than that of the most northerly *cachinnans* populations. For comparison, the earliest breeding dates for the northern form *heuglini* are indicated by the following: a nest on the Yamal Peninsula tundra, examined on 27th June, held three eggs close to hatching; and, on the Kola Peninsula, the first newly hatched chicks were observed on 29th June (Danilov *et al.* 1984; Filchagov & Semashko 1987).

Table 1 compares egg sizes of two populations of *barabensis* with those of other gull populations of the Black Sea-Caspian Sea region and Siberia. There appears to be a tendency towards a decrease in egg size from southwest to northeast, from the breeding range of *cachinnans* to that of *barabensis*. In both *barabensis* populations, egg width differs highly significantly¹ from that of the nearest *cachinnans* breeders, at Tengiz Lake. The same applies to differences in length between eggs from the latter locality and those of the Chany Lakes *barabensis*, while egg-length difference between *cachinnans* and the population of *barabensis* from Saltaim Lake (56°N, 72°E) is not significant. The eggs of both populations of *barabensis* are significantly longer² than those of *heuglini* from the Gulf of Ob', while those of Chany Lakes *barabensis* are also significantly narrower³, but egg-width difference between *heuglini* (Gulf of Ob') and *barabensis* (Saltaim Lake) is not significant.

In summary, the egg size of *barabensis* seems to be rather close to that of *heuglini* populations from both the Kola Peninsula and the Yamal Peninsula. Farther east, throughout the breeding range of *taimyrensis*, increase in egg size is gradual, apparently a result of the influx of *vegae*

¹ $P < 0.001$.

³ $P = 0.01$.

² $P < 0.01$; $P < 0.05$.

genes from eastern Siberia. The whole picture of geographical variation accords well with data on clinal variation in body size among gulls of the taxa chain *cachinnans-barabensis-heuglini-taimyrensis-vegae* (see below).

Morphometric features of *barabensis* populations

As can be seen from table 2, *barabensis* is characterised by its relatively small size. In almost all measurements it tends to be smaller than gulls from the breeding range of nominate *cachinnans* (especially those *cachinnans* of the Black Sea region). At the same time, *barabensis* seems to be slightly larger than *armenicus*, although the latter has, on average, a relatively longer wing. In general, it can be said that, in terms of size and proportions, *barabensis* is intermediate between *cachinnans* of the Caspian region and adjacent eastern areas and more northerly *heuglini*; our supposition is that *barabensis* is the product of secondary intergradation between those two taxa. Supplementary arguments to support this hypothesis are presented below.

We believe the apparent similarity in biometrics between *barabensis* and *taimyrensis* to be the result of two independent processes, namely the interbreeding of *heuglini* with two of its neighbours whose breeding ranges are situated to, respectively, the south (*cachinnans*) and the east (*vegae*) of the range of *heuglini*. Bearing in mind the considerable similarity between *cachinnans* and *vegae* in size, proportions and coloration, it is not surprising that, in both cases, hybrid populations with similar characters have arisen: *barabensis* to the south of the range of *heuglini* and *taimyrensis* to the east (see also Discussion).

Garner & Quinn (1997) suggested that *barabensis* is characterised by its 'noticeably small (sometimes very thin) bill'. Our data show, however, that the bill of *barabensis* is not, on average, shorter than that of *taimyrensis*, which is usually regarded as a large-billed gull. Moreover, the two taxa are similar in bill depth, although the gonydeal angle of *barabensis* is, possibly, less prominent than on *taimyrensis* and *cachinnans*. Compared with *cachinnans*, the bill of *barabensis* is, in general, shorter and nar-

Table 2. Some morphological variables (in mm and g) of *barabensis* in comparison with those of other representatives of the *Larus argentatus-cachinnans-fuscus* complex. Figures show means with (in parentheses) S.D., range and sample where available. Sources: own measurements; Micrauskas *et al.* (1991), Dement'ev (1951), Danilov *et al.* (1984), Buzun (1993), Cramp & Simmons (1983) and Dolgushin (1962). Note that all data for *armenicus* are from Buzun (1993).

