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Hybridization and changes in the distribution of Iceland gulls (*Larus glaucoides/kumlieni/thayeri*)

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Abstract

Three Iceland gull taxa were defined mainly from adult wingtip melanism. Up until about 1860, nominate *glaucoides* (no melanism) was known to breed from Greenland to western High Arctic Canada, but by about 1900 it was essentially confined to Greenland. Until 1860, *thayeri* (most melanism) was known only from western High Arctic Canada, but from 1900 to 1980 it was found throughout High Arctic Canada and in a small part of north-west Greenland. At high latitudes in Canada it replaced *glaucoides*, with which it was formerly sympatric in the west and probably interbred. The first known *kumlieni* (intermediate, variable melanism) were from west Greenland in the 1840s, and by 1900 the western and northern limits of most of its breeding range in the eastern Canadian Low/High Arctic were known. The range of *kumlieni* lies between those of *thayeri* and *glaucoides* and overlaps both; *kumlieni* bred in Greenland by 1964. It freely interbreeds with *thayeri* and probably with *glaucoides*. Winter ranges of *glaucoides* and *thayeri* have changed little since they were first determined for *glaucoides* by 1860 and for *thayeri* by the 1920s. However, winter adult *kumlieni* was unknown from Greenland to the British Isles until 1900; there were a few records prior to 1915 and progressively more after 1950. The study adds to the evidence that *kumlieni* represents introgressive hybridization by western *thayeri* into eastern *glaucoides*.

Key words: Iceland gull, distribution changes, taxonomy, hybridization

INTRODUCTION

The Iceland gull *Larus glaucoides* Meyer 1822 is an Arctic species, which is presently regarded as comprising three subspecies: *L. g. glaucoides* from Greenland; *L. g. kumlieni* mainly from Baffin Island; and *L. g. thayeri* mainly from High Arctic Canada. However, relationships between the Iceland gull and herring gull *L. argentatus* and between Iceland gull taxa have been debated for 180 years (E. Sabine, 1819, 1824; MacGillivray, 1824; Swainson & Richardson, 1831; Kumlien, 1879; Dwight, 1906, 1917, 1925; Brooks, 1915; Taverner, 1933; Rand, 1942; MacPherson, 1961; Smith, 1966; Knudsen, 1976; Weber, 1981; Gaston & Decker, 1985; Godfrey, 1986; Snell, 1989, 1991*a*, 1993; Chu, 1998). Iceland gull taxa have been treated as varieties or subspecies of the herring gull or of the glaucous-winged gull *L. glaucescens*, or as separate species, or as three taxa of one species.

During the twentieth century the frequency of *kumlieni* in winter adult Iceland gull populations greatly increased in the eastern Atlantic (Weir *et al*., 1995). This suggestion of instability in the distributions of two taxa prompted us to review distribution data for all three taxa, from the earliest reference to the Iceland gull in 1771 (Winge, 1898) to the present day. Our aim was to investigate the relationships and validity of the taxa from any changes in their respective distributions over time. Unstable distributions may indicate genetic instability and possible hybridization (Barton, 1989).

We defined taxa essentially from variations in the degree of adult wingtip melanism and noted relationships with colours of some soft parts. Non-correlated combinations of these features are usually good indications of hybridization between other species of large, white-headed *Larus* gulls, although in one case reduced wingtip melanism in a new population might have been due to a founder effect (Patten & Weisbrod, 1974; Harris, Morley & Green, 1978; Ingolfsson, 1970, 1987, 1993; Snell, 1991*a*,*b*, 1993; Bell, 1996; Chu, 1998). Our arbitrary, operational definitions of taxa based on published descriptions were necessary for this morphological study and imply no pre-judgement of the genetic relationships between them.

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Table 1. Definitions of Iceland gull taxa mainly from adult upper surface wingtip melanism based on a variety of sources

Features	*thayeri*	*kumlieni*	*glaucoides*
Number of primaries with melanism	(3)4–6	1–5	0
Melanism scores P 10–6	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, 1991*a*, *b*; additional Iceland gull data by us from specimens, after Snell (1991*b*).

DEFINITIONS OF TAXA

Differences in extent and intensity of upper surface wingtip melanism and other external characters of adults for three operationally defined taxa of the Iceland gull are presented in Table 1. Wingtip melanism varies more or less continuously from none in *glaucoides* to darkest and most extensive in *thayeri* (Dwight, 1925; Fjeldså & Jensen, 1985; Snell, 1989). There is consequently overlap or only marginal separation between taxa (Table 1). Nominate *glaucoides* has been defined as lacking any wingtip melanism from E. Sabine (1819); to Boertmann (1994), but melanism varies geographically in the other two taxa (MacPherson, 1961; Ingolfsson, 1967, 1970; Knudsen, 1976; Fjeldså & Jensen, 1985; Gaston & Decker, 1985; Snell, 1989).

Wingtip melanism and bill size in Iceland gulls were not correlated in partly sympatric *thayeri* and *kumlieni* (Snell, 1989). Wing and tarsus length and bill size did not differ significantly between winter samples of *kumlieni* and *glaucoides* measured in Iceland, the Faroe Isles and the UK (Weir *et al*., 1995), but *kumlieni* was slightly larger-billed than *glaucoides* in other samples measured (Dwight, 1906, 1925; Rand, 1942; Ingolfsson, 1967).

Iris colour and wingtip melanism tend to be correlated in breeding adult Iceland gulls (Table 1). The iris colours for Iceland gulls (Table 1) are from mainly allopatric populations; the relationship between colour of iris and wingtip melanism breaks down where sympatric *thayeri* and *kumlieni* freely interbreed with each other (Gaston & Decker, 1985; Snell, 1989).

Although not wholly satisfactory, wingtip melanism is the best character for distinguishing between the Iceland gull taxa. Genetic differences between these and other taxa of large white-headed *Larus* gulls are extraordinarily slight and probably all at sometime interbreed with one or more other taxa (Ingolfsson, 1970, 1987, 1993; Snell, 1991*a*,*b*, 1993; Bell, 1996).

METHODS

We examined possible changes with time in the wingtip melanism of adult Iceland gulls throughout their geographical range. We also examined stability of distribution of other large gulls of the region, in case changes were due to a common set of external variables. Because *L. a. smithsonianus* is readily confused with *thayeri* and may interbreed with Iceland gulls, we examined old records of 'herring gulls' at high latitudes.

We assigned specimens and published records to our definitions of taxa, but differences in definition have occurred between us and other workers. Sight records were often problematical. We excluded most records of immature Iceland gulls because they are highly variable and we knew of no reference specimens of known-origin older than newly fledged juveniles (Weir *et al*., 1995). We list collections where we examined specimens or from which we sought data (Table 2). Specimens examined for this paper and Weir *et al*. (1995) differ from those examined in other studies of Iceland gulls or Arctic *smithsonianus* (MacPherson, 1961; Ingolfsson, 1967, 1970; Fjeldså & Jensen, 1985; Godfrey, 1986; Snell, 1989).

