narfjall and Skrudur, appear from primary pigmentation to be so close to pure *hyperboreus* and pure *argentatus*, respectively, that it seems somewhat unlikely that they would exhibit a marked increase in size variability, detectable in relatively small samples. A study of the more intermediate populations in Iceland would have been of greater interest (but admittedly much more difficult due to the small sizes of these populations).

Snell did not find consistent correlation between primary pigmentation and the 16 skeletal characters he measured in the Skrudur gulls. This agrees with my previous findings on gulls from this colony. However, Snell did not mention that my earlier results from Horn and Hromundarey in eastern Iceland showed clear correlations between degree of pigmentation and size, scarcely understandable without resorting to an explanation involving hybridization between the larger *hyperboreus* and the smaller *argentatus*. My earlier findings indicated that this correlation was becoming weaker with time. This is to be expected if genes for body size and primary melanism are not closely linked.

In addition, I was able to find significant correlation for degree of pigmentation, time of molt and breeding success within colonies (Ingolfsson 1987). Again, this is very difficult to explain except by assuming that a mixing of two gene pools was taking place.

As Snell stated, *argentatus* with reduced melanism on the primaries were found in European populations prior to the immigration of *argentatus* to Iceland. However, he neglected to note that the pattern of reduced melanism is significantly different from that found in Icelandic gulls. In Iceland, assumed hybrids have a black pattern involving the sixth, seventh and eight primaries that is typically diffuse. In gulls with reduced pigment from European populations, this is usually not so; the reduction in pigment is most pronounced on primaries 9 and 10 (Ingolfsson 1970:356). Therefore, the underlying causes are presumably different. Gulls from northern Norway and adjacent Kola Peninsula are exceptions, where many birds are similar to Icelandic hybrids.

It is clear that Icelandic gulls, contrary to Snell's conclusion, show both phenetic intermediacy and increased variability in comparison to *hyperboreus* and *argentatus* from most other areas. This is, as Snell (1991b:340) stated, "strong evidence in support of hybridization." However, Snell also correctly pointed out that failure to find such a pattern is only weak evidence against the hypothesis of hybridization (see also Schueler and Rising 1976). Thus, his final conclusion (Snell 1991b:340) that "It is likely that the variable plumage in the Icelandic populations of *argentatus* simply represents heretofore unrecognized intraspecific variation" is quite puzzling.

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Variably Plumaged Icelandic Herring Gulls: High Intraspecific Variation in a Founded Population

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When phenotypic variability within a species is not adequately understood or is underestimated, "unusual" character states in a population may be erroneously interpreted as evidence of hybridization (Schueler and Rising 1976). First, characters (or character states) thought to be taxon-specific markers may be present in a second taxon at low frequency; such joint occurrence may simply reflect recent common ancestry. Second, character states thought to be intermediate between parental taxa actually may be historically present at low frequency in a portion of a species' geographic range. Third, the spread of seemingly intermediate or unusual character states throughout a species' range or to newly colonized geographic regions may be misinterpreted as hybridization.

Reduced and variable patterning on primary feathers of some Icelandic *Larus argentatus* (Herring Gulls)

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and faint melanism on some Icelandic *L. hyperboreus* (Glaucous Gulls) are unusual phenotypic characteristics that have been interpreted as evidence of hybridization (Ingolfsson 1970, 1987, 1993, Snell 1989). As Ingolfsson (1993) stated, he "described a situation in Iceland where apparent extensive hybridization occurred when Herring Gulls . . . immigrated to Iceland starting about 1920 and encountered Glaucous Gulls . . . ." At issue is whether these variably plumaged gulls are hybrids, as Ingolfsson (1970) hypothesized, or whether, as I (Snell 1991:329) suggested, such birds may more simply represent light-winged *argentatus* founders, possibly dispersed from Scandinavia.