	<i>cachinnans</i> (Black Sea)	<i>cachinnans</i> (Caspian region)	<i>barabensis</i>	<i>beuglini</i>	<i>talmyrensis</i>	<i>armenicus</i>
Males						
Wing	464.6 (1.6; 35)		437.9 (10.2; 428-445; 8)	450.0 (435-465; 28) 443 (432-457; 4)	457.0	439.8 (12.5; 411-458; 18)
Bill length (culmen chord)	62.1 (0.4; 34)	60.0 (3.2; 53.9-63.4; 6)	58.1 (2.2; 55.3-61.2; 7)	54.7 (3.0; 49.2-58.8; 15)	55.3 (3.1; 51.9-59.2; 4)	52.3 (2.3; 48.1-56.5; 18)
Bill length (from nostril)	25.2 (21.9-28.2; 4)	24.6 (3.0; 21.3-28.8; 6)	25.3 (1.9; 23.2-28.7; 7)	24.8 (2.0; 20.7-27.3; 15)	25.5 (1.8; 23.7-27.9; 4)	22.9 (1.2; 21.2-25.4; 18)
Bill depth (at gonys)	19.5 (0.2; 35)	18.9 (0.7; 17.8-20.0; 6)	18.4 (0.7; 17.6-18.8; 7)	18.4 (0.9; 17.0-20.0; 15)	19.2 (1.1; 18.4-20.8; 4)	18.6 (1.0; 16.8-20.1; 18)
Bill depth (at nostril)	18.0 (15.6-19.7; 4)	17.5 (0.9; 16.5-18.8; 5)	17.5 (0.4; 16.8-17.9; 7)	17.4 (0.8; 15.8-18.4; 14)	17.5 (1.5; 16.0-19.5; 4)	17.2 (0.8; 15.5-18.3; 18)
Bill width	10.9 (8.9-11.8; 4)	10.8 (0.4; 10.1-11.3; 6)	10.9 (0.4; 10.5-11.5; 7)		10.6 (0.5; 9.9-11.2; 4)	
Combined head+bill length	133.6 (0.5; 35)		126.7 (3.0; 122.0-129.5; 6)			121.0 (2.6; 115.6-125.9; 18)
Sternum keel	86.2 (0.5; 35)		83.9 (3.9; 73.6-79.7; 6)			80.2 (2.6; 76.8-85.1; 17)
Tarsus	72.3 (0.4; 35)	70.2 (3.0; 65.4-73.7; 6)	67.3 (2.6; 63.6-70.5; 7)	66.4 (2.7; 61.2-71.2; 15)	67.0 (3.4; 65.0-72.4; 4)	68.7 (2.3; 64.3-73.7; 18)
Weight (g)	1317 (160.7; 1200-1500; 3)	835 (750-1193; 27)	1012 (97.9; 900-1070; 6)	1124 (113.0; 1015-1300; 5)	1260; 1300 (2)	857 (66.7; 785-960; 9)
				1179 (990-1350; 4)		

Table 2. cont.

	<i>cachinians</i> (Black Sea)	<i>cachinians</i> (Caspian region)	<i>barabensis</i>	<i>bengali</i>	<i>taimyrensis</i>	<i>armenicus</i>
Females						
Wing	440.8 (1.0; 71)		417.9 (10.2; 404; 430; 7)	434.5 (410; 455; 20)	453.0 (32.8; 432; 470; 3)	419.1 (400; 436; 23)
Bill length (culmen chord)	56.3 (0.3; 71)	56.4 (4.2; 49.9; 63.1; 6)	51.4 (1.9; 49.7; 54.1; 11)	51.4 (3.7; 47.6; 57.4; 6)	50.6 (2.2; 47.8; 57.4; 8)	46.3 (2.1; 41.3; 50.6; 22)
Bill length (from nostril)		23.7 (1.7; 20.9; 26.1; 6)	23.5 (1.6; 21.7; 26.5; 11)	24.4 (1.6; 21.8; 26.2; 6)	24.3 (0.6; 23.7; 25.2; 8)	20.7 (0.8; 19.1; 22.6; 22)
Bill depth (at gonys)	17.2 (0.1; 71)	17.4 (1.3; 16.5; 20.0; 6)	16.2 (0.9; 15.4; 18.6; 11)	17.3 (1.0; 16.5; 19.2; 6)	17.7 (0.7; 16.7; 18.8; 8)	16.5 (0.51; 15.5; 17.4; 22)
Bill depth (at nostril)		16.1 (1.0; 15.1; 17.9; 6)	15.2 (0.7; 14.3; 17.2; 11)	15.9 (1.2; 15.0; 18.2; 6)	16.3 (0.9; 15.4; 17.3; 8)	15.3 (0.7; 14.0; 16.5; 21)
Bill width		9.8 (1.0; 8.4; 11.3; 6)	9.7 (0.3; 8.7; 10.6; 11)		10.3 (0.5; 9.6; 11.2; 8)	
Combined head+bill length	122.9 (0.3; 71)		115.5 (2.3; 113.4; 118.9; 6)			111.5 (3.0; 105.8; 119.6; 22)
Sternum keel	80.4 (0.4; 71)		76.9 (2.3; 73.6; 79.7; 6)			74.8 (3.1; 64.9; 81.0; 23)
Tarsus	66.9 (0.3; 71)	65.6 (4.1; 62.3; 72.5; 5)	61.3 (4.9; 58.2; 65.6; 11)	64.6 (3.4; 60.5; 69.8; 6)	62.8 (3.0; 59.7; 67.6; 8)	64.1 (2.6; 58.4; 68.0; 22)
Weight (g)		772 (700; 1050; 16)	824.8 (100.1; 680; 950; 9)	983 (924; 1050; 7)	983 (121.0; 890; 1120; 3)	708 (55.7; 605; 775; 17)