The ornithology of the Arctic is so recent that the apparent expansion of a taxon's range over time may be real, an artefact of increasing knowledge or a combination of both. Conversely, a major range contraction with time may be demonstrably real; there may be good

Table 2. Collections in which we examined Iceland gull specimens, or from which we sought data on specimens for this study and Weir *et al*. (1995). Acronyms are given for these and others referred to in the text

Collection (acronym)	Taxa
Examined by us	
Aberdeen University Natural History Museum (AUNHM)	T K
Glasgow Art Gallery and Museum (GAGM)	G
National Museums of Ireland (NMI)	T G possible hybrid
National Museums and Galleries on Merseyside (NMGM)	G
Natural History Museum, Tring (NHM)	T K G
National Museums of Scotland (NMS)	K G
Examined by others	
Museum Faroe Islands and J.-K. Jensen Coll. Nolsøy, Faroe Islands (MFI)	T K G
Icelandic Museum of Natural History (IMNH)	K G
University Zoology Museum, Copenhagen (ZMK)	K G
Smithsonian Institution (USNM)	possible G and T
Others in text	
Museum Comparative Zoology, Harvard (MCZ)	G or K

Taxa: T, *thayeri*; K, *kumlieni*; G, *glaucoides*.

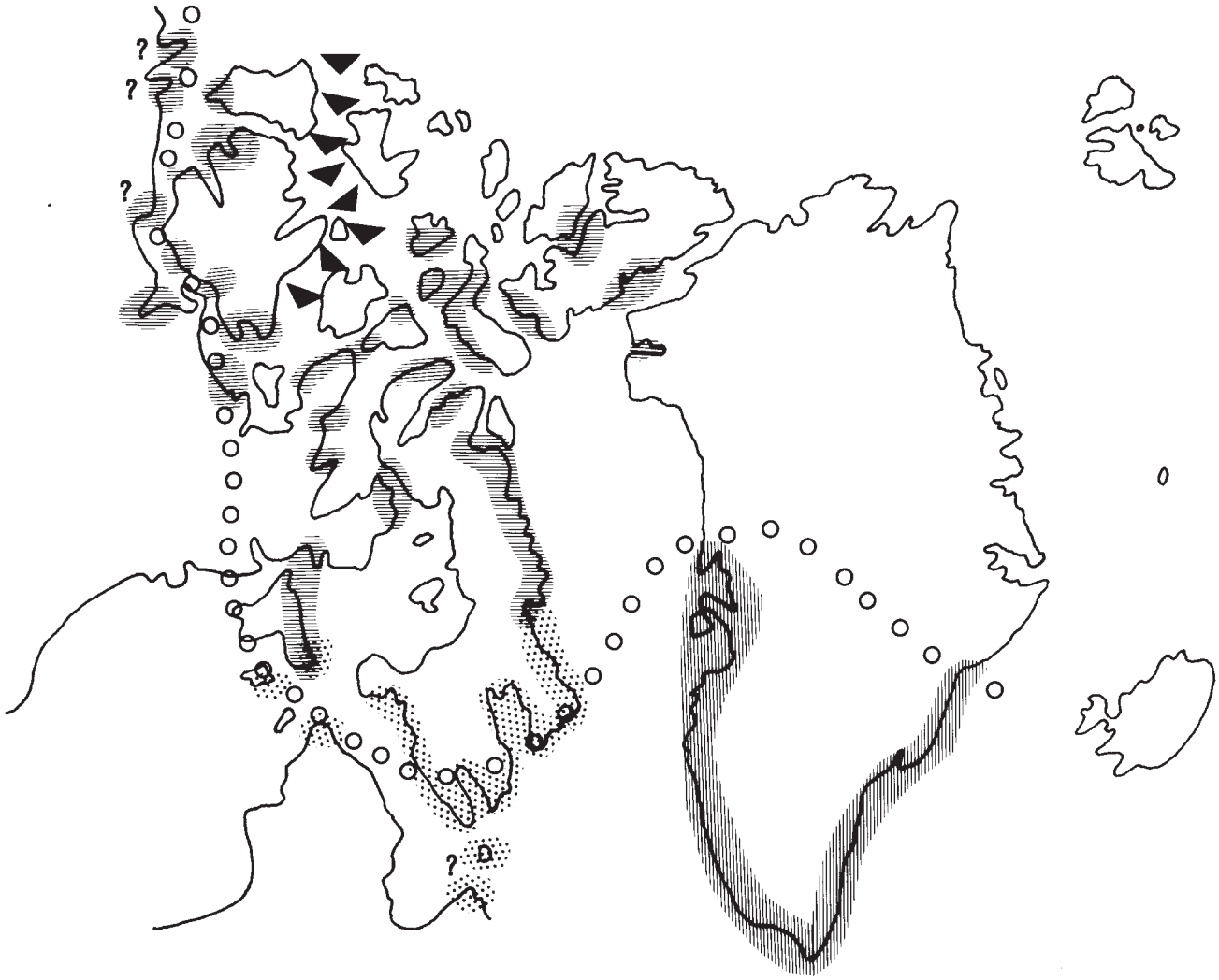

Fig. 1. Breeding records for three Iceland gull taxa *c*. 1950–95: *glaucoides* ▥ ; *kumlieni* ⁘ ; *thayeri* ▤ . Complete breeding distributions of all three taxa are still uncertain (= ?), and a few *thayeri* records are from up to 20 years before 1950. ▼ indicates the main southward thrust of thick, multi-year accretions of pack ice; o o postulated southern limit to High Arctic.

specimen evidence that it once bred where it is not now found. Therefore apparent range expansion by one Iceland gull taxon was most likely to be real if it corresponded in space and time to a known range contraction by another.

It was fortunate that Royal Navy (RN) and associated explorations of the Northwest Passage in 1818–60 included studies of natural history (Neatby, 1970) and happened to traverse almost the entire breeding range of the Iceland gull. Most specimens from the earliest of these are now lost but full descriptions of proposed types or some new geographical records remain. As Arctic ornithology became less novel (J. Sabine, 1824; Ross, 1826; Richardson, 1836) there were fewer descriptions for the period *c*. 1825–50, and very few specimens survive today. However, most specimens from after *c*. 1850 are still extant. We examined critically the literature from these explorations in which records were mainly for Arctic Canada. There were references to Greenland birds in early Scandinavian literature from the Viking Sagas onwards and these were critically reviewed by Winge (1898).

RESULTS

Present breeding distribution

Post-1950 breeding distributions of Iceland gull taxa are shown in Fig. 1. Distributions are much more clumped and discontinuous than can be shown at this scale (MacPherson, 1961; Joensen & Preuss, 1972; Gaston *et al*., 1986; A. J. Gaston, *in litt*.). The main southward thrust of thick, multi-year accretions of pack ice that block the Northwest Passage (Neatby, 1970) is shown with a southern boundary of the High Arctic (Bliss, 1977, in Sage, 1986). These indicate that present distributions are High Arctic for *thayeri*, Low to High Arctic for *kumlieni* and *glaucoides*, and that Iceland gulls are absent from the coasts most affected by thick ice. The

range of *kumlieni* lies between those of *thayeri* and *glaucoides*, and *kumlieni* is sympatric with both.