Ingolfsson (1993) stated Snell made "an unfortunate, but understandable, choice of Skruder as a study colony in eastern Iceland. This colony contains a higher proportion of *argentatus*-like birds than most other colonies in eastern and southern Iceland. My previous account (Ingolfsson 1970) should have made this clear." In fact, what is clear from Ingolfsson's previous account is that the *argentatus* colonies with high proportions of light-winged birds have or had small populations, often containing fewer than 30 individuals. Some Icelandic colonies, such as at Horn, are likely abandoned. I chose Skruder as a sample site, on Ingolfsson's advice, as it is one of the few if not the only *argentatus* colony in Iceland large enough to withstand, without adverse effect on the breeding population, the collection of a sample of adequate size to allow for the statistical analysis of variation in variability. Of 53 adult *argentatus* Snell collected at Skruder, eight birds (17%) have plumage melanism scores of 4 or less (Snell 1991:fig. 3) and would be considered as "hybrids" according to Ingolfsson's (1970) criteria.

Ingolfsson (1993) wrote that "Snell (1991b) stated that his samples of *hyperboreus*-like gulls . . . do not differ significantly in melanism scores. This is not so. Significantly larger numbers of gulls have traces of melanistic patterns on their primaries at Bjarnarhafnarfjall (11 of 53) than in Svalbard . . . and Home Bay (0 of 48)." In fact, Ingolfsson (1993) has compared the results of tests of different statistical parameters (Fisher's exact test and ANOVA). As well, although Ingolfsson (1993) does not mention it, the results of the Fisher's exact test are evidently based on the Icelandic birds I collected (Ingolfsson's and my sample sizes are the same, and both of us independently examined my Icelandic samples of *argentatus* and *hyperboreus*).

Ingolfsson (1993) coded the melanism of the gulls using a binary character: having "traces of melanistic patterns" or not. Coding plumage melanism of *hyperboreus* as a binary character is simplistic, as the difference between a vanishingly small trace of melanism and no melanism is both exceedingly slight and substantially less than the difference between a vanishing "trace" and a distinct though reduced melanistic pattern on the 9th and 10th primary. Ingolfsson (1993) compared the frequency of presence/absence of "traces" using Fisher's exact test.

By comparison, I (Snell 1991) scored the degree of melanism in plumage patterns of all his *argentatus* and *hyperboreus* samples using Ingolfsson's (1970) criteria (an index that takes into account degree of darkness of primaries). I (Snell 1991:332) tested for among-population differences in mean plumage melanism scores using ANOVA followed by *a posteriori* comparisons, reporting "First, the three *hyperboreus* populations [Iceland, Home Bay and Svalbard] are composed of exceedingly light-winged birds, which do not differ significantly in mean melanism score, and which are significantly less melanistic than other populations."

Regardless, these results (Snell 1991, Ingolfsson 1993) are not incompatible, contradictory, or evidence of hybridization. The *hyperboreus* with "traces of melanistic patterns" from western Iceland and Svalbard are light-winged or exceedingly light-winged individuals (Snell 1991: fig. 2), with plumage melanism index values of less than 1. Mean values of plumage scores within populations are very low, and do not differ significantly (Snell 1991). The significant differences in plumage of *hyperboreus* are in the frequencies of birds having very similar appearance. Reflecting the common misperception among ornithologists and other observers that adult *hyperboreus* invariably lack pigmentation on primary feathers, faint patterning on *hyperboreus* is likely often overlooked in the field. Where observed, faint patterning is easily misinterpreted as evidence of hybridization.

Faintly patterned primary feathers were present in some *hyperboreus* prior to the colonization of Iceland by *argentatus* in the 1920s. For instance, an adult *hyperboreus* from Greenland (unnumbered), collected before 1841, is distinctly patterned on the inner vane of the 9th and the inner and outer vanes of the 10th primary (Fig. 1). While faint traces of patterns on primary feathers of some *hyperboreus* are unusual, these patterns need not imply hybridization. Rather, interpopulational differences in frequency of patterned primary feathers can more simply be interpreted as intraspecific geographic variation.

Initially, Ingolfsson (1970:342) dismissed or ignored the possible relevance of light-winged Norwegian *argentatus*, stating that the number of these birds "is so low as to be of little importance in analysing hybrid situations such as that found in Iceland." Ingolfsson (1993) wrote, in relation to plumage variation in *argentatus*, "I had noted that some birds from northern Norway and the adjacent Kola Peninsula in Russia were so hybridlike that extensive hybridization in the area was suspected."