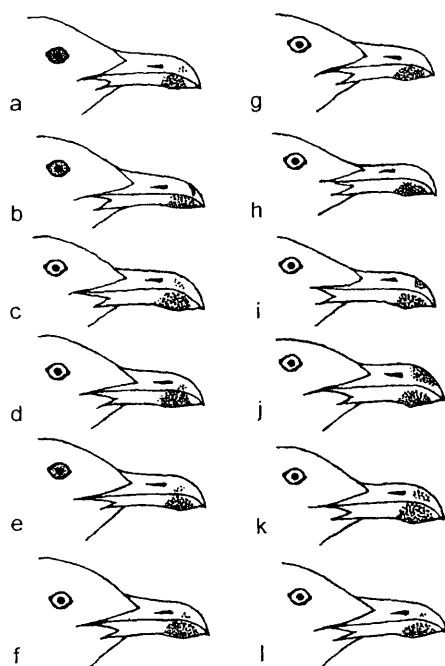


Fig. 2. Variations in bill shape and coloration and eye colour of *barabensis* gulls inhabiting the Chany Lakes.

Left six (a-f) males, right six (g-l) females. Slight admixture of brown tones in individuals b (also on rectrices), c, d, e, g and h. Dark pigmentation occupies about 80% of iris in individual a, about 50% in b and e, and 1-5% in f, h, j and l; in all others, iris completely yellow. (Individuals f, i and j also had wingtip pattern partly similar to that of typical *Cacchymimus*; on others, pattern closer to that of *heuglini*.)

rower, but it does not look disproportionately small when the compact appearance of the bird itself is taken into account. In the field, *barabensis* should definitely appear longer-billed than *armenicus*, since bill depth is practically the same in both taxa. It should also be emphasised that the size and shape of the bill of *barabensis* are quite variable; as fig. 2 shows, relatively small-billed (of the *beuglini* type) and large-billed (of the *cachinnans* type) individuals occur among both males and females.

Plumage coloration

Just as with body size and proportions, *barabensis* is intermediate between *cachinans* and *beuglini* in all colour characteristics, being closer to the latter. The mantle is slate-grey, obviously lighter than on *beuglini*,

but tends to be a shade darker than on many birds from the breeding range of *taimyrensis*. Typically, it has a brownish tinge that is normally absent on *taimyrensis*, the upperparts of which appear bluish-grey. In contrast to *taimyrensis*, on which the tone of the mantle is quite variable, *barabensis* has a rather constant mantle colour, although lighter-mantled individuals sometimes occur (such birds usually have certain other colour characteristics which give them a *cachin-nans*-like appearance).

It is apparent from fig. 3 that mean values of almost all features of the wingtip pattern of *barabensis* are also intermediate between those of *cachinnans* and those of *heuglini*. Within populations, we determined the proportions of individuals showing various intensities of black pigmentation on the primaries. This was assessed in terms of (1) the number of primaries bearing subterminal black markings; (2) the presence or absence of a white spot on the tip of the 9th primary (P9); (3) the maximum length of such a spot on P10 (and, if present, on P9); and (4) the size of the gap between the distal end of the grey wedge on P10 and P9 and the tip of the respective feather. In the last two characters, *barabensis*, being intermediate between *cachinnans* and *heuglini* and closer to the latter, does not differ, on average, from *taimyrensis*; significantly, however, in characters (1) and (2) it seems more closely to resemble *heuglini* than it does *taimyrensis*. The typical wingtip patterns of *barabensis* and of all other taxa under consideration are presented in fig. 4 (on page 237).

