

Glacial survival or *tabula rasa*? The history of North Atlantic biota revisited

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Up to the 1960s, there was nearly complete consensus that disjunctions and endemism in the North Atlantic cannot be explained without *in situ* survival during the glaciations (the “nunatak hypothesis”). The alternative “*tabula rasa* hypothesis” of postglacial immigration was regarded to be of merely historical interest. Herein we review recent geological, molecular, taxonomic, and biogeographic data to re-examine this view. There is now strong geological evidence for some ice-free North Atlantic areas within the maximum limits of the Late Weichselian/Wisconsinian ice sheets, but no fossils have been found to prove continuous *in situ* existence of life in these areas. Molecular data suggest that many plants and animals have migrated recently across the Atlantic, even if they lack mechanisms promoting long-distance dispersal. In other species, there are deep trans-oceanic phylogeographic splits suggesting survival in two or more refugia, but these refugia may have been located outside the ice sheets. For vascular plants, we provide an updated list of 77 north boreal, alpine, and arctic taxa accepted as North Atlantic endemics. The degree of endemism is very low (0.0–1.9% single-region endemism). Forty endemics occur in more than one of the isolated Atlantic regions, indicating extensive migration and complicating inferences on the location of refugia. Thirty-four endemics are probably not hardy enough for nunatak survival and are explained by postglacial immigration (or *in situ* evolution). Among the 43 “hardy” endemics, there is not a single outcrossing diploid that could suggest long-term evolution. Most of the hardy endemics are asexual or self-fertilizing polyploids, some of postglacial hybrid origin. Others are preglacial polyploids which immigrated postglacially or survived *in situ*. Some ice-free areas, such as the extensive Greenlandic ones, may have supported survival of some hardy organisms. The evidence accumulated since the 1960s suggests, however, that endemism and disjunctions in the North Atlantic can be explained without invoking *in situ* glacial survival.

KEYWORDS: biogeography, endemism, long-distance dispersal, molecular phylogeography, North Atlantic region, nunatak hypothesis, *tabula rasa* hypothesis.

INTRODUCTION

The possibility that northern refugia for arctic and boreal biota existed in geographic regions other than Beringia during the ice ages has stimulated continuous debates among botanists, zoologists, and geologists. A voluminous literature has accumulated presenting biogeographic and other evidence to propose numerous high-latitude refugia, such as nunataks protruding above the ice caps and exposed coastal shelves. Similar discussions have addressed possible “intraglacial” refugia in southern mountain regions, for example the European Alps (reviewed by Stehlik, 2002, 2003; Tribsch & Schönswetter, 2003).

In this paper, we revisit the evidence proposed to support the hypothesis of “*in situ* glacial survival” (the

“*nunatak*” hypothesis; originally formulated by Blytt, 1876, 1882; Warming, 1888; and Sernander, 1896) or the alternative “*tabula rasa*” hypothesis stating that postglacial immigration is responsible for the entire present-day biota in various North Atlantic regions. Up to the 1960s, there was virtually complete consensus among biogeographers that the occurrence of endemics and disjunct distributions in this area could not be explained without postulating *in situ* survival, at least during the last glaciation. In the concluding remarks for the Reykjavik Symposium on the *North Atlantic Biota and their History*, the Icelandic botanist Áskell Löve (1963: 391) stated that the theory of survival of plants within the glaciated areas replaces “the now merely historical *tabula rasa* idea”.

In Scandinavia, many mountain plants were thought

to be glacial survivors (e.g., Nordhagen, 1936, 1963; Dahl, 1955, 1963). Among the proposed glacial survivors in Greenland are most vascular plants (Warming, 1888), even the relatively thermophilous woodland birch (*Betula pubescens* Ehrh.; Böcher, 1956), and many beetles (Lindroth, 1963). In Iceland, survival of 50% of the present-day vascular plants and many beetles was proposed (Lindroth, 1931; Steindórsson, 1963). The most radical proponents of glacial survival in Svalbard (Hadac, 1963; Rønning, 1963) suggested that because of the isolated position of this high-arctic archipelago, most plants were probably glacial survivors, even the most thermophilous ones, which are very rare under the current climatic conditions. However, even if the proponents of glacial survival dominated the literature from 1930 to 1960, there was also throughout this period an undercurrent of scepticism in the Nordic area, mainly represented by palynologists (e.g., Fægri, 1960; cf. also Danielsen, 1971).

There are also more recent suggestions of glacial survival along the Norwegian coast, even of relatively thermophilous plants such as the spruce (*Picea abies*; Kullman, 2000) and the forest herb *Melica nutans* (Tyler, 2002). Many other organisms, such as marine algae (van Oppen & al., 1995), lichens (Lynge, 1939; Cernohorský, 1963; Printzen & al., 2003), marine invertebrates (the isopod *Idotea balthica*; Wares & Cunningham, 2001), earthworms (Omodeo, 1963), birds (Holder & al., 1999), and mammals (the Norwegian lemming; Fedorov & Stenseth, 2001), have also been proposed as *in situ* glacial survivors in various North Atlantic regions.

The two basic arguments used to support the glacial survival hypothesis were (1) the occurrence of numerous postulated endemic taxa, in particular of vascular plants, which was taken as definite evidence for long-term *in situ* evolution; the current postglacial period (or even several glacial cycles) was assumed to be too short for evolution of new plant species (cf. Dahl, 1987, 1989b); and (2) the lack of typical long-distance dispersal mechanisms in many disjunctly distributed species, in particular those with their only North European occurrences within the glaciated areas. In her studies of arctic-alpine poppies (*Papaver*), the Norwegian botanist Gunvor Knaben (1959b: 80) concluded: "It is evident that the races...have been separated from each other through periods of quite another duration than that of post-glacial times". The Swedish entomologist Carl Lindroth (1957, 1963) explained the lack of endemic animal species in the North Atlantic islands by Tertiary extinctions; the present fauna immigrated later across a land bridge and survived *in situ* through one or several glaciations.

Several of the North Atlantic beetle species are flightless or almost so (Lindroth, 1957, 1963), many animals such as earthworms are ampho-Atlantic disjuncts in

spite of being soil-dwelling (Lindroth, 1963; Omodeo, 1963), and the majority of the arctic-alpine plant species occurring in the North-Atlantic regions lack obvious traits to promote long-distance dispersal (Dahl, 1963). Hultén (1937) believed that ampho-Atlantic plant species had lost their dispersal capacity after repeated isolation and depauperation in small refugial populations: "Even if the explanation given for this peculiarity...will not stand criticism, the fact itself remains and cannot be rejected" (pp. 138–139). It was thus concluded that postglacial dispersal of arctic-alpine plants and animals across the North Atlantic ocean was virtually impossible: "...whatever is the explanation of the ampho-Atlantic distribution pattern, it is not a matter of long-distance dispersal" (Dahl, 1963: 183; but see, e.g., Danielsen, 1971 for the opposite view). Hultén and Dahl therefore believed that the populations of plant species occurring on different sides of the Atlantic had been separated throughout the entire Quaternary. They found the most convincing evidence for this hypothesis by the presence of so-called "west-Arctic" species in Scandinavia, a subset of the ampho-Atlantics which are absent from the Central European mountains and from the areas eastwards in Russia. A similar "east-Arctic" element in North America, restricted to assumed unglaciated areas in Greenland and the stretch from North Labrador across Newfoundland to Gaspé, has been explained in the same way (e.g., Fernald, 1925; cf. also Marie-Victorin, 1964). Another type of disjunction used as an argument for nunatak survival is the so-called "centric" species in Scandinavia, which were believed to have survived in separate refugia in southern and northern Scandinavia (centricity was also discussed for Icelandic plants, cf. Steindórsson, 1963).

For Scandinavia, the two last comprehensive reviews of the botanical and geological evidence referred to in the glacial survival discussion were published in 1987 (Dahl, 1987; Nordal, 1987). Dahl (1987) interpreted the available data to provide strong support for *in situ* glacial survival. Nordal (1987) challenged, however, the conclusion from the Reykjavik Symposium (Löve & Löve, 1963). She regarded postglacial long-distance dispersal caused by drifting ice, icebergs, or birds as the most probable explanation for the ampho-Atlantic disjunctions, and suggested that isolation of small populations during 10,000–15,000 years is sufficient to explain the reported endemism in *Papaver*: "I shall have to reject the commonly presented postulation, that endemisms, centricity and occurrence of West Arctic species in Scandinavia, necessarily presupposes ice-free refugia" (Nordal, 1987: 385).

Since these two reviews were published in 1987, many new studies providing data relevant for the glacial survival discussion in Scandinavia and other North

Atlantic regions have accumulated. In many areas, the reconstructions of the maximum extent of the Late Weichselian ice sheets have been revised based on recent geological investigations with improved techniques, in particular dating technology (e.g., Funder & Hansen, 1996; Landvik & al., 1998; Svendsen & al., 1999; Dyke & al., 2002; Mangerud & al., 2002). There is now quite abundant information on molecular variation and speciation in North Atlantic plants and animals (partly summarized in Brochmann & Steen, 1999; Weider & Hobæk, 2000; Abbott & Brochmann, 2003). The taxonomy of many North Atlantic organism groups has been critically revised. For vascular plants, new comprehensive critical checklists and floras are available, e.g., for Norway (Elven, 1994), Svalbard (Elven & Elvebakk, 1996), the entire Nordic area including Iceland (*Flora Nordica*; Jonsell, 2000, 2001, in press, and unpublished parts), and for the entire circumarctic area (*The Panarctic Flora Checklist*; Elven & al., 2003; cf. also Nordal & Razzhivin, 1999). There is also abundant new evidence from paleoecology and phytogeography (partly summarized in H. J. B. Birks, 1993, 1996; H. H. Birks, 1994; Bennike, 1999; see also Paus, 1988, 1989a, b, 1990, 1992; Alm & Birks, 1991).

For Greenland, Bennike (1999) reviewed evidence from paleoclimatology, paleoecology and biogeography relevant for potential glacial survival of plants, humans, and other animals, and concluded that if any biota survived at all, they probably only contained very few, exceptionally hardy species. This conclusion was mainly based on recent climatic reconstructions from the ice core projects, which suggest that the glacial temperatures in Greenland were much lower than previously believed, and on fossil evidence, suggesting that migration rates were high and that recolonization of Greenland rapidly followed deglaciation. In her review of plant macrofossil evidence for the eastern Atlantic area, H. H. Birks (1994) noted that no fossils yet have been found to provide definite evidence supporting the nunatak hypothesis; the increasing number of plant remains from beyond the ice margins suggest that the plants colonized new areas as rapidly as the ice melted. For Iceland, Rundgren & Ingólfsson (1999) summarized paleoclimatological data and presented new pollen data from the Younger Dryas stadial, and argued for local survival throughout the Weichselian. For Scotland, H. J. B. Birks (1997) reviewed paleoecological and geological data and concluded that the nunatak hypothesis was not necessary to explain the observations.

In Scandinavia, the island of Andøya in northern Norway has been central in recent discussions on glacial survival. At or close to the late glacial maximum in this area, there is evidence of vascular plants (since 22,000 years BP), inferred from pollen deposits in a lowland

lake (Vorren & al., 1988; Alm & Birks, 1991; Alm, 1993). This lowland lake had, however, earlier been covered by the glacier (Vorren & al., 1988; Alm, 1993). Thus, there is so far no fossil evidence of plant life continuity in the period from before and through the glacial maximum at Andøya, but the findings have frequently been cited to support the nunatak hypothesis (e.g., Tarasov & al., 2000; Tyler, 2002). An intriguing possibility is that plants in any case could have overwintered at Andøya in the true sense of the word; survival of seeds in the permafrost environment for some hundreds to one thousand years might have been sufficient because the climatic fluctuations were abrupt and short-lasting (T. Alm, pers. comm.; cf. also McGraw & al., 1991).