Canada

It is usually thought that *glaucoides* as defined here no longer breeds anywhere in Canada (Snyder, 1957; MacPherson, 1961; Godfrey, 1966, 1986; Ingolfsson, 1967; Fjeldså & Jensen, 1985). However, the palest-winged birds at 69° N in east Baffin Island were thought to be indistinguishable from *glaucoides* (Snell, 1989), and a few adult 'Iceland gulls' were found with breeding *thayeri* at 73° N (Reynaud, Johnson & Finley, 1981).

Kumlieni is found in variably-spaced colonies with the highest numbers in east Baffin Island, from Meta Incognita to Cumberland Sound, and with the palest-winged birds in a minority (MacPherson, 1961; Fjeldså & Jensen, 1985; Gaston & Decker, 1985; Gaston *et al*., 1985, 1986; Snell, 1989; A. J. Gaston, *in litt*.). These sources estimated numbers of *kumlieni* for the Foxe Basin coasts, south Baffin Island and part of east Baffin Island, and more recent information for other potential range within these limits was added, suggesting a total Canadian breeding population of 10 000 pairs ± 50%. Possibly no *kumlieni* breed west of Southampton Island (A. J. Gaston, in Snell, 1989), although there were at least three 1930s to 1950s records of *kumlieni* as defined here from *thayeri* colonies further north or north-west (Bray & Manning, 1943; Manning *et al*., 1956; Parmalee & MacDonald, 1960). The boundary between *kumlieni* and *thayeri* in northern Hudson Bay and Hudson Strait does not seem to have shifted in the last 20 years (A. J. Gaston, *in litt*.). Nor did that in Home Bay, east Baffin Island, between 1960 and 1987 (Smith, 1966; Snell, 1989).

Numbers of *thayeri* range from relatively many, large colonies in south-western Foxe Basin to few, small colonies on the northernmost breeding islands (Ellis, 1956; Ellis & Evans, 1960; Manning *et al*., 1956; Tuck & Lemieux, 1959; Parmalee & MacDonald, 1960; MacPherson, 1961; Savile, 1961; Parmalee, Stevens & Schmidt, 1966; Nettleship, 1974; Gaston *et al*., 1986; Godfrey, 1986; Snell, 1989). The most recent information suggests a Canadian population of 4000–6000 pairs, with highest numbers in the Frozen Strait/Lyon Inlet area (Smith, Whitney & Storm, 1995; Smith, Saunders & Whitney, 1996). There are few very recent data for the mainland coast west of *c*. 90° W.

In east Baffin Island there may have been a gap between the southern limits of *thayeri* and northern limits of *kumlieni*, but the present southern limits of *thayeri* were correctly predicted by MacPherson (1961), and determined by Smith (1966).

Greenland

The distribution of *glaucoides* shown in Fig. 1 is from Salomonsen (1979*a*); see also Evans (1984). Recent local declines in west Greenland were attributed to over-shooting (Salomonsen, 1967). Northern limits in east Greenland may be further south than in Fig. 1 (Boertmann, 1994; J. Fjeldså, *in litt*.). Evans (1984) gave no estimate of the breeding population, but it may be less than 80 000 pairs (Boertmann, 1994).

The current breeding population includes unknown numbers of probably widespread *kumlieni*. Different samples of 10 and five June–July adult specimens were all *glaucoides* (Fjeldså & Jensen, 1985; Weir *et al*., 1995), but 12 of 19 (63%) from June–August had some wingtip melanism, which was very subdued in nine (Ingolfsson, 1967). Many of the same specimens were examined by Ingolfsson (1967) and Fjeldså & Jensen (1985), so that most of Ingolfsson's summer *kumlieni* must have been from August rather than June–July, and were treated as taken after the breeding season by Fjeldså & Jensen. More recently there were a further five specimens or sight records of summer adults with evident wingtip melanism (Olsen, 1991; Boertmann, 1994). Some of the above birds presumably bred, and there was a definite record from Søndre Strømfjord in west Greenland in 1964 where chicks taken into captivity developed subdued wingtip melanism and olive-brown or olive-buff irises when adult (Goethe, 1986). Many pale-winged *kumlieni* are indistinguishable from *glaucoides* in the field (Fjeldså & Jensen, 1985), and Goethe (1986) did not mention adult *kumlieni*, although he made prolonged observations at the colony where he took the chicks. Pale-winged *kumlieni* may often be overlooked in Greenland.

Salomonsen (1967) gave a very restricted distribution for *thayeri*. Breeding birds were not found in west Greenland by Thing (1976, *contra* Evans, 1984), but seven adults and fledged young were seen just south of the breeding area in August 1987 (Olsen, 1991). A few summer adults were seen both coastally and at sea north and south of the breeding area (Brown, 1986; Boertmann, 1994).

Past breeding distribution

Distribution data to *c*. 1900 and 1950 are shown with selected dates of first records in Figs 2 and 3. Up to *c*. 1900 both *thayeri* and *kumlieni* were known only from very small ranges, with *thayeri* only in the north-west of the present range. Even up to *c*. 1950, known ranges of both were smaller than now. However, travel to many breeding areas of both taxa remains very difficult to the present day. Thus the concentration of *thayeri* in Frozen Strait/Lyon Inlet was only found in the last decade, but extensive development of *Caloplaca* lichens suggests that gull colonies have used the cliffs for a long time (A. J. Gaston, *in litt*). The range of *glaucoides* before 1900 extended far into High Arctic Canada, where it was sympatric with *thayeri*. The apparent range expansion of *thayeri* as shown in Figs 1–3 corresponds partly in space and well in time to the known range contraction of *glaucoides*. In specific

