Historical and taxonomic review of the Iceland Gull *Larus glaucoides* complex

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The Iceland Gull *Larus glaucoides* is now generally regarded as comprising three subspecies: *L. g. glaucoides*, which breeds in Greenland, *L. g. kumlieni* ('Kumlien's Gull'), which breeds mostly on Baffin Island, and *L. g. thayeri* ('Thayer's Gull'), which breeds throughout the Canadian High Arctic (fig. 1). Iceland Gull taxa have at various times, however, also been treated as subspecies of Herring Gull *L. argentatus* or Glaucous-winged Gull *L. glaucescens*, or as three separate species. The relationships among the three Iceland Gull taxa have been debated by ornithologists for 180 years, from Sabine (1819) to Chu (1998), without a clear resolution, which gives some idea of the problems presented by this group.

In an earlier paper, Weir *et al.* (1995) reported that the frequency of *kumlieni* among wintering adult Iceland Gulls in the eastern Atlantic had increased substantially during the twentieth century. This change

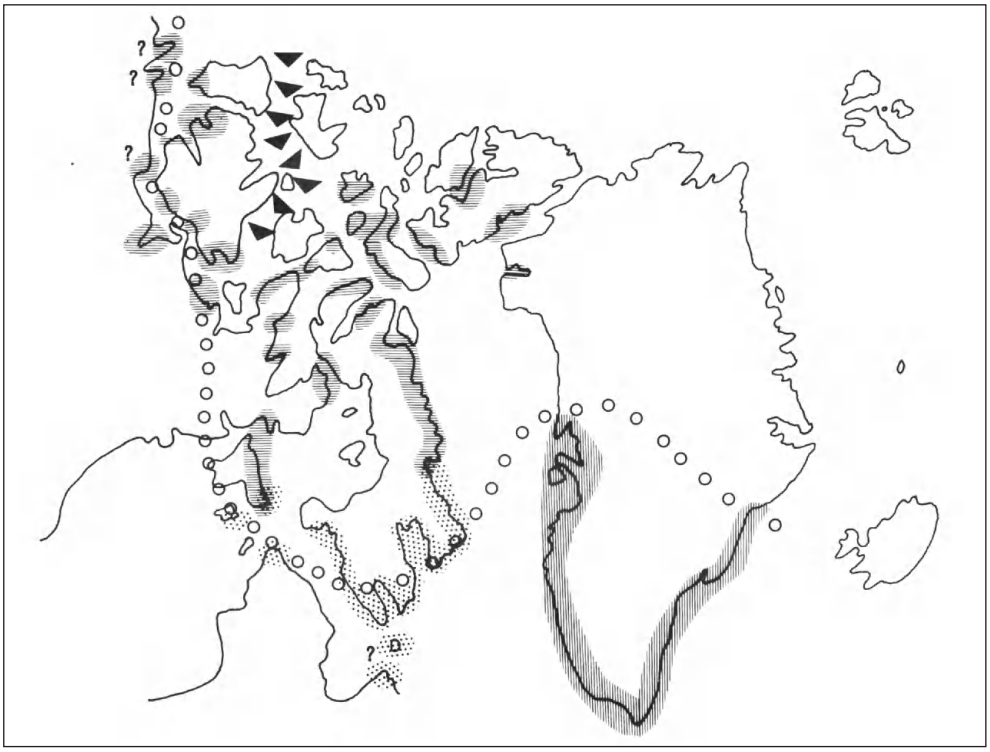

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Fig. 1. Breeding records for three Iceland Gull *Larus glaucoides* taxa, about 1950-95: *glaucoides* ▒; *kumlieni* ⁙; *thayeri* ▤. Complete breeding distributions of all three taxa are still uncertain (=?), and a few *thayeri* records are from up to 20 years before 1950. ▼ indicates the main southward thrust of thick, multi-year accretions of pack ice; line of open circles shows postulated southern limit of High Arctic.

prompted us to review historical distributional data for all three Iceland Gull taxa. We suspected that any changes in their respective distributions that could not be explained by changing environmental factors might help to elucidate the relationships among, and the validity of, the three taxa. By carrying out a detailed historical and morphological review of Iceland Gull taxa over the past 200 years, we hoped to develop hypotheses on their relationships that could be tested by molecular studies.

Specimens were routinely collected by members of Royal Navy and other explorations of the Northwest Passage, from 1818 to 1860, which covered almost the entire range of the Iceland Gull. Although only a few of the earliest bird specimens collected still exist, many full descriptions can be found in published expedition reports and zoological literature. It is clear from these studies that most early naturalists were able to distinguish readily between the nominate race of Iceland Gull *L. g. glaucoides* and the larger Glaucous Gull *L. hyperboreus*, a fact which it is important to note when interpreting descriptions from these early accounts.