According to the most prominent supporters of the glacial survival hypothesis in Scandinavia, the botanists Nannfeldt (1935, 1960), Nordhagen (1936, 1963), Selander (1950), Dahl (1955, 1958, 1963, 1987, 1989a, b, 1991, 1992), Gjærevoll (1963, 1973; Gjærevoll & Sørensen, 1954; Gjærevoll & Ryvarden, 1977), and Rønning (1963), and the entomologist Lindroth (1957, 1963), it is a necessity to invoke *in situ* survival to explain the occurrence of the endemics and disjunctions. In the following, we revisit this postulate and will mainly refer to arctic-alpine species because *in situ* glacial survival of more thermophilous lowland species can be regarded as quite improbable in light of recent geological and paleoclimatic reconstructions (for reviews of lowland endemism in Scandinavia, see, e.g., Borgen, 1987; Jonsell, 1988, in press). In this respect we follow the view of Buckland & Dugmore (1991): "If this is a refugium, why are my feet so bloody cold?"

We omit detailed discussion of the centrality argument because it has been demonstrated that present-day ecological factors are sufficient to explain the distribution of the centric species in Scandinavia (H. J. B. Birks, 1993, 1996; see also Berg, 1963), and because several molecular studies of plants and animals have suggested that such disjunctions either have originated by recent dispersal (e.g., Brochmann & al., 1992a; Aares & al., 2000; Hagen & al., 2001), independent polyploid (hybrid) origins (e.g., Brochmann & al., 1992b), or by different postglacial migration routes into Scandinavia (e.g., Nordal & Jonsell, 1998; see also Berglund & Westerbergh, 2001; Taberlet & al., 1998; and Jaarola & al., 1999, for some examples of plants and animals with more continuous south-north distributions). We also omit discussion of postulated endemics in mosses (see reviews by Schuster, 1983, and Dahl, 1998; cf. also Flatberg, 1993), lichens (see Dahl, 1998), and animals, because critical evaluation of these groups is beyond our competence.

GEOLOGICAL RECONSTRUCTIONS OF MAXIMUM ICE SHEET EXTENT

In several regions, the reconstructions of the Late Weichselian ice sheets have been revised and improved as a result of recent geological investigations. Better techniques, especially for dating, have contributed to improved control on lateral as well as vertical extent of the last ice sheets. Figure 1 shows the maximum extent of the Late Weichselian ice sheets compiled from several recent reconstructions. In most areas, the mapping of past ice margins has been based on two different approaches: (a) mapping and dating of glacial deposits such as subglacially formed till, moraines formed at the ice sheet margins, and ice-dammed lakes, and (b) mapping and dating of subaerially formed deposits which prove non-glaciation, such as lake deposits and wind-blown deposits.

The development of exposure age dating has provided a break-through in distinguishing between formerly glaciated and unglaciated areas. When rocks are continuously exposed to cosmic rays, stable isotopes of Al, Be, Cl, and other elements are formed. The formation process stops when the rock is covered by glacial ice or

soil. When we know the formation rate of these isotopes, the duration of ice-free periods can be calculated from the content of isotopes accumulated in the rocks (see e.g., Gosse & Phillips, 2001).

The Late Weichselian maximum extent of the ice sheets is not a synchronous event, but represents the maximum extent the ice sheets experienced in each area during the Late Weichselian period (25,000–10,000 years ago; Fig. 1).

The British Isles and Fennoscandia. — Recent compilations for these regions show ice margins that have been generally accepted during the last couple of decades (e.g., Svendsen & al., 1999). The Fennoscandian and British Ice Sheets coalesced in the central and northern North Sea (Sejrup & al., 2000). Due to the simultaneous global sea level lowering of ca 135 m (Yokoyama & al., 2000), the southern North Sea was dry land and connected to continental Europe (Fig. 1). Studies of sediment cores show that the two ice sheets split up 22,000 years ago. The central and southern part remained dry land until 7,000 years ago.

In Scotland, several nunataks probably existed in the mountains in the northwest and on the Outer Hebrides (Stone & al., 1998; Ballantyne & al., 1998a, b). At the

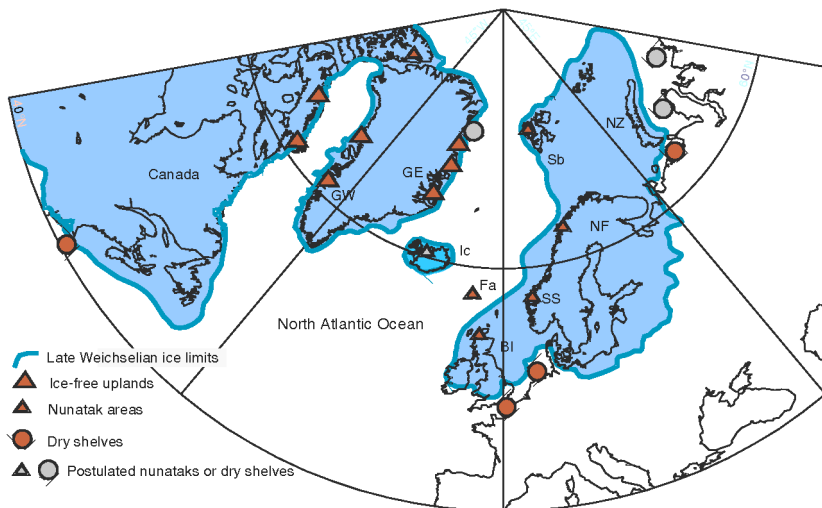


Fig. 1. Reconstruction of the Late Weichselian (25,000–10,000 years ago) maximum ice limits in the North Atlantic area compiled from various sources (Funder & Hansen, 1996; Landvik & al., 1998; Svendsen & al., 1999; Dyke & al., 2002; Mangerud & al., 2002). Occurrences of extensive ice-free uplands, nunatak (ice-free mountain) areas, and ice-free dry shelves in the North Atlantic region at the time of the Late Weichselian maximum ice extent are indicated. Red symbols represent ice-free areas for which strong geological evidence is available; grey symbols represent areas suggested in recent literature but for which strong evidence is not yet available. The ice-free coastal shelves along the margins of the Greenland and North American ice sheets are potential refugia relevant for the nunatak hypothesis of glacial survival. The ice-free coastal shelves south and northeast of the coalesced North European ice sheets, on the other hand, were directly connected to the periglacial continental tundras and may have served as important source areas for post-glacial immigration. See the text for details and references. The nine geographic regions analyzed for endemic vascular plant taxa are indicated: GW - Greenland, West and South (SE to Lindenowfjord); GE - Greenland, East (N of Lindenowfjord); Sb - Svalbard including Bear Island and Franz Josef Land; NZ - Novaya Zemlya (excl. Vaigach); Ic - Iceland; Fa - The Faroes; BI - Northern British Isles; SS - Scandes, southern part; NF - Fennoscandia, northern part including the Kola Peninsula.

same time, the ice sheet probably extended across the entire adjacent shelf, and its western margin continued across the mouth of the Norwegian Channel and can be continuously mapped along the shelf edge off Norway until it coalesced with the Barents Sea Ice Sheet. However, on Andøya in northern Norway, the maximum ice margin was close to the present coast, and the western part of this island was deglaciated as early as 22,000–21,000 years ago (Vorren & al., 1988; Alm, 1993). If this limited ice extent is correct, several mountains must have been ice-free in this area throughout the Late Weichselian (Vorren & al., 1988). A series of nunataks has also been proposed in the mountains along the western coast of southern Norway based on geomorphological studies (Nesje & Dahl, 1992) and exposure age dating (Brook & al., 1996). Nunataks probably existed also in other areas in northern Norway, such as the Lofoten region (Fig. 1).

Svalbard and the Barents Sea Ice Sheet. —

The Late Weichselian glaciation of the Svalbard archipelago has been subject to an intensive debate for several decades (reviewed by Landvik & al., 1998). Large ice-free areas have been postulated along the west coast of Svalbard (e.g., Miller, 1982; Forman & Miller, 1984; Miller & al., 1989; Andersson & al., 1999, 2000) based on ages of >100,000 years obtained from amino acid racemization of subfossil shells in beach deposits. This was taken as definite evidence for long-lasting coastal refugia by Dahl (1987). In contrast, later studies of the floor of the fjords and shelf (Svendsen & al., 1992, 1996) show that the coastal areas were overrun by Late Weichselian glaciers, which extended to the edge of the continental shelf (see reviews by Mangerud & al., 1992, 1998; Landvik & al., 1998). Thus, the previous findings of old shells demonstrate that extensive marine deposits were left undisturbed in spite of being glaciated, not only during the last, but probably several glaciations.

The present compilation of the ice margin is based on mapping of glacial deposits shown to be of Late Weichselian age (Landvik & al., 1998). The ice sheet extended to the shelf edge west and north of Svalbard, and covered all coastal lowlands. However, Landvik & al. (in press) suggest, based on exposure age dating, that small areas on some mountains in the northwest of Spitsbergen have been ice-free for 70,000 years, and that they penetrated the Late Weichselian ice sheet as nunataks (Fig. 1). The eastern margin of this ice sheet did not extend into continental Russia and Siberia, as suggested by, e.g., Grosswald & Hughes (1995, 2002), but terminated along the western margin of the Kara Sea (Mangerud & al., 2002). Frans Josef Land and Novaya Zemlya were also covered by this ice sheet, but more eastern areas such as the Taymyr Peninsula have not been glaciated since the Early Weichselian (Alexanderson &

al., 2001).

Iceland and the Faroe Islands. — These islands were covered by separate ice caps. Existence of ice-free areas in northwest Iceland was suggested by Nordahl (1991), mainly based on geomorphological arguments. This view was supported by Rundgren & Ingólfsson (1999) in their study of the vegetation during the Younger Dryas stadial. However, recent marine geological studies around Iceland suggest that the last ice sheet covered the entire island as well as the continental shelves (Andrews & al., 2000). The Faroe Islands were previously assumed to have been completely covered by an ice cap (see discussion in Humlum, 1998). However, recent studies using exposure age dating suggest that ice-free areas existed during the Late Weichselian (O. Humlum, pers. comm.).

Greenland. — The Late Weichselian Greenland ice sheet was larger than today. Along its western and southeastern margins, it terminated on the continental shelf (Funder & Hansen, 1996). However, in East Greenland, there is strong evidence for ice-free lowlands on Hochstetter Forland, and probably on the adjacent shelf (Funder & al., 1998). There is also strong evidence for extensive ice-free uplands penetrating the ice sheet in Jameson Land (Funder & al., 1998) and Germania Land (Landvik, 1994). In southwest Greenland, the ice sheet covered the continental shelf, but large ice-free uplands probably existed around 67°N and 72°N (Funder & Hansen, 1996). Further north, the Greenland ice sheet coalesced with the ice sheet over Ellesmere Island (Blake, 1992; England, 1999). In Peary Land, the northernmost part of Greenland, Funder & Hansen (1996) suggested that the Greenland ice sheet extended over the coast into the Arctic Ocean. This was supported by Landvik & al. (2001), who concluded that the southern parts of Peary Land had been overrun by a larger Greenland Ice Sheet until 8,000 years ago.

Eastern North America. — In Figure 1, the Late Weichselian ice margins in eastern North America are reproduced from a compilation by Dyke & al. (2002), who also present a thorough review of the geological data. Based on marine geological data, they suggest that the Late Weichselian (named the Late Wisconsin in North America) ice sheet covered the shelves off Nova Scotia and Newfoundland. Thus, the new evidence contradicts the previous assumptions (e.g., Pielou, 1991) of ice-free areas on, for example, the Grand Banks during the last glaciation. From Labrador to the coalescence with the Greenland Ice Sheet in northernmost Baffin Bay, the ice margin was probably situated close to the present coastline and characterized by ice streams draining out the major fjords and sounds. Along the coast of Baffin Island and Ellesmere Island, the latest reconstruction is to a large degree based on recent advances in

marine geology and exposure age dating (reviewed by Miller & al., 2002). The recent reconstructions contradict previous models of limited ice extent proposed by, e.g., Løken (1966) and Miller & Dyke (1974). However, there is still general agreement that a series of ice-free uplands and nunataks existed along this coastline (Fig. 1).