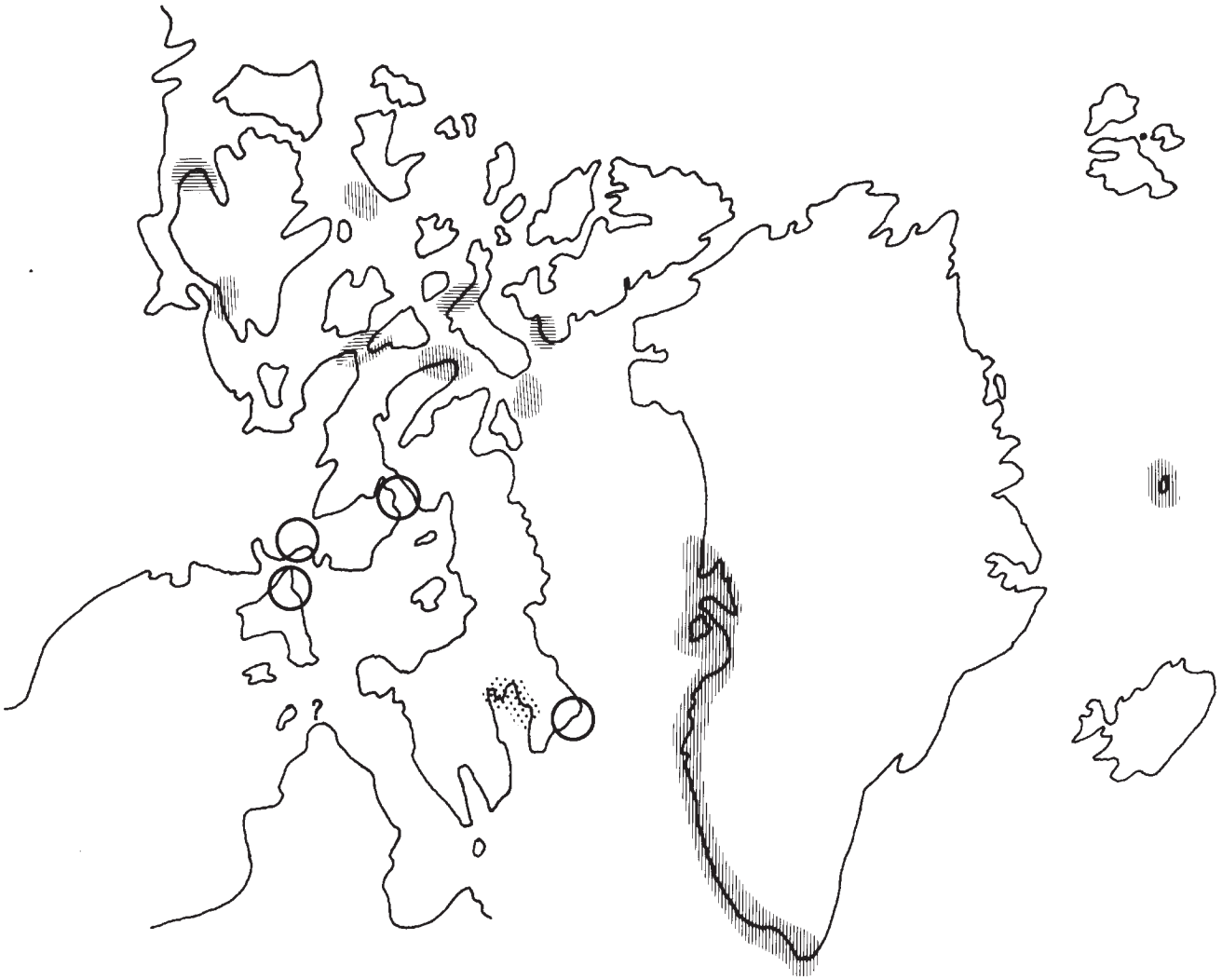

Fig. 2. Known breeding distribution with dates of first records for three Iceland gull taxa to *c*. 1900: *glaucoides* ▥; *kumlieni* ⁘; *thayeri* ▤; *glaucoides* or *kumlieni* (taxon not verified) = ?. The first most northerly breeding records for *L. a. smithsonianus* are also shown ◯.

areas *thayeri* replaced *glaucoides*, probably in south-east Victoria Island, and certainly in Bellot Strait and the north-east coast of Prince Regent Inlet.

Canada

Iceland gulls and herring gulls were looked for from the earliest RN Arctic explorations (E. Sabine, 1819, 1824; MacGillivray, 1824; J. Sabine, 1824; Richardson, 1825, 1831, 1836; Ross, 1826, 1835). Extant specimens and early descriptions prove or suggest the identities of gulls at 14 locations from 10 explorations in 1818–59 (Table 3). The data refute two subsequent assumptions: firstly, that glaucous gull *L. hyborboreus* or *thayeri* were mistaken for *glaucoides* (Taverner, 1933; Salomonsen, 1950; MacPherson, 1961; Parmalee *et al*., 1966); and secondly, that all 'herring gulls' at high latitudes were *thayeri* (Dwight, 1925; MacPherson, 1961). Early identifications were mostly accurate despite assumptions by some later workers. Besides the specimen records, the best evidence for Canadian *glaucoides* was from the Parry Isles in 1819–20 and Prince Regent Inlet in 1829–32, the second and fifth voyages listed in Table 3.

The Canadian *glaucoides* colonies in Fig. 2 were spread over a large area, but *glaucoides* was definitely recorded in only four of the 10 explorations in Table 3 and might then have been scarce in Canada. In three publications from Parry's first voyage (1819–20) there were more than 20 references to glaucous gull in Canada, compared with only two for Iceland gull (Griffiths, 1821; E. Sabine, 1821, 1824).

Dark-winged gulls collected at six locations (Table 3) were, or probably were, *smithsonianus*. The first *thayeri* specimens from two areas and a record inferred from present distribution in a third, were from the north-west of its present range and from the first three voyages in the search for Sir John Franklin, which explored widely the western Canadian High Arctic (Neatby, 1970). Evidence that *thayeri* then bred east of 90° W or south