The most reliable character for defining Iceland Gull taxa is the intensity and extent of wingtip melanism in adults, although this varies more or less continuously from none in *glaucoides*, through the intermediate *kumlieni*, to darkest and most extensive in *thayeri*. A secondary, but less reliable, character involves the iris colour of breeding adults. Details of the differences separating the three forms are given in table 1.

Most records of immature Iceland Gulls had to be excluded from our study owing to the highly variable nature of the plumage of such individuals and the lack of ringed birds of known origin. We then assigned each historical specimen and each individual described in published records to one of our three defined taxa, in order to determine changes in both the breeding and the winter distributions of these taxa over the last two centuries. Historical data were relatively few compared with the availability of more recent information (e.g. post-1950). Further details, including sample sizes, are given in Weir *et al.* (2000). We also examined changes in the distributions of other large gulls in the same region, to determine whether these were due to a common set of environmental or ecological variables.

We found that, until about 1860, nominate *glaucoides* bred from Greenland to the western High Arctic of Canada, but by about 1900 it was essentially confined to Greenland (fig. 2). Until 1860, *thayeri* was known only from the western Canadian High Arctic, but from 1900 to 1950 it was found throughout the High Arctic of Canada and in a small area of northwest Greenland (fig. 3).

At high latitudes in Canada, therefore, *thayeri* had evidently replaced *glaucoides*, with which it was formerly sympatric in the west and with which it probably interbred. The first known *kumlieni* were recorded from west Greenland by the 1850s, and by 1900 the western and northern limits of most of its breeding range in the eastern Canadian Low/High Arctic were known. By

Table 1. Definitions of Iceland Gull *Larus glaucoides* taxa, based on adults only. The melanism score of the primaries is derived from the extent and relative intensity of melanism on the upper surface of the wing.

Feature	*thayeri*	*kumlieni*	*glaucoides*
Number of primaries with melanism	(3)4-6	1-5	0
Melanism scores P10-P6	2.0-4.5	0.2-2.5	0
Iris colour of breeding adults	dark (purple/brown speckling)	intermediate	clear greyish-yellow

Sources: Dwight 1906, 1917, 1925; Salomonsen 1950; MacPherson 1961; Fjeldså & Jensen 1985; Godfrey 1986; Ingolfsson 1967, 1970; Snell 1989, 1991a, b; Weir *et al.* 2000.

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Fig. 2. Known breeding distribution of three Iceland Gull *Larus glaucoides* taxa, in about 1900: *glaucoides* ▒; *kumlieni* ⁙; *thayeri* ▤; *glaucoides* or *kumlieni* (taxon not verified) = ?. The first northerly records of Herring Gull *L. argentatus smithsonianus* are shown as open circles.