INTRASPECIFIC MOLECULAR DIFFERENTIATION IN NORTH ATLANTIC VASCULAR PLANTS

Many plant species occur disjunctly on both sides of the Atlantic, but are absent from areas eastwards in Eurasia and westwards in North America (see maps in Hultén, 1958). The question of how these species crossed the Atlantic, or if they crossed it at all, has been continuously debated in the phytogeographic literature. A subset of the amphi-Atlantic disjuncts, the “west-Arctic” species, is absent from the Central European mountains and contains some 30 species occurring in Scandinavia/Svalbard and Greenland, with or without extension to continental North America (Dahl, 1963, 1987; Nordal, 1987). Their entire current distribution on the European side is situated within the area of the Weichselian glaciers, cited by many as providing the strongest evidence for *in situ* glacial survival in Scandinavia and Svalbard. Similar arguments were used for northeastern North America with respect to the “east-Arctic” species (Fernald, 1925).

Hultén (1937, 1958, 1962, 1971) proposed that the amphi-Atlantics are fragmented remnants of formerly circumpolar species. Both currently circumpolar species and amphi-Atlantic species were thought to have reached a circumpolar distribution early in the Quaternary, with the two sides of the Atlantic representing endpoints of different migration waves. According to Hultén's hypothesis, the currently amphi-Atlantic species were exterminated by the glaciations except along the Atlantic coasts, and the contemporary east and west Atlantic populations of both circumpolar and amphi-Atlantic species have thus been separated throughout the Quaternary. Other phytogeographers, in particular Dahl (1958, 1963, 1987), agreed with Hultén that the North Atlantic is a strong barrier against plant dispersal. In an analysis of the arctic-alpine flora of Fennoscandia, he showed that the majority of the species have no special adaptations to long-distance dispersal such as winged seeds and fleshy fruits. Dahl (1987) rejected a hypothesis of postglacial immigration of the amphi-Atlantic species to Scandinavia from the south, partly because there are many more amphi-Atlantic taxa shared among Scandinavia, Iceland, and the British Isles, than between these areas and the Alps. In contrast to Hultén, however,

he explained the amphi-Atlantic disjunctions by migration across a late Tertiary North Atlantic land bridge and *in situ* glacial survival on both sides of the Atlantic during the Quaternary.

Other phytogeographers have argued that long-distance dispersal of arctic-alpine plants can be more common than expected from their lack of specialized dispersal mechanisms (e.g., Berg, 1983; Nordal, 1985a, b, 1987). During the last decade, molecular data have been obtained for several such species, providing support for this hypothesis.

West-arctic and other amphi-Atlantic species. — In an early analysis of allozyme variation in the diploid, west-Arctic grass *Vahlodea atropurpurea*, there was no variation at 17 loci, suggesting a recent bottleneck as well as recent dispersal across the Atlantic (Haraldsen & al., 1991). In the amphi-Atlantic diploid *Lychnis alpina*, most of the allozyme diversity was found among populations within geographic regions (such as northern and southern Scandinavia) rather than among populations from different sides of the Atlantic (Haraldsen & Wesenberg, 1993). Hagen & al. (2001) presented the first DNA-based analysis (RAPDs and SCARs) of a west-Arctic species, *Cerastium arcticum* s.l. (Figs. 2, 3). This high-polyploid is composed of two highly divergent lineages (now recognized as different taxonomic species; *C. arcticum* s. str. and *C. nigrescens*; see also Brysting & Borgen, 2000; Brysting & Elven, 2000). Although both lineages are disjunctly distributed across the Atlantic, there is very little intra-lineage geographic structuring (Fig. 3). The occurrence of very similar, in some cases even identical, multilocus genotypes of such regularly self-fertilizing, fixed-heterozygous allopolyploids on both sides of the Atlantic is most probably caused by postglacial dispersal.

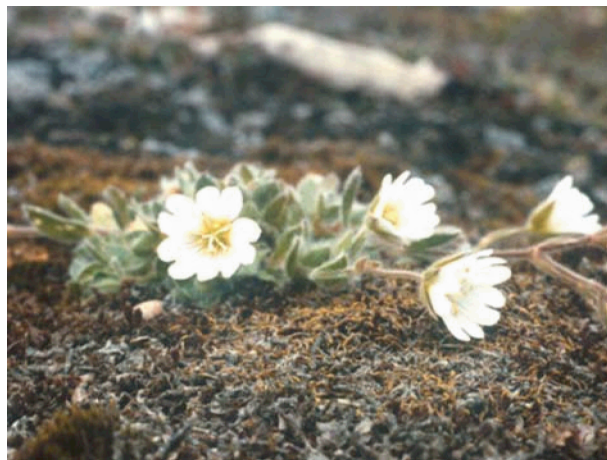


Fig. 2. One of the amphi-Atlantic disjuncts, the “west-Arctic” *Cerastium arcticum* s.str., which has no special mechanisms for long-distance dispersal. Photo: Christian Brochmann (Svalbard).

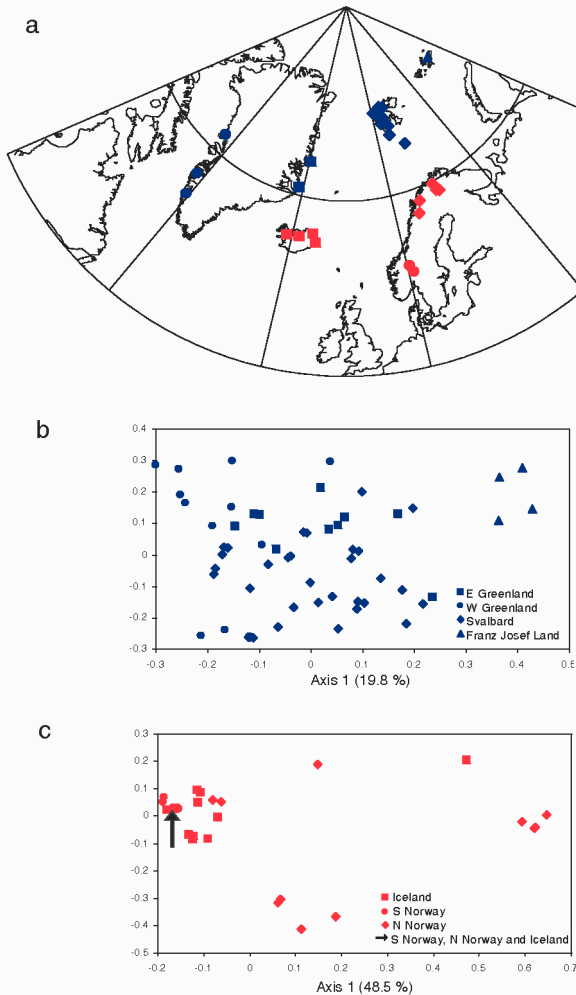


Fig. 3. Results of the first DNA-based analyses (RAPDs) of one of the West-arctic species, the high-polyloid and regularly self-fertilizing *Cerastium arcticum* s.l. (modified from Hagen & al., 2001). a, distribution of sampled populations; b, c, principal coordinate analysis of the RAPD data. This species was shown to comprise two highly divergent lineages (now recognized as two separate species, *C. arcticum* s.str., blue symbols, and *C. nigrescens*, red symbols; cf. Brysting & Elven, 2000). Although both lineages occur disjunctly across the Atlantic, there is virtually no geographic structuring of their intra-lineage variation. *Cerastium arcticum* s.str. also occurs in north-eastern Canada, but no material from this region was available for analysis.

Circumpolar “short-distance dispersers”. —

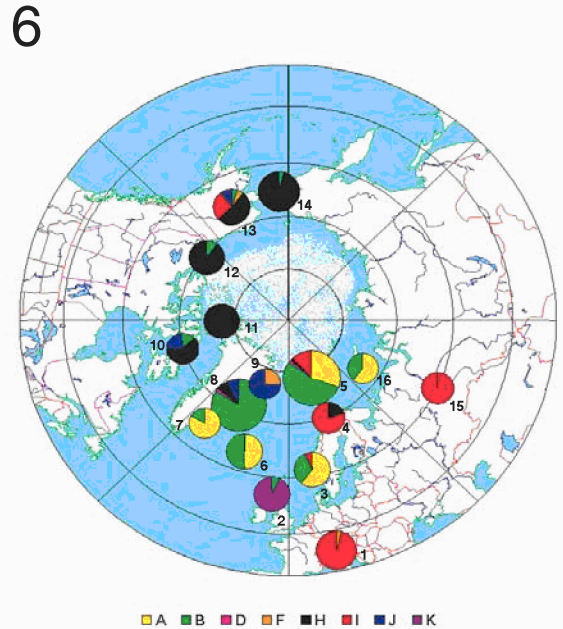
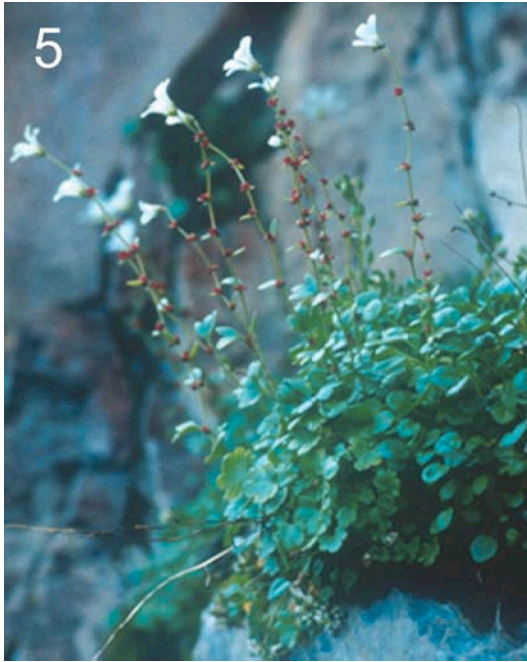
Similar evidence for continuous gene pools in the entire North Atlantic area is also available for several circumpolar species. In a cpDNA analysis of the sexual and out-crossing purple saxifrage, *Saxifraga oppositifolia* (Fig. 4), two divergent, main clades of haplotypes were identified (the “American-Beringian” and the “mainly Eurasian” clades; Abbott & al., 2000). The mainly

Eurasian clade extends westwards across the Atlantic, and even two closely related haplotypes (A and B) belonging to this clade are amphi-Atlantic. Both occur in most North Atlantic regions including Scandinavia, Svalbard, and eastern continental North America. In East Greenland, however, there is also one low-frequent haplotype (C), which is derived from the common Atlantic haplotype B and not found elsewhere, possibly indicating local survival in this area. In the same species, recent dispersal among three eastern Atlantic regions (Svalbard, N and S Scandinavia) was invoked using nuclear markers (RAPDs; Gabrielsen & al., 1997).

A similar pattern was observed in a recent study of circumpolar cpDNA and nuclear (AFLP) variation in the nodding saxifrage, *Saxifraga cernua* (Figs. 5, 6; Bronken, 2001; Bronken & al., 2001), which is a bulbil-reproducing but occasionally sexual allopolyploid with high clonal diversity even at small spatial scales (Brochmann & al., 1998; Gabrielsen & Brochmann, 1998; Brochmann & Håpnes, 2001; Kjølner & al., 2000; Kjølner, 2001). More cpDNA markers and more samples from the Siberian area are needed for this species, but the markers obtained so far identify several haplotypes with different geographic distributions (Fig. 6). The Beringian-American area is dominated by one haplotype (H) that also extends eastwards across the Atlantic to Svalbard and northern Fennoscandia, and high diversity was observed in Alaska. Another haplotype (I) dominates in the Ural Mountains and the European Alps but extends into northern Fennoscandia and Svalbard, suggesting immigration to this area from the northeast. As in the purple saxifrage, the North Atlantic area is dominated by two very similar haplotypes (A, B), and both of them are amphi-Atlantic (Fig. 6). The analysis of AFLP multilocus phenotypes in *Saxifraga cernua* also indicated consider-



Fig. 4. The purple saxifrage, *Saxifraga oppositifolia*, a “short-distance-dispersed” circumpolar species analysed for cpDNA variation in its entire arctic range (Abbott & al., 2000). Photo: Arnodd Håpnes (Svalbard).