Actually, there is no evidence of either current or historical secondary contact between *argentatus* and *hyperboreus* in Svalbard, northern Norway or the Kola Peninsula in Russia. *Larus hyperboreus* does not breed in these regions. In Svalbard, where *hyperboreus* is abundant, *argentatus* is absent. In the other two regions,

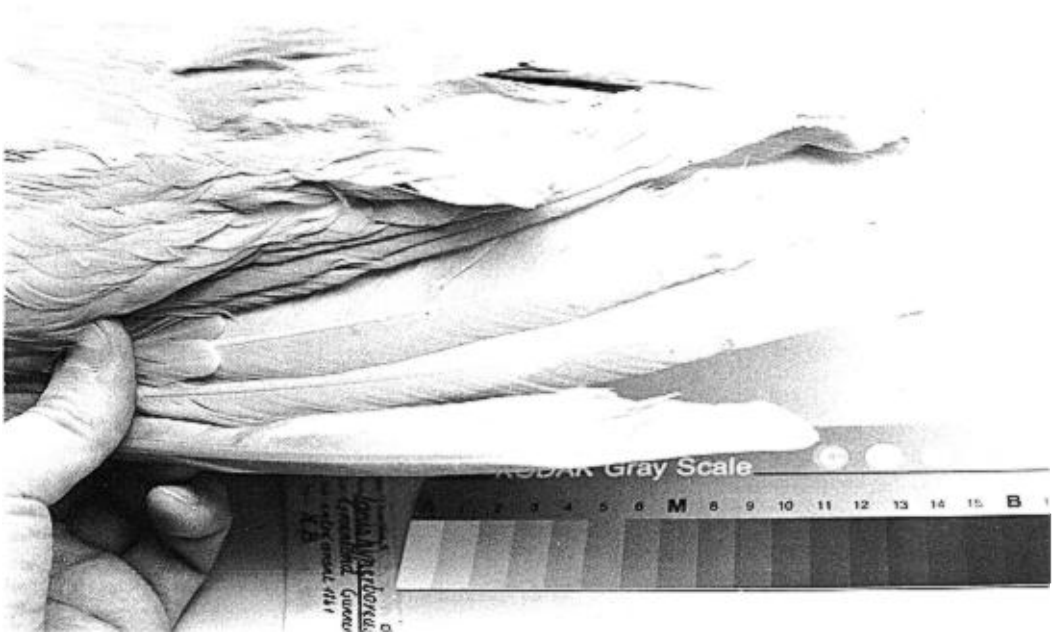

Fig. 1. *Larus hyperboreus* collected at Greenland, before 1841, housed at Brussels in the Institut Royal des Sciences Naturelle de Belgique. Specimen examined courtesy of Pierre Devilliers. Primary feathers have pigmented regions on the outer 9th vane, inner 10th vane, and outer 10th vane.

more than 600 km south of Svalbard, *hyperboreus* does not breed, whereas *argentatus* is common.

Ingolfsson (1993) stated "In any case, some of the Icelandic *argentatus*-like populations, especially those I studied at Hromundary and Horn (Ingolfsson 1987), are considerably more variable in degree of primary melanism than those from Europe, including northern Norway." This statement is entirely consistent with my (Snell 1991) hypothesis that variably plumaged Icelandic *argentatus* reflect founders not hybrids. If the original founders included light-winged individuals, highly variable plumage patterns in some founded *argentatus* colonies would be expected, especially at colonies of small size such as Hromundary and Horn.

Ingolfsson (1993) wrote "It is not possible to attach much significance to Snell's conclusion that the variability in 16 skeletal measurements of Icelandic gulls he studied was no greater than found in allopatric populations. The two populations he analysed in Iceland . . . appear from primary pigmentation to be so close to pure *hyperboreus* and pure *argentatus*, respectively, that it seems somewhat unlikely that they would exhibit a marked increase in size variability, detectable in relatively small samples." Indeed, as I (Snell 1991:fig. 2) demonstrated, the degree of variability in primary-feather pigmentation of Icelandic *argentatus* is extremely similar to that of northern Norwegian conspecifics, a population Ingolfsson (1970: 342) had considered, as noted above, "to be of little importance in analysing hybrid situations such as that found in Iceland." However, in comparison to the *argentatus* populations sampled elsewhere, in eastern Canada and France (Snell 1991:fig. 2), the level of variability of Icelandic *argentatus* is very high. Of course, in hindsight, had the degree of plumage variability of the northern Norwegian populations been recognized, there would have been no need for Ingolfsson (1970, 1987) to invoke the hypothesis of *argentatus* × *hyperboreus* hybridization as the explanation of the variable plumage in the founded Icelandic *argentatus* colonies.