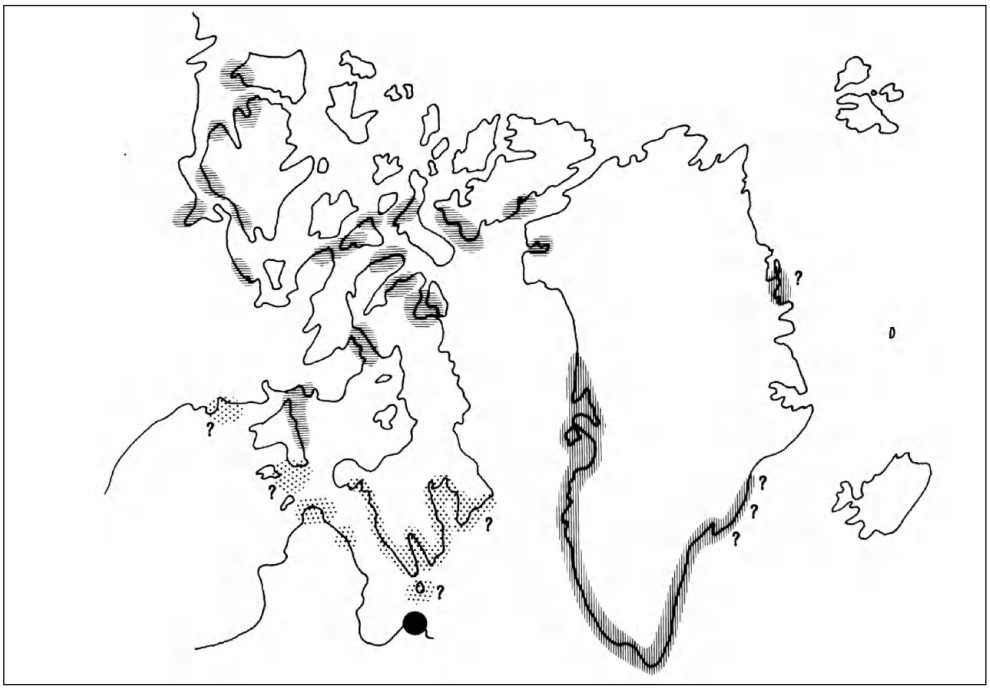

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Fig. 3. Breeding records for three Iceland Gull *Larus glaucoides* taxa, about 1950: *glaucoides* ▒; *kumlieni* ⁙; *thayeri* ▤; *glaucoides* or *kumlieni* (taxon not verified) shown as filled circle; uncertain or disputed records = ?.

1964, *kumlieni* was recorded breeding in Greenland (not shown in fig.1). The current breeding range of *kumlieni* is restricted, lying between those of *thayeri* and *glaucoides* and overlapping both; *kumlieni* freely interbreeds with *thayeri* (Gaston & Decker 1985; Snell 1989) and probably with *glaucoides*. In contrast to their changing breeding distributions, the winter ranges of *glaucoides* and *thayeri* were found to have changed little since they were first determined, by 1860 and by the 1920s respectively. Winter adult *kumlieni*, however, was unrecorded in the north Atlantic between Greenland and the British Isles until about 1900; it remained rarer than *glaucoides* until 1915 (when samples were 75-100% *glaucoides*), but became progressively more common after 1950 (when samples were 33-80% *kumlieni*).

There is clear evidence that *glaucoides* was replaced by *thayeri* on the breeding grounds, involving an eastward shift of 40° longitude, whereas, in contrast, the distributions of other large gulls of the region shifted mainly northwards. Therefore, whatever factors had caused the eastward movement of *thayeri* were different from those which affected the distributions of other large gulls. We also noted, however, that *thayeri*, as it spread eastwards, hybridised with *glaucoides*, giving rise to the variable form known as *kumlieni*.

Hybrid populations are often distinguished from valid taxa by their inherent instability, both through time and in their geographical distribution. Otte & Endler (1989) set out fairly simple criteria by which unstable, hybrid populations can be recognised. Five of these criteria demonstrate that *kumlieni* is not a valid taxon, but a variable intermediate form resulting from introgressive hybridisation between *thayeri* and *glaucoides* lineages:

1. Specimen data confirm that the postulated parent taxa (*glaucoides* and *thayeri*) formerly bred sympatrically and may have hybridised.
2. Known range contraction by one parent taxon (*glaucoides*) corresponds spatially and temporally to known or apparent range expansion by the other parent taxon (*thayeri*).
3. Non-assortative breeding by the intermediate is known to occur with one parent (i.e. *kumlieni* × *thayeri*), and is strongly suspected to occur with the other.
4. The form *kumlieni* is highly variable in key morphological characters, being intermediate between the two parent taxa in wingtip melanism and iris colour, and this variation tends to be geographical with respect to the parent taxa.
5. The present range of the intermediate is limited, lying between and overlapping in part with those of the parent taxa; in addition, the hybrid has not spread into the High Arctic, where *thayeri* has directly replaced *glaucoides*.

This may not, however, have been the first time that *thayeri* and *kumlieni* have met. Their populations may have advanced and retreated several times in the Arctic in response to climate change during the present and past interglacials. They may not have hybridised at every meeting and, when they did, gene flow may have been in either direction. It appears that the brief systematic ornithology of the Arctic happened to coincide with the most recent hybridisation between *thayeri* and *glaucoides*, and the eastward shift by *thayeri* of about 40° of longitude, followed by further introgression by the intermediate into the remaining population of the Atlantic parent.

Hybrid zones are common ornithological phenomena. In northern regions, most are explained by secondary contact during the present interglacial, though most species do not move far (Hewitt 1989). Hybrids are presumed to be adaptively less fit, and they tend to occur in density troughs between the parental peaks (Barton 1989). In the case of the Iceland Gull, the distributions of both parent taxa and the hybrid form shifted rapidly, but *kumlieni* is now probably more numerous than *thayeri*, and *glaucoides* may be ten times more abundant than either of them.

Other workers (e.g. Dwight 1906; Snell 1989) have suggested that *kumlieni* is an intermediate taxon between *glaucoides* and *thayeri*, and our recent paper (Weir *et al.* 2000) presents strong new evidence to support this. The next step should involve molecular studies to test the hypotheses which we have presented concerning distributional change, hybridisation and continuing introgression.

Acknowledgments

The figures and table in this paper are reproduced from Weir *et al*. (2000) by kind permission of the Editor of *Journal of Zoology*.

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