Figs. 5–6. 5, the nodding saxifrage, *Saxifraga cernua*, another “short-distance-dispersed” circumpolar species, analyzed for AFLP and cpDNA variation by Bronken (2001; see also Bronken & al., 2001). Photo: Gunvor Berge (Norway). 6, geographic distribution of cpDNA haplotypes (denoted A-K) observed in the nodding saxifrage, *Saxifraga cernua*, based on analysis of 274 plants from 71 populations. Haplotype frequencies are given for each of 16 geographic regions. Pie size reflects sample size. Modified from Bronken (2001; see also Bronken & al., 2001).

able intermingling among different regions in the North Atlantic (Bronken, 2001; Bronken & al., 2001).

Although both of these circumpolar species of *Saxifraga* and the amphi-Atlantic species discussed above are “short-distance dispersers” in the sense of Dahl (1963), there is strong evidence for recent migrations across the Atlantic. Molecular evidence for recent migrations among various regions in the North Atlantic has also been provided for other “short-distance dispersers”, including the tetraploid, selfing grass *Phippsia algida* (Aares & al., 2000), the decaploid, selfing *Draba alpina* and several other species of *Draba* (Brochmann & al., 1992a, 1996), the octoploid, partly selfing *Saxifraga cespitosa* (Fig. 7; Tollefsrud & al., 1998), the regularly outcrossing diploid *Silene acaulis* (Abbott & al., 1995), and even the strictly outcrossing (self-incompatible) diploid *Arabis petraea*, of which at least two diaspores must have been dispersed simultaneously (Jonsell & al., 1995; this species is now named *Arabidopsis petraea*, see O’Kane & Al-Shehbaz, 1997). The latter species is highly disjunct and occurs in Iceland, the Faroes, the British Isles, and southern Norway, and it also has isolated populations in small areas along the rocky Baltic coast of Sweden and at Lake Onega in Russia. Jonsell & al. (1995) focused on the history of the Swedish Baltic populations, which belong to an element proposed to be con-

nected to the White Sea area along narrow strips of land present in early postglacial times (the “White Sea - Baltic Corridor”). Allozyme analysis of *Arabidopsis petraea* suggested, however, that the Swedish Baltic population is closely related to the southern Norwegian and the Icelandic populations, and only distantly to the Russian ones. Thus, the Atlantic populations as well as the Swedish Baltic ones were suggested to descend from early postglacial immigrants from south-southwestern periglacial refugia (cf. Fig. 1; Jonsell & al., 1995).

Bird- and wind-dispersed circumpolar species. — One bird-dispersed circumpolar species, the bilberry (or arctic blueberry; *Vaccinium uliginosum* s. lat.; Fig. 8), has recently been analyzed for variation in cpDNA, ploidy levels, and morphology (Alsos & al., 2001; Alsos, 2003; cf. also Alsos & al., 2002). High cpDNA diversity was observed in this di- to hexaploid species (Fig. 9). Three well-supported lineages were resolved, one circumpolar arctic-alpine (corresponding to the mainly diploid ssp. *microphyllum*), one amphi-Atlantic boreal/low arctic (corresponding to the tetraploid ssp. *uliginosum*), and one amphi-Pacific boreal/low arctic (the latter with high diversity and so far unresolved taxonomic structure). The lineages were estimated to have diverged between 0.7 and 3.0 million years ago. One mainly high-arctic cpDNA haplotype (C)



Fig. 7. *Saxifraga cespitosa*, a circumpolar “short-distance-disperser” analyzed for RAPD variation in Scandinavia and Svalbard (Tollefsrud & al., 1998). Photo: Arnodd Håpnæs (Svalbard).

of *ssp. microphyllum* not only occurs across the Atlantic, but has a complete circumpolar distribution, demonstrating the extreme dispersal ability of this bird-dispersed species (Fig. 9). Another haplotype (H) has an extremely disjunct distribution, occurring in Taymyr in Siberia and in the White Mountains in eastern North America. In the amphi-Atlantic lineage, one haplotype (K) is widespread in Europe and extends across the Atlantic to southeastern Greenland, and a closely related haplotype (I) occurs in continental Northeast America. Two arctic-alpine haplotypes (E and G) are only found in Greenland and northeastern Canada, possibly suggesting local glacial survival (Alsos & al., 2001; Alsos, 2003). In an ongoing



Fig. 8. The first circumpolar, bird-dispersed species analyzed for cpDNA variation, the bilberry or arctic blueberry, *Vaccinium uliginosum* s.l. (Alsos & al., 2001; Alsos, 2003). Photo: Inger Alsos (northern Norway).

analysis of a wind-dispersed species, the dwarf birch (*Betula nana*), one of the identified cpDNA haplotypes occurs in southern Norway and Svalbard, across the Atlantic to Greenland, and in the Canadian Arctic and Alaska, suggesting that this species has a dispersal abili-

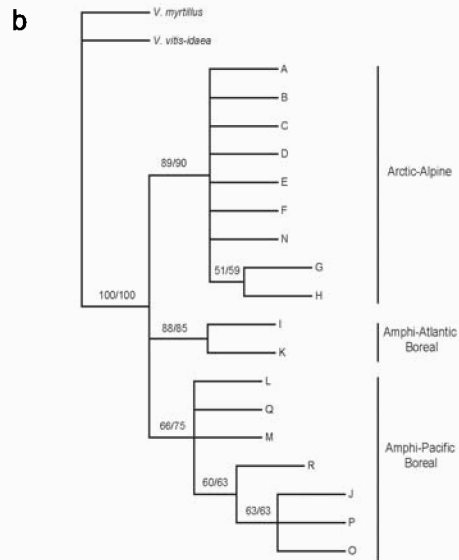
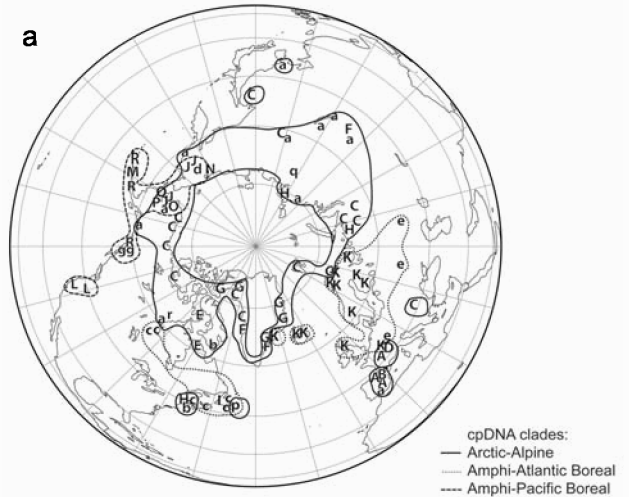


Fig. 9. Geographic distribution (a) and phylogenetic relationships (b) among cpDNA haplotypes (based on *trnL/F* and *trnS/G* spacer region sequences) observed in 122 populations of the bilberry or arctic blueberry, *Vaccinium uliginosum* s.l. Upper case letters denote combined haplotypes, lower case letters denote single-region haplotypes (based on either *trnL/F* or *trnS/G*). The strict consensus tree of 18 equally most parsimonious trees is shown (consistency index = 0.760; retention index = 0.815); the numbers are bootstrap support for maximum parsimony/maximum likelihood analysis. Modified from Alsos (2003).

ty similar to the bilberry (Alsos, Taberlet & Brochmann, unpubl.).

What does it mean? — There are so far few molecular-clock estimates available for the species discussed above, but the hypothesis of isolation of the trans-Atlantic populations during the entire Quaternary as suggested by Hultén (1937, 1958, 1962, 1971), Dahl (1958, 1963, 1987), and many other authors, can be rejected with reasonable certainty. Although the chloroplast DNA molecule has low mutation rates, more sensitive nuclear fingerprinting markers such as AFLPs and RAPDs are also available for several of the fixed-heterozygous, mainly clonal or selfing allopolyploid species. The patterns observed with such markers in this type of species provide strong evidence for recent trans-Atlantic migrations, probably late- or post-Weichselian. Even if they lack particular adaptations, “short-distance dispersers” can probably be chance-dispersed by strong winds over frozen sea (Savile, 1972) or by icebergs, drift ice and driftwood (Nordal, 1987; Johansen & Hytteborn, 2001).

It is also commonly observed that North Atlantic lineages within species and subspecies have low intra-lineage diversity, and that in the circumpolar taxa, divergent lineages with deeper phylogeographic histories can occur in the Beringian-Siberian area. This pattern suggests that the North Atlantic lineages often have experienced recent bottlenecks, and that it is sufficient to postulate survival in a single Weichselian refugium and subsequent post-glacial range expansion. The question remains as to where this refugium was situated in each case. By far the most important refugia were probably situated on the vast tundras to the south, east, and northeast of the North European ice sheets, and to the south of the eastern North American ice sheet. It is nevertheless possible that some hardy species also may have survived in the “intraglacial” North Atlantic ice-free areas indicated in Figure 1, such as the extensive ice-free uplands in East Greenland (as discussed above for *Saxifraga oppositifolia* and *Vaccinium uliginosum*).

INTRASPECIFIC MOLECULAR DIFFERENTIATION IN OTHER NORTH ATLANTIC ORGANISMS

In the following, we review some relevant molecular case studies of intraspecific variation in organisms other than vascular plants. We have excluded studies with little focus on or only few samples from the North Atlantic area. Some of the studies included here were also reviewed by Weider & Hobæk (2000) in their more general survey of arctic organisms, but herein we have re-examined these papers to put particular emphasis on those results that are relevant for dispersal and potential

glacial survival in the North Atlantic area. In addition, several new studies have appeared in this rapidly expanding field since their review.

Mosses. — Compared to vascular plants, moss species much more frequently occur disjunctly among different continents (Derda & Wyatt, 1999; Shaw, 2001). There are, however, opposing views regarding the explanation for this pattern. It has been thought that mosses spread very efficiently because of their small and light spores. Alternatively, mosses may have lower evolutionary rates (e.g., Stenøien & Sæstad, 1999), possibly because deleterious mutations immediately are expressed in their haploid main generation, and/or because genetic drift is slow because of large effective population sizes. In an allozyme analysis of 71 populations from America and Europe (including Fennoscandia) of the moss *Polytrichum commune*, Derda & Wyatt (1999) found that populations that border Pleistocene glacial margins in North America and Europe were more similar to each other than either was to other populations from the same continent. These authors suggested that the patterns observed in this species reflected survival in numerous refugia and that occasional long-distance dispersal from them occurred. Stenøien & Sæstad (1999) used allozyme and RAPD markers to assess genetic structure in three peat mosses (*Sphagnum*); trans-Atlantic populations were analyzed for one of them (*S. angustifolium*; two populations from Norway and two from Newfoundland). Although the populations of *S. angustifolium* were highly variable at RAPD loci, they were only weakly differentiated for any marker, even across continents. Stenøien & Sæstad (1999) concluded that their findings could best be explained by assuming low evolutionary rates, inferring that high levels of molecular variation not necessarily are incompatible with slow evolution. Their preferred explanation for the lack of differentiation between continents was a combination of low mutation rates, low migration rates, and slow genetic drift, suggesting very high effective population sizes, although other explanations such as recent intercontinental migration were not entirely ruled out (Stenøien & Sæstad, 1999).

Lichens. — There are two recent studies of intraspecific molecular variation in lichen species, interestingly with quite different conclusions. In their study of *Letharia vulpina*, Högberg & al. (2002) proposed that the European populations of this lichen had originated via long-distance dispersal from the American ones. However, their conclusion was based on sequence variation in a few populations only of this very widespread species, and alternative explanations were also considered possible (Högberg & al., 2002). In contrast, in a comprehensive study of the strongly oceanic lichen *Cavernularia hultenii*, which is widely disjunct across North America and across the North Atlantic to north-

westermost Europe, Printzen & al. (2003) concluded that the disjunctions in this species most probably are quite old. Their study was based on sequence variation in nuclear ribosomal DNA (ITS/part of IGS) among 300 samples from 62 populations representing three main geographic areas: northwestern North America, eastern North America (Newfoundland), and western Europe (Norway and Scotland). Four common haplotypes inferred as ancestral were shared among all three areas, whereas all of the numerous derived haplotypes were restricted to a single area. Printzen & al. (2003) proposed that the species survived the last glaciation in at least two, probably several, refugia in North America, and in one European refugium, which may have been located on the western Norwegian coast. This location of the European refugium is, however, unlikely if the recent ice sheet and paleoclimate reconstructions are correct (cf. Fig. 1); *Cavernularia hulthenii* exclusively grows on tree species such as spruce (most commonly), pine, and birch.