We could not ascertain any features that permit distinction between downy young of *barabensis* and those of other members of the '*L. argentatus-cachinnans-fuscus* complex'. On the few juvenile *barabensis* that we examined, the pale tertial fringes were not thin and of uniform width as is characteristic of nominate *cachinnans*, but were broad and extensively scalloped, in this respect matching those of typical *beuglini*. Examination of specimens in the Museum of Zoology (Moscow State University) showed that the latter type of tertial pattern occurs on many juvenile gulls from northeastern Kazakhstan (in particular, from the Semipalatinsk region).

Fig. 3. Comparison of the characteristic shape of the *cachinnans* (tail) and *armenicus* (tail) by asterisk, and **a:** proportion of P10-P5 (operation) (black). **b:** proportion of P10 and P9 (operation). **c:** max. length of P10 and tip of P9. **d:** max. length of P10 and tip of P9. **e:** distance between P10 and tip of P9. **f:** distance between P9 and tip of P10. (For c-f, mean values of *armenicus*, 1

All 12 individuals in the hand had no dark spots, 1-5% of the individuals had about 50% orange and 80% on orange (fig. 2). The color was from orange tinged red.

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Fig. 3. Comparison of some wingtip patterns characteristic of *barabensis* (bar) with those of *cachinnans* (ca), *beuglini* (heu), *taimyrensis* (tai) and *armenicus* (arm). (Data on *armenicus* from Buzun 1993, where some values, indicated by asterisk, are lacking.)

a: proportions of birds with black markings on P10-P5 (open bar), P10-P4 (shaded), P10-P3 (black).
b: proportions with white spots on tip of both P10 and P9 (open bar) and only on P10 (black).
c: max. length of white subterminal spot on P10.
d: max. length of white subterminal spot on P9.
e: distance between distal end of grey wedge on P10 and tip of feather.
f: distance between distal end of grey wedge on P9 and tip of feather.
 (For c-f, means, S.D. and ranges are shown; for *armenicus*, range values for c and e lacking.)

Bare-part colours

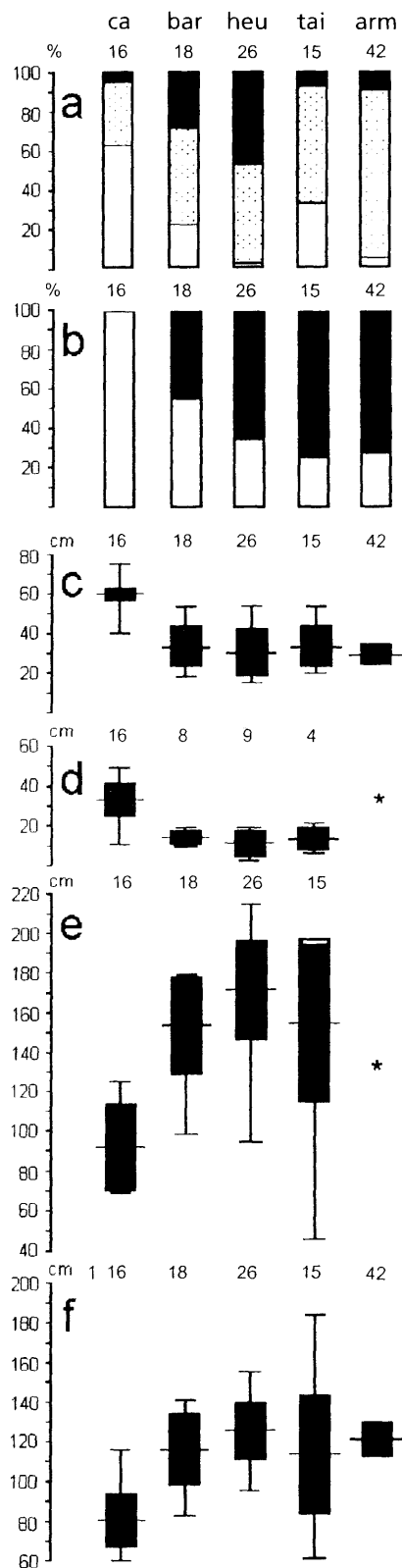
All 12 individuals of *barabensis* examined in the hand had a pale yellow iris. Five of these had no dark pigmentation, while four others had small dark brown speckles occupying 1-5% of the iris area; dark speckles covered about 50% of the iris on two individuals and 80% on one, so that their eyes looked dark (fig. 2). The colour of the eye-ring varied from orange with a yellow tint to orange-tinged red, being orange-red in most cases.