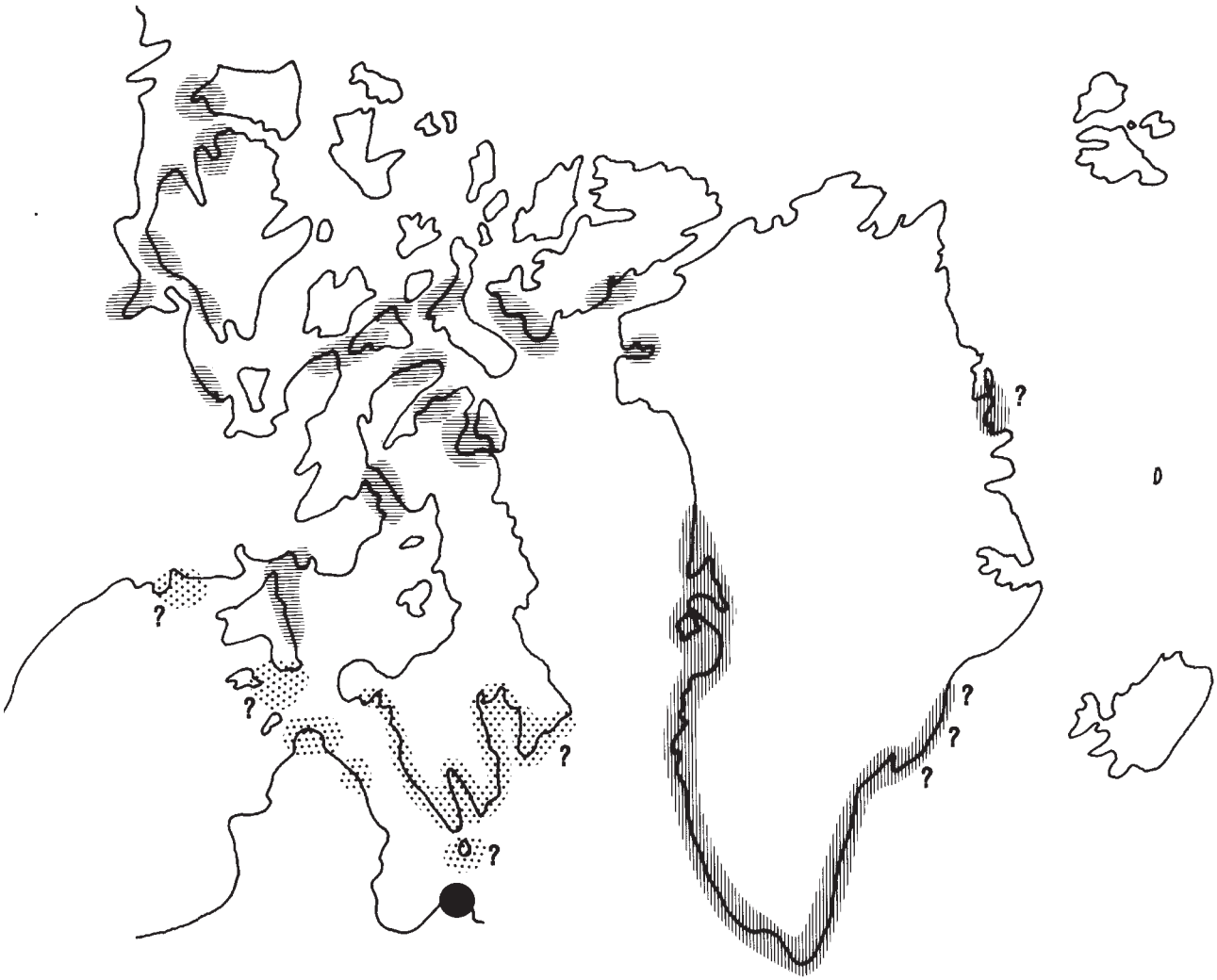

Fig. 3. Breeding records for three Iceland gull taxa *c*. 1900–50: *glaucoides* ▥; *kumlieni* ⁘; *thayeri* ▤; *glaucoides* or *kumlieni* ●; uncertain or disputed records = ?.

of 70° N was lacking, but the early explorers did not reach important breeding areas (see above).

Many other early records lack specimens or descriptions. We traced specimens of eggs of 'Iceland gulls', taken for USNM in 1861–65 on the lower Anderson River east of the Mackenzie Delta (MacFarlane, 1891). The 'Iceland gull' eggs were thought to be of the small *barrovianus* race of the glaucous gull (Taverner, 1933) and the 18 extant sets of MacFarlane's eggs in the USNM (14) and NMS (four) are all now regarded as glaucous gulls (R. Schmidt, *in litt*.; this study).

A very pale adult specimen of the Iceland gull breeding near the Digges Isles in 1886 was lost (Feilden, 1889). It might have been either *glaucoides* or pale *kumlieni*; most Digges Sound birds now are typical *kumlieni*, but range from birds with heavily pigmented wingtips to almost unpigmented (Gaston *et al*., 1985; A. J. Gaston, *in litt*.). A similarly pale and probably breeding adult female from Cape Chidley, north Labrador, in 1934 was identified as *leucopterus* (= *glaucoides*) at MCZ (Gross, 1937). We have not examined it, but Snyder (1957) gave the range of *kumlieni* as extending to Cape Chidley, possibly from this record.

Although the first breeding *kumlieni* recorded at Cumberland Sound, east Baffin Island in 1878 had evident wingtip melanism, 'white-winged' adults also were present, but not breeding (Kumlien, 1879). Apart from Digges Sound (see above) no other colony was reported in the nineteenth century, but those two areas are near the western and northern limits of the present range (Fig. 1). An increasingly wider breeding range in and near Baffin Island was reported in the middle part of the twentieth century (Taverner, 1933; Soper, 1940, 1946; Rand, 1942; Wynne-Edwards, 1952; Snyder, 1957). Range limits in Snyder (1957) are exceeded in most directions by present limits (Fig. 1). This most likely resulted from increased knowledge, but major twentieth century range expansion cannot be wholly discounted (A. J. Gaston, *in litt*.).

Table 3. Known or probable identities of 'Iceland gulls' and 'herring gulls' from nine Royal Navy and one Hudson's Bay Co. explorations of Arctic Canada, 1818–59

Voyage	Locality	Date	Taxa[a]	n	Sex	Age[b]	Museum[c]	Comments	References[d]
Ross First, 1818	Davis Strait	July 1818	G	1		A	NMGM	From series used to distinguish G from H	14, 16, 20
Parry First, 1819–20	Davis Strait, Baffin Bay, Melville I.		G + S	> 1					11, 15
	Melville I.	6 June 1820	? G	1					5
Parry Second, 1821–24	Duke of York Bay, Southampton I.	August 1821	S	1		J	(NMS)		4, 6
	Igloolik I.	Sept 1821	S	1	F	A	(NMS)		7
	NE Melville Peninsula	June–Sept 1822	S	6		A	NMS - 4		6, 11, 19, contra 2, 8
Parry Third, 1823–25	Prince Regent Inlet		? S	> 1					4, 12
Ross Second, 1829–32	Prince Regent Inlet		G	> 1				Mixed colony with H above G	13, 16, 17
Back, 1836	route to Repulse Bay		S	1		A	(NHM)		18
Rae, 1855	Repulse Bay		S	1		A	(NHM)		18
McClure, 1850–54	Devon I.	1852	T	2		A, J		Originally identified as S, but T nests there now	9
Collinson, 1853	NW Prince Albert Land	1853	T	1	M	A	NHM		3, 18
	SE Cambridge Bay	1853	G/T	3		E	NHM		1, 3, 10
M'Clintock, 1857–59	Bellot Strait	1859	G	2		A	NMI	Re-feathering brood patches	21
	Bellot Strait	1859	T	1		J	NMI		4, 21
	Bellot Strait	1859	K	1		J	NMI	Identification uncertain	21

[a]Taxa: G, *glaucoides*; S, *smithsonianus*; T, *thayeri*; K, *kumlieni*; H, *L. hyperboreus*.
[b]Age: A, adult; J, juvenile; E, egg.
[c]Specimens deposited in museums; acronym as Table 2; specimen lost if acronym in parentheses.
[d]References: (1) Bent, 1921; (2) Dwight, 1925; (3) Feilden, 1879*a*; (4) Godfrey, 1986; (5) Griffiths, 1821; (6) MacGillivray, 1824; (7) MacGillivray, 1852; (8) MacPherson, 1961; (9) M'Cormick, 1854; (10) Oates, 1901; (11) Richardson, 1931; (12) Ross, 1826; (13) Ross, 1835; (14) Sabine, 1819; (15) E. Sabine, 1824; (16) Solomonsen, 1950; (17) Solomonsen, 1967; (18) Salvin, 1896; (19) Stenhouse, 1930; (20) Taverner, 1933; (21) Walker, 1860*a*.