Birds. — The rock ptarmigan (*Lagopus mutus*), one of the few bird species spending their entire life cycle in the arctic tundra, was studied by Holder & al. (1999) using mtDNA and nuclear DNA (ITS1 and the Gapdh intron) sequencing. Focusing on North America, they found that several postulated glacial refugia were geographically concordant with the distribution of several groups of mtDNA haplotypes as well as with several morphologically distinct subspecies, including ssp. *islandorum* in Iceland and ssp. *welchi* in Newfoundland. Divergence times based on the mtDNA data were estimated to 15,000–78,000 years; i.e., during the last glaciation and mainly before the last glacial maximum. However, the support obtained in the mtDNA phylogeny was weak, and no eastern Atlantic populations were included in this study. All samples had identical ITS1 sequences, and although some differentiation was observed for the Gapdh intron, all populations but one shared the most common allele.

In the dunlin (*Calidris alpina*), a distinct global population structuring was observed based on mtDNA sequence variation by Wenink & al. (1993). The dunlin is a long-distance migrant shorebird with a circumpolar breeding range, and it is morphologically variable with up to nine subspecies recognized. Among 33 control-region haplotypes, 30 were specific to populations of different geographic origin, whereas three indicate dispersal between southern Norway and Taymyr in Siberia. Five mtDNA lineages were identified, suggested to have diverged in different Pleistocene refugia: Alaska, western North America, Gulf of Mexico (currently breeding around Hudson Bay in Canada), western Europe, and Taymyr. No birds were included, however, from the northeastern coast of North America or Greenland. The western European lineage included very similar, inter-

mingling haplotypes from populations sampled at their breeding sites in Iceland and southern Norway, and at their wintering sites in Germany and the Netherlands. The split between the European lineage and the more closely related Taymyr/Alaska lineages was estimated to have occurred 350,000 years ago (Wenink & al., 1993). This species was also studied in detail using various molecular markers by Wennerberg & al. (1999) and Wennerberg (2001a, b), but these studies concentrated on the Palearctic populations.

Terrestrial mammals. — *In situ* glacial survival through the last glacial maximum was recently suggested for one Scandinavian endemic, the Norwegian lemming (*Lemmus lemmus*; Fedorov & Stenseth, 2001). Low diversity was found in the mitochondrial control region, and statistical analyses of the data indicated a population bottleneck followed by expansion, estimated to have happened around the last glacial maximum. This result can either be explained by an *in situ* bottleneck in a Scandinavian refugium, or by survival of the Norwegian lemming in a periglacial area followed by founder events during early postglacial colonization (Fedorov & Stenseth, 2001). The former explanation is (slightly) preferred by the authors. However, *in situ* survival of the lemming does not appear to be likely if the current ice sheet reconstructions are correct (Fig. 1).

Many other recent studies have addressed molecular variation in various species of lemmings (true lemmings, *Lemmus*, and collared lemmings, *Dicrostonyx*; see e.g., Fedorov, 1999; Fedorov & al., 1999a, b; Fedorov & Goropashnaya, 1999; Fredga & al., 1999; Ehrich & al., 2000; Fedorov & Stenseth, 2002), but only few of these studies have included material from the North Atlantic. The analysis of the arctic collared lemmings by Fedorov & Goropashnaya (1999) was circumarctic, but was also based on limited sampling from the North Atlantic. Their mtDNA phylogeny supports recognition of four species, one Eurasian and three North American (including Greenland), suggested to have radiated during the Pleistocene. Postglacial colonization history of various other rodent species in Fennoscandia, including the wood lemming (*Myopus schisticolor*), was reviewed by Jaarola & al. (1999); three main patterns of late- and postglacial immigration (from the northeast, from the south, and from both directions) were demonstrated.

Reindeer (*Rangifer tarandus*) is a highly migratory and morphologically complex circumpolar species with eight subspecies. Fossil evidence shows that at the last glacial maximum, reindeer was found south of the ice sheets in Eurasia and North America, and in Beringia. Banfield (1961) suggested that the arctic island forms survived the last glaciation north of the ice sheets in tundra refugia in Arctic Canada and/or on northern Greenland, that the continental tundra forms survived in

Beringia and possibly in central Europe, and that the forest forms survived in temperate refugia south of the ice sheets. His hypotheses were tested in a recent circumpolar analysis based on mtDNA sequencing (Flagstad & Røed, 2003). They identified three major lineages, suggested to represent three separate refugial populations. Two lineages were small and strongly supported, one (currently occurring in Taymyr, southeastern Finland, and Norway) indicating survival south or east of the ice in western Eurasia, and another (currently occurring around Quebec and in the Northwest Territory) indicating survival south of the ice in North America. The third and largest lineage was diverse and poorly supported, interpreted to represent a large, continuous glacial population on the vast tundras in Beringia and far into Eurasia. This glacial lineage probably contributed to the gene pool of all extant subspecies and comprises haplotypes currently occurring in populations from the entire circumpolar area. The delimitation of subspecies of reindeer does thus not reflect its mtDNA phylogeny, leading Flagstad & Røed (2003) to suggest that morphological differentiation occurred rapidly as adaptive responses to postglacial environmental change. Seven of the eight subspecies occur or occurred in the North Atlantic region, including three recognized as exclusively arctic and endemic (ssp. *platyrhyncus* in Svalbard, the extinct ssp. *eogroenlandicus* in E Greenland, and ssp. *pearyi* in N Greenland and the arctic Canadian archipelago). These subspecies exclusively contain haplotypes originating from the large Beringian-Eurasian glacial population, suggesting that they have a common postglacial origin on the continental tundras.

Freshwater organisms. — One of the most intensively studied groups of arctic animals during the last two decades is the *Daphnia pulex* complex, an asexual species assemblage of primarily polyploid microcrustaceans occurring in ponds (briefly summarized in Weider & Hobæk, 2000; see also Colbourne & al., 1998, Weider & al., 1999a, b; Weider & Hobæk, 2003). Two major groups, the *D. tenebrosa* and *D. pulicaria* groups, with two and five distinct intragroup lineages, respectively, were identified in this complex based on mtDNA variation. The *D. tenebrosa* and *D. pulicaria* groups were estimated to have diverged 5.0–2.2 million years ago, and the intragroup lineages diverged during the Pleistocene. There is strong evidence for recent long-distance (passive) dispersal of some lineages, and especially high clonal diversity is found in some areas, partly explained by secondary contact between lineages derived from different glacial refugia (Weider & Hobæk, 2000).

Within the *Daphnia tenebrosa* group, one lineage is strictly European (extending northwards to northern Fennoscandia and northern Russia) and one (*D. tenebrosa*) is circumarctic, occurring in northernmost

Fennoscandia/Russia, in Svalbard, and across the Atlantic to Canada (Weider & al., 1999a). However, the large sequence divergence between Eurasian and North American populations within *D. tenebrosa* suggests that they have been isolated throughout most or all of the Pleistocene.

All lineages within the mainly Nearctic *D. pulicaria* group, on the other hand, contain extremely widespread haplotypes indicating rapid dispersal across large distances. Weider & al. (1999a) concluded that at least two of the five *D. pulicaria* group lineages have crossed the North Atlantic from North America after the last glaciation and colonized sites in northern Europe, possibly with migrating waterfowl such as geese and ducks. The “Panarctic *D. pulex*” lineage occurs in Fennoscandia, Iceland, Greenland, and North America and is basal to a clade in which *D. middendorffiana* (Svalbard, Greenland, and N America) is sister to three lineages referred to *D. pulicaria* (eastern, western, and polar *D. pulicaria*); the eastern and polar lineages are also amphiatlantic.

Interestingly, one case of high mtDNA diversity in Svalbard (higher than in Beringia and Europe) could clearly be explained by multiple colonization of Svalbard by divergent groups within *Daphnia* (Weider & al., 1999a). In another, recent study of allozyme and mtDNA variation (Weider & Hobæk, 2003), recently deglaciated regions such as the eastern Canadian Arctic were shown to have lower richness of *Daphnia* clones than western regions closer to Beringia. Thus, extremely complex phylogeographic patterns have been revealed in arctic *Daphnia*. Intra- as well as intercontinental diversification is sometimes blurred by long-distance dispersal of lineages, and each lineage has its own, unique postglacial history.

In another freshwater crustacean, the water flea *Sida crystallina*, Cox & Hebert (2001) suggested based on allozyme and mtDNA markers that the European and North American populations diverged before the Pliocene and probably should be recognized as different species, and that the four allopatric groups identified in North America were derived from different Pleistocene refugia. Thus, in contrast to the *Daphnia pulex* complex discussed above, it was concluded that long-distance dispersal of *Sida crystallina* either does not occur or occurs so rarely that it has not counteracted the development of a deep phylogeographic structure (Cox & Hebert, 2001). However, the focus of this study was on North America; only three central European populations of this widespread species were included.

One species of fish, the freshwater/anadromous Arctic charr (*Salvelinus alpinus* L.), has been proposed to be a glacial survivor in Svalbard (Svenning, 1993). However, recent geological data indicate that no coastal

lakes existed at the last glacial maximum (Landvik & al., 1998, in press). In a recent circumpolar analysis of mtDNA variation in the Arctic charr (Brunner & al., 2001), which comprises many subspecies, five divergent lineages with little within-lineage variation were identified. The lineages probably separated in the early- to mid-Pleistocene, and were suggested to have survived in different glacial refugia and rapidly colonized their present range 10,000–20,000 years ago. The Svalbard haplotype is closely related to haplotypes in Baikal and Taymyr and belongs to the “Siberian lineage”, which probably expanded westwards after the last glaciation. The “amphi-Atlantic lineage” contains populations from the European Alps, Fennoscandia, Ireland, Iceland, South Greenland, and eastern North America. Two individual haplotypes are amphi-Atlantic and must have dispersed over immense distances; one occurs in Scandinavia, Ireland, and eastern North America, and one occurs in Scandinavia, southern Greenland, and in the landlocked populations in the European Alps. South Greenland is a meeting point for the amphi-Atlantic lineage and a lineage occurring in Canada, Alaska, and easternmost Siberia.

Marine organisms. — Although the marine connections in the Atlantic region during the Pleistocene glaciations were more or less continuous, in contrast to the terrestrial ones, we include marine organisms in this review because several of them have been proposed to be glacial survivors. The arctic to cold-temperate North Atlantic red alga *Phycodrys rubens* was studied for ITS variation by van Oppen & al. (1995). Three lineages were identified: one West Atlantic, one East Atlantic (France, Ireland, and the Barents Sea), and one North Sea/Baltic. The divergences between a Pacific outgroup species and the two European lineages suggest that they have been separated since 5.3–2.1 myr. However, the divergence between the West Atlantic lineage of *Phycodrys rubens* and the Pacific species was only 0.35%, suggesting a recent trans-Arctic passage. Thus, van Oppen & al. (1995) suggested that *P. rubens* colonized the North Atlantic from the Pacific twice; first shortly after the opening of the Bering Strait, and then again after the last glaciation. The two divergent lineages found along the European coast were suggested to be remnants of the first colonisation event that survived in small ice-free refugia, thought to have existed along the northern coast of Scotland and Norway (van Oppen & al., 1995). However, the possibility for survival in different periglacial refugia south of the European ice sheets cannot be excluded based on these results.

The red alga *Ceramium tenuicorne* is currently only known to occur along the South Norwegian coast and into the Baltic Sea, an area that was completely glaciated in the late Weichselian (Gabrielsen & al., 2003).