The legs and feet of all 12 were deep yellow, on some very brightly coloured. The feet of one had an orange tint.

The bill is bright yellow, with a reddish-orange gonydeal angle. Only two of the 12 individuals examined showed small blackish markings near the tip of the upper mandible, and on one the marking was reddish. These findings differ dramatically from observations made some 360 km northwest of our study area, on Saltair Lake: there, dark markings of varying size were present on the bill (mostly the upper mandible) of 18 out of 29 adult *barabensis* examined in the hand during the breeding season (Filchagov 1993).

Some features of behaviour

By the beginning of our study on Uzkoredkiy Island, most gulls had already left the nesting colony and were on the water close to the shore. Groups comprising one or two adults together with up to three juveniles, and thus perhaps intact family parties, were seen only rarely at that time. The majority of juveniles

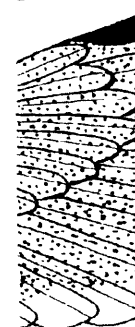




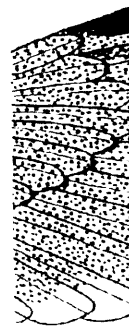
132 - 136. Gulls of the form *Larus beuglini barabensis*, Russia, July 1997. All by E. N. Panov

were gathered in varying numbers, from a few to about 100 ('crèches') with a few gulls, with a colony in the vicinity of the nesting site, competing for the food involved in incubation, such as the *cachinnans* at 1981).

a



c



e



Fig. 4. Wing (c), *beuglini*

were gathered in loose aggregations of varying composition and containing from a few to about 15 individuals. These groups ('crèches') were very attractive to adult gulls, with a continual interchange of birds in the vicinity of such sites. Many adults, competing for the role of chick guardians, were involved in incessant antagonistic interactions, such as those previously described for *cachinnans* at Tengiz Lake (Panov & Zykova 1981).

Frequent conflicts were invariably accompanied by numerous Long-call displays. In the overwhelming majority of cases, the motor components of the displays were a quick lowering of the head down to the water surface, followed by stretching of the neck upwards and forwards at an angle of about 20-30°. This, the so-called 'argentatus-like' version of the Long-call display, is the one most frequently observed in most populations belonging to the '*L. argentatus*-