The type series of *thayeri* is mainly summer adults from south-east Ellesmere Island collected in 1901 (Brooks, 1915). 'Kumlien's gull' eggs collected by J. S. Warmbath from south-east Ellesmere Island in 1900 were assumed to be *thayeri* (Bent, 1921), but earlier field descriptions of two adult 'stragglers' there fitted *glaucoides* (Greeley, 1886). No dark-winged gulls or Iceland gulls were recorded there by Feilden (1877; 1879*b*).

Subsequent determination of the range of *thayeri* was complicated by debate over its status and over the identity of many specimens (Dwight, 1917, 1925; Taverner, 1933; Rand, 1942; Synder, 1957; MacPherson, 1961). Dwight (1925) stated that there was a clinal transition from *smithsonianus* to *thayeri* north and west from Hudson's Bay. The two taxa were shown as narrowly allopatric by Snyder (1957); birds in Foxe Basin south of those limits had all been described simply as 'herring gulls' (Bray & Manning, 1943). To summarize past and recent Canadian data, *thayeri* was known only from the north-west of its present range until *c*. 1860, to present north-east limits by 1900, to present southern limits in Foxe Basin by 1960 (Smith, 1966) and to those in east Baffin Island by 1960. Again, increased knowledge is suspected to account for its presence at Foxe Basin and Baffin Island (A. J. Gaston, *in litt*.), but in some northern areas *thayeri* replaced *glaucoides* (see above).

Greenland

According to Winge (1898), the earliest reference to the Iceland gull was in a publication of 1771; the Inupik name for the Iceland gull differed from two for the glaucous gull, and the Inuit still distinguish by name between freshly killed breeding adults of the two species by the colour of the orbital ring (Freuchen & Salomonsen, 1957). In the 1820s, locations for type descriptions of *glaucoides* or synonyms were mostly from west Greenland coasts or waters (Salvin, 1896), but MacGillivray (1824) described a large adult given to the Edinburgh Museum by Captain Scoresby from his voyage to east Greenland. The specimen seems to have gone missing by 1860 (NMS Archives) but is by far the earliest east Greenland record.

In those parts of west Greenland known to Europeans, i.e. from Cape Farewell to 73° N, breeding Iceland gulls were widespread and common (Reinhardt, 1861; Hagerup, 1891; Winge, 1898). In adult specimens from west Greenland in ZMK there were no plumage differences between 15 Iceland gulls and 10 glaucous gulls (Winge, 1898). Slight melanism on the wingtips of glaucous gulls is extremely rare in west Greenland specimens (Ingolfsson, 1993), suggesting that the Iceland gulls were all *glaucoides* as defined here. Moreover, all remaining adult Iceland gulls in ZMK which Winge could have included in his sample are *glaucoides* (J. Fjeldså, *in litt*.).

Early records of adult Iceland gulls in the High Arctic of Greenland and Canada were thought to be misidentified glaucous gulls (Taverner, 1933; Salomonsen, 1950) but Table 3 refutes this for records up to 1859. We did not re-examine all records which Salomonsen rejected, but he rightly rejected those of Nares (1878) whose expedition naturalist did not mention Iceland gulls (Feilden, 1877; 1879*b*).

Iceland gulls were said to breed to *c*. 73° N in west Greenland in the nineteenth century (see above) and present limits are *c*. 72° N (Joensen & Preuss, 1972; Boertmann, 1994). Two clutches of eggs were taken there at almost 75° N in 1934 (Dalgety, 1936). Comparison of Dalgety's egg measurements with those in Makatsch (1974) confirm them as Iceland gull eggs. Northern limits may have changed little in west Greenland. The distribution of many bird species in east Greenland remains poorly known (Boertmann, 1994) and there is no consensus on the present northern limits of Iceland gulls there (see above). A breeding record north of 75° N (Pedersen, 1934) was further north than any ever recorded and is highly doubtful (Løppenthin, 1932; Salomonsen, 1950, 1979*a*; Elander & Blomqvist, 1986; Boertmann, 1994; J. Fjeldså, *in litt*.).

A gull from west Greenland with subdued wingtip melanism was named *L. chalcopterus* by Lichtenstein in 1854. Wingtip melanism of the specimen was not evident to Dwight (1906, 1925) nor to Salvin (1896), who thought this might be due to poor lighting in the Berlin Museum. Moreover, Holboell saw three similar specimens in west Greenland about the same time (Reinhardt, 1861). Some observers looked for summer adult *kumlieni* in west Greenland as soon as the taxon was described (Hagerup, 1891), but the first published records were from the 1980s (Olsen, 1991; Boertmann, 1994). However, we note a breeding record for the 1960s (Goethe, 1986) and summer specimens examined by Ingolfsson (1967) must have included birds which were taken some or many years earlier.

The first summer adult *thayeri* was taken just south of the breeding area in 1914 and about six more records up to 1939 included eggs (Salomonsen, 1950). The early naturalists had looked unsuccessfully for dark-winged gulls off north-west Greenland (E. Sabine, 1819, 1824; Walker, 1860*b*; Feilden, 1877, 1879*b*).

Winter distribution in the Nearctic

October–April distributions are summarized for North America to west Greenland. Those of *thayeri* and *kumlieni* were outlined by Bent (1921) and Dwight (1925) and remain very similar (American Ornithologists Union, 1983). However, the Pacific winter range of *thayeri* in those sources lies well south of the southern boundary of the Marine Subarctic (Hartmann & Johnson, 1977), whereas the western Atlantic winter range of *kumlieni* straddles the comparable Atlantic boundary shown in Stonehouse (1971). The Pacific continental shelf is narrow, but *thayeri* is non-pelagic there (Campbell *et al*., 1990; Morgan, Vermeer & McKelvey, 1991). By contrast, the winter range of

Table 4. Composition by taxon, from wingtip melanism (see text), of autumn to early spring samples of adult Iceland gull specimens. The region covers Atlantic wintering range from Greenland to the British Isles and the samples are wholly or mainly pre- and post-1950

Region	*glaucoides* %	*kumlieni* %	*n* birds	Source
Pre–1950				
Greenland to 1898[a]	100	0	15	Winge (1898)
Northeast Iceland 1907–13	90	9	11	this study
British Isles 1869–1915	75	25	4	this study
post–1950				
Greenland[b]	67	33	45	Fjeldså & Jensen (1985)
Sowth-west Iceland 1966	38	62	139	Ingolfsson (1967)
South–north-east Iceland1954–89	50	50	10	Weir *et al*. (1995)
Faroe Isles 1983	20	80	25	Fjeldså & Jensen (1985)
Shetland Isles 1993–94	56	42	7	Weir *et al*. (1995)

[a] summer and winter birds combined.
[b] must include some older specimens.

kumlieni extends to or beyond the breaks of the much wider western Atlantic shelves (Brown *et al*., 1975; Powers, 1983; Brown, 1986).