However, it is possible that this putatively endemic species is more widespread; it belongs to a taxonomically partly unresolved complex (the “*C. strictum*” complex). The postglacial colonization history of this red alga was recently inferred based on sequencing of one mtDNA region (cox2-3) and RAPD markers (Gabrielsen & al., 2002). The mtDNA data revealed two geographically separated lineages (Oslofjorden vs. Skagerrak-Baltic region), which diverged in the Tertiary, whereas the RAPD data revealed a continuous cline corresponding to a strong salinity gradient ranging from Oslofjorden, via Kattegat, and into the Baltic Sea. The combined data suggest colonization from a genetically diverse Atlantic glacial gene pool (of unknown location), followed by lineage sorting of ancestral mtDNA polymorphisms and strong differential selection among nuclear genotypes along the salinity gradient (Gabrielsen & al., 2002).

The ocean quahog (*Arctica islandica*), a bivalve found on continental shelves throughout much of the North Atlantic, was investigated for mtDNA sequence variation by Dahlgren & al. (2000). Only three haplotypes were observed along the U.S. coastline, whereas five haplotypes were observed in Iceland alone. The Icelandic populations were more similar to the western Atlantic populations than the eastern ones. Dahlgren & al. (2000) suggested that a warm Holocene climatic optimum rather than glacial refugia shaped the genetic structure in the species, whereas Wares & Cunningham (2001; see below) interpreted the data to support a refugium hypothesis for Iceland.

In a comparative study of six cold-temperate invertebrate species, Wares & Cunningham (2001) examined mtDNA sequence variation among amphi-Atlantic populations of three obligate rocky intertidal species (one barnacle, *Semibalanus balanoides*, and two gastropods, *Nucella lapillus* and *Littorina obtusata*), and three habitat generalist species (one seastar, *Asterias rubens*, one mussel, *Mytilus edulis*, and one isopod, *Idotea balthica*). The study included populations from several North American sites including Nova Scotia and Newfoundland, and from several European sites (Ireland, Iceland, Norway, and France). The dispersal type of the species ranged from broad planktonic dispersal (*Asterias*, *Mytilus*, *Semibalanus*) to low dispersal (*Idotea*; “crawl-away”-type for the two gastropods). The European populations of these species were characterized by high allelic diversity and many unique haplotypes, suggesting that they are much older than the last glacial maximum. Based on the lower haplotype diversity, estimated age of the most recent common ancestor, and that all North American haplotypes either were shared with Europe or descended from European haplotypes, five of the six species (except the mussel) showed

evidence of colonization of America from Europe, even for the “crawl-away”-dispersed gastropods. The patterns were consistent with full postglacial recolonization except for the barnacle, in which one of the two American clades appeared to have survived the last glaciation. In spite of the broad planktonic dispersal type of the mussel *Mytilus edulis*, this species probably has long histories in both continents. It has high levels of endemic diversity in both regions and only one shared American-European haplotype, which was identified as the root haplotype (Wares & Cunningham, 2001). In five of the species, it appears that the close relationships among the southernmost European populations (France) and all other European populations are consistent with survival south of the ice sheet and northwards postglacial expansion (see Wares & Cunningham, 2001: Fig. 1). In the isopod *Idotea balthica*, however, the Icelandic populations formed a divergent clade with low haplotype diversity, estimated to have diverged from the other European populations investigated more than 200,000 years ago. This result was interpreted by Wares & Cunningham (2001) as evidence for glacial *in situ* survival in Iceland.

Narwhal (*Monodon monoceros*) populations from eastern Canada, West Greenland, and East Greenland were studied by Palsbøll & al. (1997) using mtDNA sequencing and RFLP analysis. Extremely low nucleotide diversity and low genetic distances between haplotypes were observed, suggesting a recent expansion from a single, small founder population in connection with the last glacial period.

In a worldwide mtDNA sequence analysis of the harbor seal (*Phoca vitulina*), Stanley & al. (1996) estimated that the Atlantic stocks were differentiated from the Pacific ones in the early Pleistocene, 2.2–1.7 mya. The east Atlantic populations (ssp. *vitulina*; Iceland, Ireland, Scotland, England, The Netherlands, Germany, Norway, Sweden) were estimated to be derived from the west Atlantic ones (ssp. *concolor*; NE Canada) 0.9–1.3 mya. The average sequence divergence among the west Atlantic populations was much greater than that among the east Atlantic ones. The results suggest that the contemporary, closely related east Atlantic populations were recruited after the last glaciation from a southern east Atlantic refugium, probably along the French or Spanish coast (Stanley & al., 1996).

Cronin & al. (1994) estimated based on mtDNA RFLP analysis that the two subspecies of walrus, the Atlantic one (*Odobenus rosmarus* ssp. *rosmarus*) and the Pacific one (ssp. *divergens*), diverged 0.8–0.5 mya. Andersen & al. (1998) studied populations of the Atlantic walrus from Northwest Greenland, East Greenland, Svalbard, and Franz Josef Land using microsatellite and mtDNA RFLP analyses. The Northwest Greenlandic

populations were the most distinct ones; their mtDNA haplotypes were basal to a clade containing all other haplotypes. The most common haplotype was shared among East Greenland, Svalbard, and Franz Josef Land, indicating recent connections between these areas. The close relationship among these populations also at microsatellite loci suggests that they may have been derived postglacially from a single refugial population, which fossil data show existed south of the ice cap 30,000 years ago (Andersen & al., 1998). Surprisingly, one individual from East Greenland had a haplotype identical to a Pacific one observed by Cronin & al. (1994). The microsatellite data supported the hypothesis that this animal was an extremely long-distant migrant that either had crossed the Arctic Ocean or followed the Arctic coastlines east- or westwards.

Based on microsatellite typing of populations spanning the total geographic distribution of the polar bear (*Ursus maritimus*), no genetic discontinuities were found that would be consistent with evolutionary significant periods of isolation among the circumarctic populations (Paetkau & al., 1999). Four groups of populations could be distinguished, but three of them were confined to various parts of Canada, and all remaining populations (the circumarctic “polar basin” group, including Novaya Zemlya, Franz Josef Land, Svalbard, East Greenland, Canada, Alaska, and Siberia) were very similar in spite of covering a geographic area exceeding the combined area of the other groups. The results clearly demonstrate the ability of polar bears to move over extreme distances.

Some concluding remarks. — Above we have summarized available data on intraspecific molecular differentiation in a variety of biologically very different North Atlantic organisms, representing a range of major taxonomic groups, habitats, breeding systems, and modes of dispersal. Among terrestrial organisms, there are now some data available for passively dispersed groups such as mosses and lichens as well as from extremely migratory species such as reindeer and birds. Similarly, the freshwater organisms include passively dispersed microcrustaceans as well as the highly mobile Arctic charr, and the marine organisms span from “crawl-away” dispersed marine gastropods, via planktonically dispersed groups such as red algae, seastars, and mussels, to wide-ranging animals such as the walrus and the polar bear. Not unexpectedly, then, these data reveal a wide variety of different Quaternary histories representing all degrees from very shallow to very deep phylogeographic splits within species. Such variety has even been demonstrated *within* individual species or species complexes; in the *Daphnia pulex* complex, for example, one group shows deep divergence across the Atlantic whereas several other lineages are amphiatlantic with a very recent history of trans-oceanic

migrations, and in the barnacle (*Semibalanus balanoides*), one American lineage appears to be recently recruited from Europe whereas another has a long history on the American continent. These findings agree with earlier comparative studies suggesting that each species or lineage has its own unique history of glacial isolations and interglacial range expansions (e.g., Taberlet & al., 1998; Fedorov, 1999; Weider & Hobæk, 2000).

In some of the species discussed above, molecular data have tested the proposed occurrence of endemic taxa or identified new endemic intraspecific lineages. In reindeer, mtDNA data suggest that the three high-arctic, North Atlantic endemic subspecies were derived from a common continental source after the last glaciation. In contrast, in the rock ptarmigan, one bivalve (the ocean quahog), and one isopod (*Idotea balthica*), intraspecific lineages endemic to Iceland were identified. Whether the current geographic distributions of these and other endemic lineages correspond to the location of their glacial refugia, or whether they immigrated postglacially from periglacial refugia, cannot be determined with certainty without dated fossil evidence. In many organisms, abundant fossils from the last glacial period have been found south of the ice sheets, east of the North European ice sheet, and in Beringia, demonstrating that major refugia indeed were situated in these areas. In conclusion, our review of intraspecific molecular differentiation in North Atlantic plants and other organisms has revealed many cases of unexpectedly long-distant and probably very recent migrations, as well as many deep phylogeographic splits suggesting survival through several glaciations in different, but often unlocated, refugia.

ENDEMISM IN NORTH ATLANTIC VASCULAR PLANTS

The occurrence of endemic taxa within the previously glaciated area of the North Atlantic has been taken as definite evidence for long-term *in situ* evolution, necessitating nunatak survival throughout the Quaternary or at least throughout the Weichselian (Löve & Löve, 1963). The post-Weichselian period was regarded as far too short to allow for evolution of endemics. Because most arctic-alpine plants were believed to be unable to disperse over long distances, an alternative hypothesis on survival outside the ice sheets followed by postglacial immigration and subsequent extinction in their periglacial refugia, was rejected (e.g., Dahl, 1987, 1998). It has, however, been known for a long time that plant species can originate by a rapid (few-generation) process, allopolyploidization (allopolyploidy), which involves interspecific hybridization and chromosome doubling. Thus, maintaining that the endemics provide

strong evidence for nunatak survival, Dahl (1987: 87, 1989b) called for falsification of the following statement: "There is no known instance where it can convincingly be demonstrated that a new amphimictic [sexual] vascular plant species has evolved by purely genetic processes other than allopolyploidy during the last 18 000 years".

Herein we review recent molecular, taxonomic, chromosomal, and reproductive data for the postulated endemics in the North Atlantic region. We conclude that the number of endemics previously has been grossly over-estimated, and that among those of the presently accepted endemics considered hardy enough to be putative nunatak survivors, there is not a single outcrossing diploid (i.e., "normally" sexual species, cf. Dahl's statement cited above). Most endemics are self-fertilizing or asexual polyploids. There is now strong molecular evidence for recent *in situ* origin of some of them via allopolyploidy or primary hybridization from identified, local progenitors. The polyploidizations resulting in several other endemic polyploids have, however, most likely predated the Weichselian, and in quite a few cases, the current polyploid endemics have probably originated by divergent evolution taking place after the polyploidization events. Many of the sexual endemics are predominantly, but not exclusively, self-fertilizing polyploids, in which divergent evolution can have occurred rapidly via genetic drift because of small effective population sizes.

The 77 endemic vascular plant taxa accepted by us as North Atlantic endemics are listed in Tables 1 and 2, and a list of rejected taxa is given with reasons for their rejection in the Appendix. We have only evaluated postulated endemics with regular contemporary occurrence in the northern boreal, alpine and/or arctic bioclimatic regions as defined by Elvebakk (1999) and Elvebakk & al. (1999), because the possibility for nunatak survival of more thermophilous plants can be disregarded. To be accepted, the taxa should be morphologically recognizable as distinct entities at the level of species or subspecies by the *Flora Nordica* criteria applied by Jonsell (2000). We thus decided to accept only a few, morphologically well-delimited taxa from large asexual complexes that contain numerous agamospecies (*Alchemilla*, *Hieracium*, the *Ranunculus auricomus* aggregate, and *Taraxacum*; Appendix). Admittedly, such decisions are quite subjective, but the vast majority of these very similar microspecies have nevertheless originated by recent hybridization, and are thus irrelevant for our discussion of nunatak survival and long-term evolution.