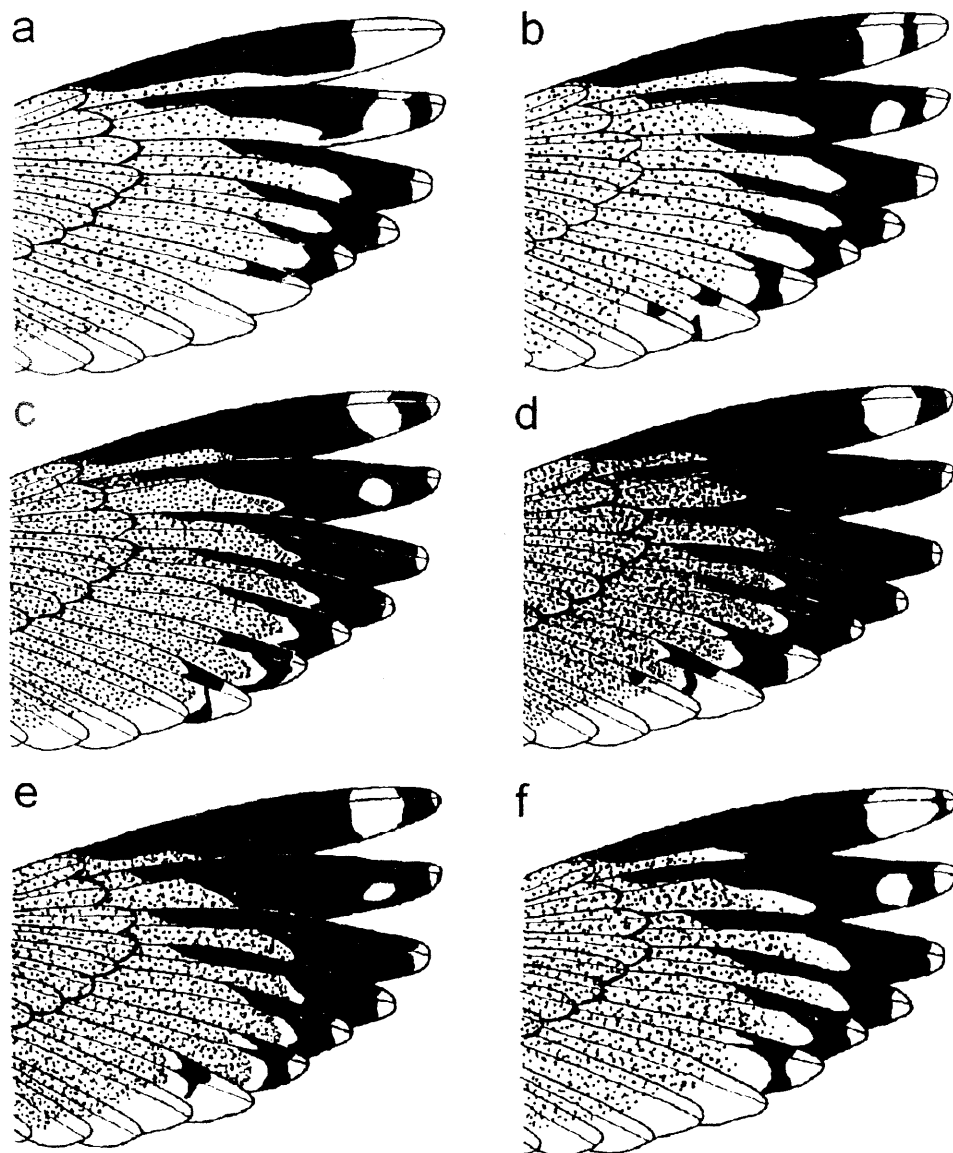


Fig. 4. Wingtip patterns most characteristic of *cachinnans* (a = lightest variant, b = darkest), *barabensis* (c), *beuglini* (d), *taimyrensis* (e) and *vegae* (f).

Gulls of the
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by E. N. Panov

cachinnans-fuscus complex'. Another version, hitherto described only for nominate *cachinnans*, was, however, observed on three occasions: the characteristic component of this version is the vertical raising of the fully extended wings during the second phase of the performance (Panov *et al.* 1991).

It is important to note that the acoustic component of the Long-call display varies conspicuously among the Chany Lakes populations of *barabensis*. There are two obviously different types of call, and a continuum of variants intermediate between them. One of these types closely resembles that characteristic of nominate *cachinnans* (compare figs. 5e and 5f), while another has a 'fuscus-

like' structure (fig. 5d) and may, therefore, prove to be the typical constituent of *beuglini* signal behaviour.

Discussion

The results of this study clearly suggest that in practically all morphological features, including size, proportions and coloration, *barabensis* exhibits the greatest degree of resemblance to *beuglini*, while at the same time showing a slight admixture of *cachinnans* characters. This forces us to conclude that *barabensis* has arisen as a result of introgression of *cachinnans* genes into *beuglini* populations which have expanded southwards from their original breeding range. Preliminary behavioural data also