British Columbia (BC) and Washington are the main wintering area for *thayeri* (Campbell *et al*., 1990; Morgan *et al*., 1991). It is 'abundant' or 'very abundant' in BC with 15 counts of concentrations of 500–2000 feeding birds (Campbell *et al*., 1990). In the Great Lakes it was a minority of wintering Iceland gulls in southern Ontario (Pittaway, 1992) and at a Québec site it was 3% of 1392 winter Iceland gulls in 14 years (Steeves, Holohan & Bathurst, 1989). It is rare on the east coasts of Canada and the USA (American Ornithologists Union, 1983; Godfrey, 1986). We know of only two pelagic records off eastern Canada (Brown, 1986; J. K. Jensen, *in litt*.).

Few early or recent records of *kumlieni* from Pacific coasts are now accepted (Weber, 1981; Godfrey, 1986; Campbell *et al*., 1990). Most Iceland gulls wintering in the Great Lakes region are *kumlieni*, i.e. in southern Ontario (Pittaway, 1992). At a Québec site it was 97% of 1392 winter Iceland gulls in 14 years (Steeves *et al*., 1989). In coastal/insular eastern Canada and the north-eastern USA it is widespread and at least locally common (Powers, 1983; Brown 1986; Godfrey, 1986; Zimmer, 1991; A. J. Gaston, *in litt*.).

Coastally and offshore 'white-winged' adults might be either pale *kumlieni* or *glaucoides* but usually were distinguished in sight records from 'typical' *kumlieni*. The abundances of white-winged birds and typical *kumlieni* at sea in winter between Canada and west Greenland were of the same order (Brown, 1986), but white-winged birds were almost unknown among Iceland gulls off north-east US coasts (Powers, 1983). Earlier, white-winged adults were said to reach those coasts mainly in invasions (Bent, 1921).

Only three specimen records of winter adult *glaucoides* from eastern Canada were accepted by Godfrey (1986). One of those is now missing from the NHM (this study). A subsequent specimen from southern Ontario in 1974 was accepted by Godfrey (Pittaway, 1992). We traced none from the USA. Only 1% of 630 recoveries of Iceland gulls ringed as chicks in west Greenland were from Canada or the USA (Salomonsen, 1967, 1979*b*). It is clear that *glaucoides* rarely reaches the North American mainland.

Greenland to British Isles winter distributions

The taxonomic composition of earlier and more recent samples of winter adult specimens are compared from Greenland to the British Isles (Table 4). Samples up to 1915 were 75–100% *glaucoides*, but those after 1950 were 33–80% *kumlieni*. The large differences apply to all areas (see below). Statistical tests were inappropriate because of the very small samples and qualifications noted in Table 4. The post-1950 samples from east of Greenland are also mainly from storm-driven invasions, when *kumlieni* is more frequent than in other years (Ingolfsson, 1967; Fjeldså & Jensen 1985; Weir *et al*., 1995).

Wintering Iceland gulls were common on the west and south coasts of Greenland (Hagerup, 1891; Winge, 1898). Greenland specimens, which were probably all *glaucoides* (see above), may have included winter birds. West Greenland birds mostly winter there; 98% of 630 recoveries of those ringed as chicks were from Greenland (Salomonsen, 1967, 1979*b*). Birds moved south in winter, with northern coastal limits at about Disko Bay (Salomonsen, 1967) and south of close ice or in polynyas at sea (Brown, 1986). Wintering gulls at a large polynya off east Greenland included no Iceland gulls (Hjort, Hakansson & Stemmerik, 1983). In September, ship surveys in the north-west Iceland–east Greenland–Jan Mayen Island triangle, only 3.2 Iceland gulls/year were recorded and all from near east Greenland coasts (I. Petersen, 1995, and *in litt*.).

Two immature specimens in winter from south-west Greenland in 1898 and 1905 were attributed to *kumlieni* (Salomonsen, 1967), but the 1898 bird was later attributed to *thayeri* (Boertmann, 1994). Identifications of variable immatures of unknown origin are speculative. At sea between Greenland and Canada adult *kumlieni*

was common in winter (Brown, 1986). Coastally it was not given as a winter visitor by Salomonsen (1950, 1967), but was regarded as regular by Olsen (1991) and Boertmann (1994).

The Iceland gull was the only gull wintering in Iceland that did not breed there (Saunders, 1882–1884). The little-known east Greenland population was thought to be the source of most birds wintering in Iceland. They are common there (below) and only 1% of 630 recoveries of birds ringed as chicks in west Greenland were from Iceland (Salomonsen, 1967, 1979*b*).

Eleven winter adult Iceland gulls collected by I. Dinesen in north-east Iceland in 1907–13 and now in ZMK, NHM and NMS, included one *kumlieni*, the first known from Iceland. Samples listed in Table 4 suggest that *kumlieni* was as common or commoner than *glaucoides* after 1954, but the proportion of *kumlieni* may be substantial, as in the 1966 sample (Table 4) and the present relative abundance of the two taxa cannot be assessed (A. Petersen, *in litt*.).

Christmas Bird Counts on 5% of all Icelandic coasts averaged *c*. 1000–3000 Iceland gulls of all ages per year, but these coasts included many which were favoured by Iceland gulls (A. Petersen & Hjartarson, 1989, 1991, 1993; A. Petersen, *in litt*.). The total winter population of both taxa combined may exceed 10 000 birds in some years (A. Petersen, *in litt*.).

Usually, small numbers of pale immature and mainly female Iceland gulls winter in the Faroe Islands (J.-K. Jensen, *in litt*.). The first known *kumlieni* specimen was in 1905 and no more were known until the adults, which predominated in the 1983 storm-driven invasion (Fjeldså & Jensen, 1985).

In the British Isles the Iceland gull formerly was a rare winter visitor (MacGillivray, 1824, 1852). Only one of four adult or subadult specimens for before 1950 was *kumlieni* from 1869 (Weir *et al*., 1995). Most sight records of adults in the storm-driven 1983 and 1993 invasions were of white-winged birds and four of seven NMS 1993 adult specimens were *glaucoides* (Weir *et al*., 1995). Numbers wintering in the Faroe Isles and British Isles combined probably exceed 1000 only during some invasions.

Hybridization

'Evidence' of hybridization between Iceland gull subspecies was formerly from specimens of unknown origin with wingtip melanism which was thought to be unusual for the location (Dwight, 1906, 1917, 1925; Taverner, 1933; Rand, 1942; MacPherson, 1961). Definitions of taxa from wingtip melanism were not agreed upon between workers (Rand, 1942). Biometrics were few; e.g. MacPherson (1961) could find measurements of only one supposed *smithsonianus* × *thayeri*. In the field complete reproductive isolation between *smithsonianus, thayeri* and *kumlieni* was reported by Smith (1966), but this aspect of his study has been discredited (Knudsen, 1976; Gaston & Decker, 1985; Snell, 1989, 1991*c*).