The western delimitation of the area of endemism considered in this paper was, for practical reasons, artificially drawn between Greenland and Canada. We do not have the necessary knowledge to evaluate the endemics proposed for eastern Canada (see, e.g., Fernald, 1925; Scoggan, 1978–1979). In addition, we found it difficult

Table 1. The 43 vascular plant taxa accepted in this paper as endemic to the glaciated part of the North Atlantic area at the specific or subspecific level and considered hardy enough (see text) to be potential *in situ* glacial survivors, given the current reconstructions of ice sheet extent (Fig. 1) and paleoclimate. The occurrence of many (23) of these taxa in more than one region may be taken as evidence for considerable dispersal capacity, suggesting that they also may have been able to disperse into the area from periglacial refugia (alternatively, the occurrence in more than one region may be caused by multiple polyploid origins or by glacial survival in multiple refugia). Such evidence on dispersal capacity is lacking for those endemics (20 taxa) restricted to a single region, and these taxa are marked in bold. *Geographic regions*: GW - Greenland, West and South (SE to Lindenojford in SE Greenland, traditionally drawn as the phylogeographic limit); GE - Greenland, East (N of Lindenojford; separated from GW by the Greenlandic ice cap); Sb - Svalbard including Bear Island and Franz Josef Land; NZ - Novaya Zemlya (excl. Vaigach); Ic - Iceland; Fa - The Faroes; BI - Northern British Isles; SS - Scandes, southern part; NF - Fennoscandia, northern part including the Kola Peninsula (separated from SS by the Middle Scandinavian lowland break in the mountain range). Repr. = *Reproductive traits*: A - Asexual reproduction predominant, by agamospermy (AA) or bulbils (AB); S - Sexual reproduction predominant; SS or SC - in the known range). Repr. = expected for sexual taxa: mainly self-fertilizing (SS) or cross-fertilizing (SC). Data for *Draba* spp. refer to Brochmann (1993), for *Papaver* spp. to Nordal & al. (1997) and Steen (1998); other references are given in the Table. *Ploidy*: 2n - Somatic chromosome number(s); Level - Ploidy level(s); D/P - Diploid (D) or Polyploid (P; i.e., tetraploid or higher). Chromosome numbers and inferred ploidy levels are provided according to the Panarctic Flora Checklist (Elven & al., 2003), for which the data were compiled based on the primary reports and the IOPB compilations (excluding the compilation by Löve & Löve, 1975). In some cases, the taxa are interpreted as diploid or polyploid based on absence or presence, respectively, of duplications at isozyme loci (cf. Brochmann & Steen, 1999). *Origin*: DD (diploid - diploid) - the endemic is diploid with closely related diploid taxa and probably originated via divergent evolution; PL (polyploid - lower ploidy) - the endemic is polyploid with its putatively most closely related taxa at the diploid or lower polyploid level(s) and has most likely originated directly via allopolyploidy (hybridization followed by chromosome number doubling); PP (polyploid - polyploid) - the endemic is polyploid with its putatively most closely related taxa at the same polyploid level (homoploid) and has most likely originated via divergent evolution (i.e.; divergence has occurred after the original polyploidization event); H (hybrid) - the endemic has probably or possibly originated recently (i.e., post-Weichselian origin considered possible) via primary hybridization or allopolyploidy. The strength of the evidence supporting the hypothesis supporting the origin varies from taxon to taxon (see references given); for some taxa, there is strong molecular evidence available.

Taxon	Geographic region(s)										Ploidy			Origin		Hypothesis on origin/comment/assumed closest relative, and reference (if available)
	GW	GE	Sb	NZ	Ic	Fa	BI	SS	NF	Repr.	2n	Level(s)	D/P	Origin		
<i>Antennaria affinis</i> Fernald	GW	-	-	-	-	-	-	-	-	AA	56	8	P	PL/H	Only female plants?	
<i>Antennaria alpina</i> (L.) Gaertn. ssp. <i>alpina</i>	-	-	-	-	-	-	-	-	SS	NF	AA	70 84 10 12	P	PL/H	Mainly female plants (Chmielewski, 1998)	
<i>Antennaria alpina</i> (L.) Gaertn. ssp. <i>porzildii</i> (E. Ekman) Chmel.	GW	-	-	-	-	-	-	-	-	NF	AA	56 63 70 8 9 10	P	PL/H	Only female plants	
<i>Antennaria hanzii</i> A. Kerner	GW	GE	-	-	-	-	-	-	-	AA	56	8	P	PL/H	Only female plants?	
<i>Antennaria intermedia</i> (Rosenv.) Porsild	GW	-	-	-	-	-	-	-	-	AA	56	8	P	PL/H	Only female plants?	
<i>Antennaria nordhageniana</i> Rune & Rønning	-	-	-	-	-	-	-	-	-	NF	SC	28	4	PP	The widespread Eurasian <i>A. dioica</i>	
<i>Arenaria norvegica</i> Gummerus ssp. <i>norvegica</i>	-	-	-	-	Ic	-	BI	SS	NF	S	80	8	P	(PL)/PP	The octoploid BI endemic ssp. <i>anglica</i> /direct allopolyploid derivative of the <i>A. ciliata</i> complex	
<i>Braya</i> (<i>Neotorularia</i> ?) <i>intermedia</i> T.J. Sørensen	-	GE	-	-	-	-	-	-	-	S	70	10	P	PL	The N American 4x-8x <i>Neotorularia humilis</i> complex (cf. Böcher, 1966b)	
<i>Braya linearis</i> Rouy	GW	GE	-	-	-	-	-	SS	NF	S	42	6	P	PP	The C European <i>B. alpina</i> (Böcher, 1966b)	
<i>Carex lidii</i> Hadac	-	GE	Sb	-	-	-	-	-	-	?	?	?	?	H?	Possibly a sterile hybrid (<i>Oxystedal</i> & Haaland, 1996)	
<i>Carex maritima</i> Dewey ssp. <i>pseudolagopina</i> (T.J. Sørensen) Böcher	GW	GE	Sb	-	-	-	-	-	-	SC?	64	?	?	PP?	The nearly circumpolar ssp. <i>maritima</i>	
<i>Carex saxatilis</i> L. ssp. <i>saxatilis</i>	-	-	-	-	Ic	Fa	BI	SS	NF	SC?	80	?	?	PP?	The nearly circumpolar ssp. <i>laxa</i>	
<i>Cerastium alpinum</i> L. ssp. <i>glabratum</i> (Hartm.) Á. & D. Löve Edmondston ex H.C. Watson	-	-	-	-	Ic	-	-	SS	NF	S	72	8	P	PL/PP	The broadly amph-Atlantic ssp. <i>alpina</i> /direct allopolyploid origin from low-ploidy relatives in C. Europe	
<i>Cerastium nigrescens</i> (H.C. Watson) Edmondston ex H.C. Watson	-	-	-	-	Ic	Fa	BI	SS	NF	S	108	12	P	PL	The close relative <i>C. arcticum</i> also 12-ploid, but evidence of independent allopolyploid origin (Brysting & Borgen, 2000; Hagen & al., 2001)	
<i>Cochlearia officinalis</i> L. ssp. <i>integrifolia</i> (Hartm.) Nordal & Stabthorp	-	-	-	-	-	-	-	-	-	NF	SC?	24	4	P	PP	The widely NW European ssp. <i>officinalis</i> (Nordal & al., 1986)
<i>Draba cacuminum</i> E. Ekman ssp. <i>angusticarpa</i>	-	-	-	-	-	-	-	-	-	NF	SS	64	8	P	PL/H	<i>In situ</i> allopolyploidization from <i>D. norvegica</i> (6x) X ?/ladnizensis (2x), independent of ssp. <i>angusticarpa</i> (Brochmann & al., 1992b)
<i>Draba cacuminum</i> E. Ekman ssp. <i>angusticarpa</i>	-	-	-	-	-	-	-	-	-	SS	64	8	P	PL/H	<i>In situ</i> allopolyploidization from <i>D. norvegica</i> (6x) X ?/ladnizensis (2x), independent of ssp. <i>angusticarpa</i> (Brochmann & al., 1992b)	
<i>Draba norvegica</i> Gummerus	GW	GE	Sb	-	Ic?	Fa	BI	SS	NF	SS	48	6	P	PL	Multiple allopolyploid origins, progenitors uncertain (Brochmann & al., 1992c)	
<i>Draba oxycarpa</i> Sommerf.	-	GE	Sb	NZ	Ic	-	-	SS	NF	SS	64	8	P	PL	Allopolyploid, but no close N Atlantic relatives (Brochmann & al., 1992a)	
<i>Elymus trachycaulis</i> (Link) Gould ex Shimmers ssp. <i>virescens</i> (Lange) Á. & D. Löve	GW	GE	-	-	-	-	-	-	-	S	28	4	P	PP	Closely related N American taxa	
<i>Festuca groenlandica</i> (Schol.) Fred.	GW	-	-	-	-	-	-	-	-	S				PP?	Closely related to the selfing, circumpolar hexaploid <i>F. brachyphylla</i> , but ploidy level unknown (cf. Levkovsky & al., 1979; Frederiksen, 1982)	

Table 1. (continued).

Taxon	Geographic region(s)										Ploidy		Hypothesis on origin/comment/assumed closest relative, and reference (if available)	
	GW	GE	Sb	NZ	Ic	Fa	BI	SS	NF	Repr.	2n	Level(s) D/P		Origin
<i>Luzula arcuata</i> (Wahlenb.) Sw. ssp. <i>arcuata</i>	-	GE	?	-	Ic	Fa	BI	SS	NF	S	36-48	6-8	PP	The amphi-Beringian ssp. <i>uralascensis</i>
<i>Papaver dahlianum</i> Nordh. ssp. <i>dahlianum</i>	-	-	-	-	-	-	-	-	NF	SS	70	10	PP	The circumpolar(?) ssp. <i>polare</i> (Petrovsky, 1999; Elven & Nilsson in Jonsell, 2001)
<i>Papaver lapponicum</i> (Tolm.) Nordh. ssp. <i>dasycarpum</i> Tolm.	-	-	-	NZ	-	-	-	-	-	SS	56	8	PP?	See Petrovsky (1999)
<i>Papaver radicans</i> Rothb. ssp. <i>laestadianum</i> Nordh.	-	-	-	-	-	-	-	-	NF	SS	70	10	PL	Separate allooctoploid origin; other subspecies allodecaploid (Nilsson in Jonsell, 2001; Solstad & al., in press)
<i>Papaver radicans</i> Rothb. ssp. <i>radicans</i> s.lat.	-	-	-	-	Ic	Fa	-	SS	NF	SS	70	10	PL	Allopolyploid, unclear relationships (Solstad & al., 1999, in press)
<i>Poa arctica</i> R. Br. ssp. <i>stricta</i> (Lindb.) Nannf.	-	-	-	-	-	-	SS	-	AB	38-39	5-6	5-6	PL/H	Progenitors possibly different from other taxa of the <i>P. arctica</i> complex (Nannfeldt, 1940)
<i>Poa jemtlandica</i> (Almq.) K. Richt.	-	-	-	-	Ic	-	BI	SS	NF	AB	36-38	5-6	PL/H	Originated several times from <i>P. alpina</i> × <i>flevoosa</i> (Brysting & al., 1997, 2000)
<i>Poa laxa</i> Haenke ssp. <i>flevoosa</i> (Sm.) Hyl.	-	-	-	-	Ic	-	BI	SS	NF	S	42	6	PP	Three other subspecies
<i>Potentilla insularis</i> Soják	-	?	Sb	-	-	-	-	-	-	AA	?	?	H	Parentage unknown; facultative apomict (Hansen & al., 2000; Nylén & Hamre, 2002)
<i>Potentilla lyngei</i> Jurtz. & Soják	-	?	-	NZ	-	-	-	-	NF	?	?	?	H?	Probably agamotaxon of hybrid origin, but may be sexual
<i>Puccinellia groenlandica</i> T.J. Sørensen	GW	-	-	-	-	-	-	-	-	S	56	8	P	Relationships unclear (Sørensen, 1953); taxonomically insignificant?
<i>Puccinellia palibinii</i> T.J. Sørensen	-	-	Sb	NZ	-	-	-	-	-	S	56	8	P	Relationships unclear (Sørensen, 1953); taxonomically insignificant?
<i>Puccinellia phryganodes</i> (Trin.) Scribn. & Merr.	-	-	Sb	NZ	-	-	-	-	-	AB	28	4	PL/H	Asexual part of di- to hexaploid aggregate (Sørensen, 1953)
ssp. <i>vilfoidea</i> (Andersson) Trzeveln	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Puccinellia porsildii</i> T.J. Sørensen	GW	-	-	-	-	-	-	-	-	S	56	8	P	Relationships unclear (Sørensen, 1953); taxonomically insignificant?
<i>Puccinellia rosenkrantzii</i> T.J. Sørensen	GW	-	Sb	-	-	-	-	-	-	S	42	6	P	Relationships unclear (Sørensen, 1953); taxonomically insignificant?
<i>Puccinellia svalbardensis</i> Rønning	-	GE	-	-	-	-	-	-	-	S	39-52	3-4	PL/H	Allopolyploid, <i>S. aizoides</i> × <i>oppositifolia</i> (Ferguson, 1972; Böcher, 1983)
<i>Saxifraga nathorstii</i> (Dusen) Hayek	-	-	-	-	-	-	-	SS	NF	AB	48-50	?	PL/H	Multiple <i>in situ</i> postglacial hybrid origins from <i>S. cernua</i> × <i>rivularis</i> , morphologically distinct from <i>S. svalbardensis</i> (Steen & al., 2000)
<i>Saxifraga opdalensis</i> A. Blytt	-	-	-	-	-	-	-	-	-	-	-	-	-	
<i>Saxifraga svalbardensis</i> Øvstedal	-	-	Sb	-	-	-	-	-	-	AB	c.64	?	PL/H	A single <i>in situ</i> postglacial hybrid origin from <i>S. cernua</i> × <i>rivularis</i> (Brochmann & al., 1998; Steen & al., 2000)
<i>Silene walibergella</i> Chowdhuri	-	-	-	-	-	-	-	SS	NF	SS	24	2	DD	Strongly selfing (cleistogamous) lineage diverged from the circumpolar, variable <i>S. uralensis</i> (Kurito in Jonsell, 2001)
<i>Taraxacum dovreense</i> (Trautv.) Dahlst.	-	-	-	-	-	-	-	SS	-	AA	32	4	PL/H	Agamic part of arctic(alpine) sexual to agamic complex
<i>Thymus praecox</i> Opitz ssp. <i>arcticus</i> (Durand) Jalas	GW	GE	-	-	Ic	Fa	BI	SS	NF	S	c.54	6?	PP	Other widespread European subspecies
Total no. of north boreal, alpine and arctic taxa in each region ¹	463	356	176	226	357	nc	nc	597	698					
No. endemics	13	11	9	5	11	6	7	18	22					
(% of total)	2.8	3.1	5.1	2.2	3.1			3.0	3.2					
No. single-region endemics	6	2	3	1	0	0	0	3	5					
(% of total)	1.3	0.6	1.7	0.4	0.0			0.5	0.7					