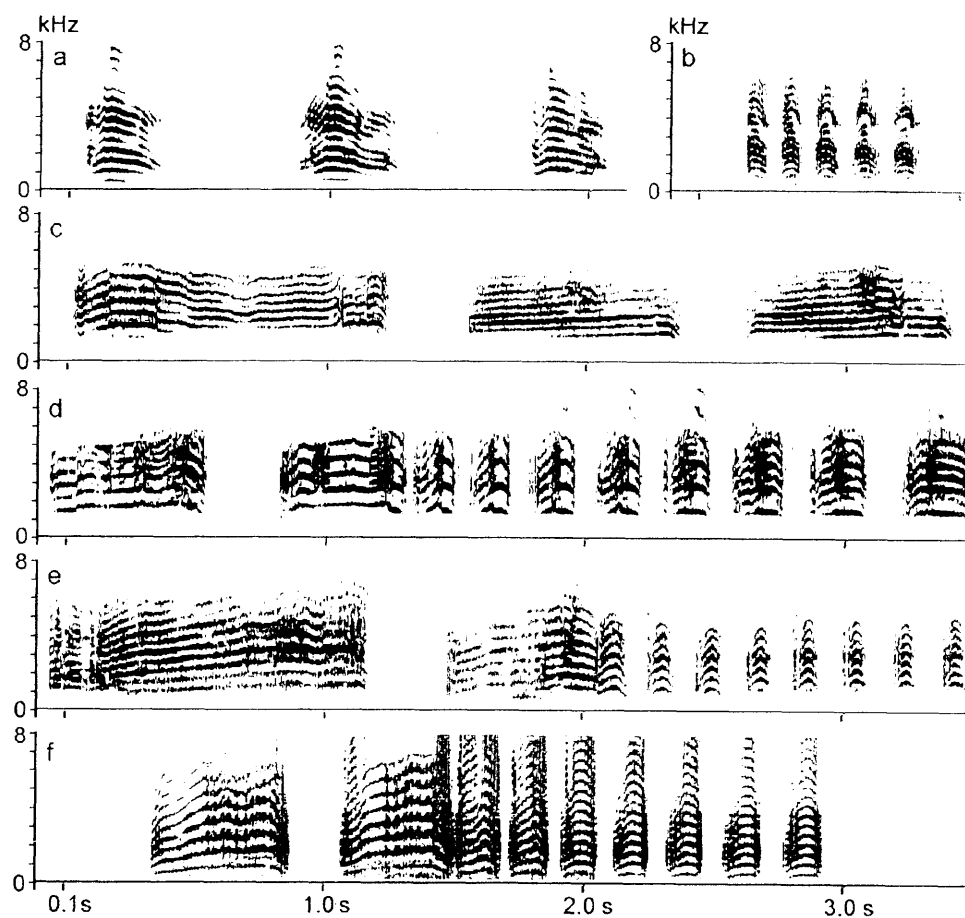


Fig. 5. Some acoustic signals of *barabensis* (a-e) and *cachinnans* (f). a: common call, used also to signal alarm; b: alarm call of 'staccato' type; c: different variants of Mew-call; d: 'fuscus-like' variant of Long-call; e: 'cachinnans-like' variant of Long-call starting with sound of Mew-call type; f: typical Long-call of nominate *cachinnans* (southeast Caspian).

Table 3. Characteristics of wingtip pattern of *barabensis* compared with some other representatives of the *Larus argentatus-cachinnans-fuscus* complex'. Data for both sexes combined. P = primary. Data for *armenicus* from Buzun (1993).

Table 3. Characteristics of wingtip pattern of *barabensis* compared with some other representatives of the '*Larus argentatus-cachimians-fuscus* complex'. Data for both sexes combined. P = primary. Data for *armenicus* from Buzun (1993).

Population	Sample	% (no.) with black markings on primaries				% (no.) with white spots on primaries			% (no.) with white spot on p9			Length in mm (S.D.; range) of white spot on primaries		Distance in mm (S.D.; range) between distal end of grey wedge and tip of primary	
		P10-P5	P10-P4	P10-P3	P10 & P9	P10 only	both webs	outer web	inner web	P10	P9	P10	P9	P10	P9
<i>cachimians</i> (Caspian region)	16	62.5 (10)	31.3 (5)	6.2 (1)	100.0 (16)	0.0	93.8 (15)	0.0	6.2 (1)	60 (3.0; 40-75)	34 (9.3; 12-50)	92 (21.9; 70-125)	80 (13.9; 60-115)		
<i>barabensis</i>	18	22.2 (4)	38.9 (7)	38.9 (7)	44.4 (8)	55.6 (10)	62.5 (5)	12.5 (1)	25.0 (2)	33 (10.1; 17-54)	15 (3.4; 11-19)	154 (24.7; 100-180)	116 (18.3; 82-140)		
<i>beuglini</i>	26	0.8 (2)	53.8 (14)	42.3 (11)	34.6 (9)	65.4 (17)	44.4 (4)	11.2 (1)	44.4 (4)	30 (11.5; 15-55)	12 (7.6; 3-20)	172 (24.8; 95-215)	126 (15.5; 95-155)		
<i>tainyrensis</i>	15	33.3 (5)	60.0 (9)	6.7 (1)	26.7 (4)	73.3 (11)	25.0 (1)	0.0 (3)	75.0 (3)	33 (9.7; 20-55)	15 (6.2; 7-22)	155 (41.0; 45-195)	113 (29.4; 60-185)		
<i>vegae</i>	38	61.8 (21)	38.2 (13)	0.0	76.3 (29)	23.7 (9)	44.8 (13)	0.0 (16)	55.2 (16)	40 (10.0; 25-60)	17 (8.0; 5-30)	115 (18.0; 90-150)	77 (14.9; 45-95)		
<i>mongolicus</i>	37	15.6 (5)	59.4 (19)	25.0 (8)	86.5 (32)	13.5 (5)	62.5 (20)	3.1 (1)	34.4 (11)	39 (12.3; 13-62)	17 (8.4; 4-39)	145 (28.1; 91-197)	111 (15.2; 87-144)		
<i>armenicus</i>	42	c.5	c.85	c.10	28.0 (11)	72.0 (31)	—	—	—	28 (5.5)	—	—	140 (9.2)		

support this hypothesis. While the southern limit of *heuglini* and the northern limit of *barabensis* are uncertain, between their known ranges lies an area approximately 1,200-1,500 km broad of impenetrable bogs and marshes; no ecological barrier therefore exists that might otherwise keep the two apart.