Within Iceland gulls sympatric *thayeri* and *kumlieni* hybridize freely and pairings are more or less random in relation to wingtip melanism and iris colour (Knudsen, 1976; Gaston & Decker, 1985; Snell, 1989). There was suggestive evidence of hybridization between *thayeri* and *glaucoides* at the only site where sympatric breeding was supported by specimens (Table 3). 'White-winged' birds in east Baffin Island were sympatric with *thayeri* at 73° N and freely interbred with *thayeri* at 69° N (Reynaud *et al*., 1981; Snell, 1989). 'White-winged' birds were sympatric with *kumlieni* in east Baffin Island as far back as 1878 (Kumlien, 1879) and the two taxa are now sympatric in Greenland (see above). The palest-winged *kumlieni* cannot have persisted for *c*. 150 years and spread if *kumlieni* only hybridizes with darker *thayeri*. Moreover, *kumlieni* tends to be darker in the west and paler in the east (above), which also suggests *kumlieni* has resulted from hybridization between *thayeri* and *glaucoides*.

Distribution changes in other large gulls

While the replacement of *glaucoides* by *thayeri* was eastwards, distributions of other large gulls of the region shifted mainly north. The southern limits of glaucous gulls moved north in eastern Canada (MacPherson, 1961). Great black-backed gulls *L. marinus* spread north in Greenland (Salomonsen, 1950, 1979*a*), and in Arctic Russia where they became sympatric with or displaced glaucous gulls (Uspenskii, 1984; Kalyakin & Ponomareva, 1999).

Birds of the herring gull complex are recent colonists of Arctic Siberia (Uspenskii, 1984). They colonized Iceland from the 1920s (Ingolfsson, 1970) and south Greenland from the 1970s (Boertmann, 1979). The exception seems to be Canada where *thayeri* was already present further north. Herring gulls bred as far north in western Foxe Basin in the 1820s (Table 3) as in the 1980s (Forbes *et al*., 1992). In Baffin Island, they bred about as far north in the 1900s (Hantzsch, 1930) as in the 1980s (Snell, 1989).

Iceland gull distribution shifts involved 40° of longitude. There were limited east-west or west-east components in the herring gull colonizations of Iceland and Greenland (above), but other longitudinal shifts involved only small numbers of large gulls in North America. Lesser black-backed gulls *L. fuscus* from Europe crossed the Atlantic and now appear to breed in eastern Canada (Godfrey, 1986; Steeves *et al*., 1989). There is slight introgression of western Pacific slaty-backed gulls *L. schistisagus* into western and south western Alaskan populations of glaucous-winged gulls (Kessel, 1989; Petersen, Weir & Dick, 1991; Bell, 1996).

DISCUSSION

Distribution shifts by Iceland gulls differed so greatly from those by other large gulls of the region that they

could not be due to the same set of external variables. We believe that *thayeri* spread east and interbred with *glaucoides*, giving rise to the variable hybrid *kumlieni*. As the eastward shift continued, the hybrid zone moved east and introgression may now extend to the eastern limits of the greatly reduced range of *glaucoides*.

Relatively simple criteria are widely considered to distinguish unstable, hybrid populations from stable, valid taxa (Otte & Endler, 1989). Five criteria identify *kumlieni* as an unstable, hybrid population: (1) specimen data confirm that the postulated parent taxa formerly bred sympatrically and may have interbred; (2) known range contraction by one parent taxon corresponds in space and time to known or apparent range expansion by the other parent; (3) non-assortative breeding by the hybrid with one parent is known and is strongly suggested with the other; (4) the hybrid is variably intermediate 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 hybrid is limited between those of the parents and overlaps both near the Low/High Arctic boundary. Also the hybrid has not spread into the High Arctic where *thayeri* has directly replaced *glaucoides*.

One genetic study shows that *thayeri*, *kumlieni* and herring gulls are very closely related, but other northern large gulls are too, and variability is greater between colonies than between species (Snell, 1991*a*). Although more *thayeri* material is still needed for another molecular study, preliminary indications are that *thayeri* differs somewhat from *kumlieni, glaucoides* and herring gulls (M. Willcox, *in litt*.). This does not preclude hybridization between *thayeri* and *glaucoides*, given its frequency in large northern gulls (Snell, 1991*a*,*b*, 1993; Bell, 1996). Also *thayeri* and *glaucoides* need not necessarily be one species; it is only necessary that *kumlieni* is intermediate between them.

Possibly *thayeri* bred in a High Arctic 'Banksian Refugium' of western Canada during the Wisconsonian Glaciation, and *glaucoides* in a Low Arctic refugium of the western Atlantic (Salomonsen, 1972). Wherever *thayeri* bred formerly, in Canada the Cordilleran and Laurentide Ice Sheets parted and circumferentially shrank early in the present inter-glacial (Pielou, 1989). This would have exposed western Arctic coasts and an overland route from the Pacific along which *thayeri* migrates today (Johnson & Herter, 1989). Salomonsen (1950, 1967) treated *glaucoides* as Low Arctic, but it bred far into the High Arctic only 150 years ago and its current restriction to more or less the Low Arctic cannot indicate a simple climatic limit.

Populations wintering in the Pacific and the Atlantic might have advanced and retreated several times in the Arctic in accordance with climatic change during the present inter-glacial. They need not have hybridized during every meeting and when they did, gene flow might have been in either direction. It appears that the brief systematic ornithology of the Arctic happened to coincide with the most recent hybridization between *thayeri* and *glaucoides*, an eastward shift in distribution by *thayeri* of *c*. 40° of longitude and further introgression by the hybrid into the remaining range of the Atlantic parent. Compared with other hybrid and parent distribution changes in northern large gulls (Snell, 1991*a*,*b*, 1993; Bell, 1996), the extent and speed of change in Iceland gulls has been extreme.

Hybrid zones are common in birds. They may be very wide and most are explained in northern regions by secondary contact during the present interglacial, but most do not move far (Hewitt, 1989). Hybrids are presumed adaptively less fit and tend to occur in density troughs between the parental peaks (Barton, 1989). In the Iceland gull there were rapidly shifting distributions of both parent and hybrid taxa, but *kumlieni* is now probably more numerous than *thayeri*, and *glaucoides* may be 10 times more abundant than either of them.

Other workers (e.g. Dwight, 1906; Snell, 1989) have suggested that Kumlien's gull is a hybrid and we present strong new evidence to support this. Further genetic studies are still desirable, although separation of large northern gulls is extremely difficult using mitochondrial DNA (Snell, 1991*a*; Bell, 1996). A study of microsatellite DNA will probably be required. Whatever taxonomic treatment is adopted, Kumlien's gull is a useful common name for the hybrid population and it commemorates a man who made an outstandingly comprehensive study of Arctic natural history in a single year.

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