Ingolfsson (1993) wrote that "A study of the more intermediate populations in Iceland would have been of greater interest (but admittedly much more difficult due to the small sizes of these populations)." Ingolfsson is correct in this regard. It would have been even more preferable to have samples collected shortly after the colonization of Iceland by *argentatus*, but such samples do not exist.

Ingolfsson (1993) wrote that "Snell did not mention that my earlier results from Horn and Hromundarey in eastern Iceland showed clear correlations between degree of pigmentation and size, scarcely understandable without resorting to an explanation involving hybridization between the larger *hyperboreus* and the smaller *argentatus*." Both Ingolfsson (1993) and I (Snell 1991) reported that correlations between degree of

pigmentation and size are inconsistent among founded colonies of Icelandic *argentatus*. I (Snell 1991:336) argued that "There is no consistent evidence for significant association between plumage melanism and morphology in these populations, and inconsistent correlations likely reflect sampling artifacts within a heterogeneously melanized population."

Ingolfsson (1993) stated that I, "neglected to note that the pattern of reduced melanism is significantly different [in European populations] from that found in Icelandic gulls .... Gulls from northern Norway and adjacent Kola Peninsula are exceptions, where many birds are similar to Icelandic hybrids."

Indeed, the nature of the patterning of many European *argentatus*, especially those from more southerly regions, differs from both Icelandic and Scandinavian conspecifics. However, as I (Snell 1991) argued, there is little reason to suspect that the founders of the Icelandic populations originally dispersed from these southern populations. The fact, as Ingolfsson (1993) agreed, that "Gulls from northern Norway and adjacent Kola Peninsula are exceptions, where many birds are similar to Icelandic hybrids," represents the fundamental and essential biological basis of my (Snell 1991:329) alternate hypothesis that the variable plumage of Icelandic *argentatus* represents "the genetic legacy of light-winged *L. argentatus* founders, possibly dispersed from Scandinavia, where light-winged *L. argentatus* individuals are present, albeit in low frequency."

In conclusion, I have taken Schueler and Rising's (1976) approach that to invoke hybridization, at the very least, data sets in addition to those that originally suggested the existence of the hybrid zone should be presented. No data sets in addition to those relating to plumage characters are available to support the hybridization hypothesis for Icelandic *argentatus*. I (Snell 1991) presented evidence that recently founded Icelandic *argentatus* populations differ little from the long-established conspecifics in northern Norway with regard to plumage and skeletal morphology, that the supposedly intermediate characteristics in *argentatus* or *hyperboreus* are historically present in these taxa, and that extant plumage patterns in Icelandic *argentatus* simply represent intraspecific variation.

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Type Specimens and Basic Principles of Avian Taxonomy

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"Ornithology" may be defined as the scientific study of birds. No aspect of avian biology, including management and conservation, can be carried out without reference *by name* to birds at some taxonomic level. Thus, the names of species of birds, and of groups of species, can fairly be considered to be of primary importance in ornithology. To be useful, these names themselves must be defined and related to biological entities. The definition of a name is accomplished by the designation of a "type." The *International Code of Zoological Nomenclature*, in paragraph (C) of Article 72 (third edition, 1985), establishes criteria for eligibility of a name-bearing type. The type of a species or subspecies name is the biological specimen defined by the name, and later use of the name implies specific or subspecific identity with the type. It is imperative, therefore, that a type be available for study and comparison so that the identity of other material with it can be established.

These principles, now considered basic by trained taxonomists, were not well established until the early part of the twentieth century. Before that, many species-group names were proposed without designation of a type and, particularly in birds, many were named on the basis of a painting or drawing. The *Code* recognizes this but establishes that the type is the spec-