Our conclusion runs counter to the view expressed by Dement'ev (1951), that *barabensis* should be regarded as the southern representative of *taimyrensis*. Furthermore, our data do not accord with the opinion of Johansen (1960), who considered *barabensis* to be a subspecies of *L. cachinnans*. The latter view is apparently based on the well-known intermingling of *barabensis* and *cachinnans* characters among large-gull populations of northeastern Kazakhstan (locality 8 in fig. 1), to the southeast of our study area. Evidently, gene-flow occurs from gulls in these regions into southern populations of *barabensis/heuglini* inhabiting lakes in the southern part of Western Siberia.

Dement'ev's (1951) suggestion that *barabensis* is a constituent of '*L. argentatus taimyrensis*' was based on a genuine similarity between these two taxa. At the same time, Dement'ev (1951, 1952) stressed the unstable nature of differences between *heuglini* and western *taimyrensis* populations, as well as the presence in the eastern part of the breeding range of *taimyrensis* of a considerable number of individuals with an admixture of *vegae* characters. Moreover, across the whole breeding range of *taimyrensis*, along with yellow-legged birds similar to *heuglini*, individuals with pink legs (*vegae* character) often occur (see e.g. colour photos in Filchagov *et al.* 1992). Analysis of the *taimyrensis* sample in the Museum of Zoology (Moscow State University) undoubtedly shows that this pink-legged form is nothing other than *heuglini* strongly influenced by *vegae* gene-flow from Eastern Siberia (see also Cramp & Simmons 1983: 815). Bearing in mind the existence of some similarity between *vegae* and *cachinnans* (see fig. 4), the deceptive superficial resemblance of two hybrid forms (*heuglini* × *vegae* = *taimyrensis*, and *heuglini* × *cachinnans* = *barabensis*) becomes readily explicable.

While the apparent phenotypic resem-

blance of *heuglini*, *barabensis* and *taimyrensis* results from their close genealogical and genetic interrelationship, the similarity between *barabensis* and *armenicus*, which has lately attracted the attention of ornithologists (e.g. Filchagov 1993; Garner & Quinn 1997), is, in our view, no more than superficial and incidental, as is, for example, that between *armenicus* and California Gull *L. californicus* (Doherty 1992). We suggest that such a resemblance is the result of convergence that manifests itself, in particular, in the parallel intensification of melanism in *heuglini* (whose characters are retained in *barabensis*) and in *armenicus*. What the causes of such a parallel evolution may be is an interesting question. Attempts to demonstrate ancient genealogical interrelationships between *heuglini-taimyrensis-barabensis* on the one hand and *armenicus* on the other (Filchagov 1993; Buzun 1993) lack adequate empirical foundation and should be viewed as pure speculation.

To summarise, we believe that *barabensis*, despite its apparent hybrid origin, should be treated as a quite well-defined taxon (contrary to Stepanyan 1975 and Yudin & Firsova 1988) that is most closely related to *heuglini*. It should be referred to as *L. heuglini barabensis*, unless the independent species status of *heuglini* (Stepanyan 1990) in relation to the Lesser Black-backed Gull is refuted by convincing argument derived from studies of comparative behaviour and genetics.

As a final point, it is worth noting that the eastern form *mongolicus* is very large, bigger even than *vegae*, and with a wingtip pattern broadly similar to that of *vegae* (cf. fig. 4f); it differs from the latter mainly in having much more black on the primaries (table 3). Comparative ethological studies (Panov & Monzikov in prep.) suggest that *mongolicus* is most closely related to *vegae*, both of which belong to the *argentatus* group within the complex, whereas *heuglini* appears to be part of the *fuscus* group. *L. cachinnans* is somewhat apart from both; although it is assumed to be closer to *fuscus* than to *argentatus*, obvious gene-flow occurs between *L. argentatus* and *cachinnans* in European Russia (see Panov & Monzikov 1999).

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