¹Total number of taxa in each region: This number is calculated as follows (not calculated for the Faroes and the northern British Isles, designated "nc" in the Table). Greenland: Based on Böcher & al. (1978), supplemented with Feilberg (1984), Bay (1992), Fredskild (1996), and the Panarctic Flora Checklist (Elven & al., 2003); sum of all species and subspecies except for introduced taxa and agamospecies in large agamic complexes. Svalbard including Bear Island and Franz Josef Land: Based on Elven & Elvebakk (1996) and Elven & al. (2003); criteria as for Greenland. Novaya Zemlya: based on Sekretareva (1999) and Elven & al. (2003); criteria as for Greenland. Iceland: based on Kristinsson (1998); sum of all species and subspecies except for introduced taxa, agamospecies in large agamic complexes, and taxa restricted to the middle boreal zone (SAW parts). Scandes, southern part: based on Elven (1994) and Stenberg & al. (1992); sum of all species and subspecies that have significant occurrence in north boreal, alpine and arctic parts, except for introduced taxa and agamospecies in large agamic complexes. Fenoscandia, northern part including the Kola Peninsula: based on Elven (1994), Stenberg & al. (1992), and Sekretareva (1999); criteria as for the southern Scandes.

Table 2. The 34 north boreal and partly low-alpine vascular plant taxa accepted in this paper as endemic to the glaciated parts of the North Atlantic area at the specific or sub-specific level but not considered hardy enough to be potential *in situ* glacial survivors, given the current reconstructions of ice sheet extent and paleoclimate (see text). The current restriction of these taxa to the previously glaciated area must, therefore, most probably be explained by postglacial immigration from periglacial areas, where they subsequently went extinct or have not yet been identified, or by rapid *in situ* speciation. See Table 1 for explanations.

Taxon	Geographic region(s)										Repr.	2n	Level(s)	D/P	Origin	Hypothesis on origin/comment/assumed closest relative, and reference (if available)
	GW	GE	Sb	NZ	Ic	Fa	BI	SS	NF	SC?						
<i>Alchemilla faeroensis</i> (Lange) Buser	-	-	-	-	Ic	Fa	-	-	-	AA	172-224	>20?	P	PL/H	Belongs to W-C European agamic complex	
<i>Alchemilla semidivisa</i> Ericsson in press	-	-	-	-	-	-	-	-	-	AA	-	-	P?	PL?/H?	Belongs to W-C European agamic complex	
<i>Alnus incana</i> (L.) Moench ssp. <i>kolaensis</i> (N.I. Orlova) A. & D. Löve	-	-	-	-	-	-	-	-	-	SC?	28	4	P	PP	The widespread European ssp. <i>incana</i>	
<i>Angelica archangelica</i> L. ssp. <i>litoralis</i> (Fr.) Thell.	-	-	-	-	Ic	-	-	-	-	SC?	22	2	D	DD	Littoral lineage; the widespread amph-Atlantic ssp. <i>archangelica</i>	
<i>Anthyllis vulneraria</i> L. ssp. <i>lapponica</i> (Hyl.) Jalas	-	-	-	-	-	BI	SS	NF	SC?	12	2	2	D	DD	Several other European subspecies	
<i>Arenaria ciliata</i> L. ssp. <i>hibernica</i> Ostentf. & O.C. Dahl	-	-	-	-	-	BI	-	-	S	-	-	-	PP?	PP?	Several other European subspecies; probably polyploid	
<i>Arenaria norvegica</i> Gunnarus ssp. <i>anglica</i> Halliday	-	-	-	-	-	BI	-	-	S	80	8	8	P	(PL)/PP	The octoploid endemic ssp. <i>norvegica</i> /direct allopolyploid derivative of the <i>A. ciliata</i> complex	
<i>Atriplex lapponica</i> Pojark.	-	-	-	-	-	-	-	-	NF	S	18	2	D	DD	Possibly the Atlantic <i>A. litoralis</i> (Gustafsson, 1986; Elven, 1984)	
<i>Cakile maritima</i> Scop. ssp. <i>islandica</i> (Gand.) Hyl. ex Elven	-	-	-	-	Ic	Fa	?	SS	NF	SC	18	2	D	DD	2-3 other European subspecies (Rodman, 1974; Elven & Gjelsås, 1981)	
<i>Calamagrostis chalybaea</i> (Laest.) Fr.	-	-	-	-	-	-	-	-	NF	AA	42	6	P	PL/H	One parent is the sexual, Russian <i>C. obtusata</i> Trin.?	
<i>Cochlearia micacea</i> E.S. Marshall	-	-	-	-	-	BI	-	-	S	-	-	-	PP?	PP?	Unknown	
<i>Cochlearia officinalis</i> L. ssp. <i>norvegica</i> Nordal & Stabbetorp	-	-	-	-	-	-	-	-	SS	NF	24	4	P	PP?	The widely NW European ssp. <i>officinalis</i> ? (Nordal & al., 1986)	
<i>Euphrasia arctica</i> Lange ex Rostk. ssp. <i>arctica</i>	-	-	-	-	-	BI	-	-	S	44	4	4	P	PP	The broadly NW European ssp. <i>borealis</i>	
<i>Euphrasia botnica</i> Kihlin.	-	-	-	-	-	-	-	-	NF	SS	44	4	P	PP	N American taxa? (Karlsson, pers. comm.)	
<i>Euphrasia hyperborea</i> Jørg.	-	-	-	-	-	-	-	-	SS	NF	S	-	PP?	PP?	Unclear relationships	
<i>Galium normanii</i> O.C. Dahl	-	-	-	-	Ic	-	-	-	NF	SS?	44	4	P	PL/H	Allopolyploid origin from the European <i>G. pumilum</i> di/polyploid complex	
<i>Gentiana aurea</i> (L.) Harry Sm.	GW	GE	-	-	Ic	-	-	-	SS	NF	18	36	2.4	D/P	Unknown	
<i>Juncus arcticus</i> Willd. ssp. <i>balticus</i>	?	-	-	-	?	BI	SS	NF	SC	80	84	?	P	PP	Other ssp. within the circumpolar <i>J. arcticus</i>	
<i>Oxytropis deflexa</i> (Pall.) DC. ssp. <i>norvegica</i> Nordh.	-	-	-	-	-	-	-	-	NF	SC	16	2	D	DD	Asian-western North American ssp. (Høiland & Laane, 1989)	
<i>Papaver lapponicum</i> (Tolm.) Nordh. ssp. <i>lapponicum</i>	-	-	-	-	-	-	-	-	NF	SS	56	8	P	PP	Other, circumpolar ssp.? (Petrovsky, 1999)	
<i>Polygonum raii</i> Bab. ssp. <i>norvegicum</i> Sam.	-	-	-	-	-	-	-	-	SS	NF	40	4	P	PP	The NW European ssp. <i>raii</i>	
<i>Potamogeton groenlandicus</i> Hagstr.	GW	-	-	-	-	-	-	-	S	26	2	2	D	DD	The N American-Siberian <i>P. subsibiricus</i>	
<i>Primula scandinavica</i> Bruum	-	-	-	-	-	-	-	-	SS	NF	72	8	P	PL/H?	Allopolyploid, but parentage unclear (isozyme data; Hultgård & Hedrén, unpubl.; cf. Knaben, 1982, and Hultgård, 1990, 1991)	
<i>Primula scotica</i> Hook.	-	-	-	-	-	BI	-	-	SS	36	4	4	P	PL/H?	Allopolyploid, but parentage unclear (isozyme data; Hultgård & Hedrén, unpubl.; cf. Knaben, 1982, and Hultgård, 1990, 1991)	
<i>Puccinellia</i> sp.	-	-	-	-	-	-	-	-	NF	S	14	2	D	DD	Relationships unknown (included in Elven, 1994)	
<i>Pyrola norvegica</i> Knaben	-	-	-	-	-	-	-	-	SS	NF	46	2?	D?	DD?	The nearly circumpolar <i>P. grandiflora</i>	
<i>Ranunculus flammula</i> L. ssp. <i>minimus</i> (A. Benn.) Padmore	-	-	-	-	-	BI	-	-	S	32	4	4	P	PP	The amph-Atlantic ssp. <i>flammula</i>	
<i>Ranunculus flammula</i> L. ssp. <i>scoticus</i> (E.D. Marshall) A.R. Clapham	-	-	-	-	-	BI	-	-	S	-	-	-	PP?	PP?	Possibly as above, but ploidy level unknown	
<i>Salicornia dolichostachya</i> Moss ssp. <i>pojarkovae</i> (N. Semenova) Piirainen	-	-	-	-	-	-	-	-	NF	SS	36	4	P	PP	The W European ssp. <i>dolichostachya</i> (Piirainen, 1991)	
<i>Salix caprea</i> L. ssp. <i>sphaecolata</i> (Sm.) Macreight	-	-	-	-	-	BI	SS	NF	SC	38	2	2	D	DD	The widespread European/W Siberian ssp. <i>caprea</i> (Berg & Christensen in Jonsell, 2000)	
<i>Salix lanata</i> L. ssp. <i>glaucoflava</i> (Flod.) Hiitonen	-	-	-	-	?	-	-	-	SS	NF	38	2	D	DD	The widespread N European ssp. <i>lanata</i> (Elven in Jonsell, 2000)	
<i>Sisyrinchium groenlandicum</i> Böcher	GW	-	-	-	-	-	-	-	S	32	4	4	P	PL/H	Allopolyploid of uncertain parentage, closely related to <i>S. montanum</i> (Böcher, 1966a)	
<i>Thymus serpyllum</i> L. ssp. <i>tanaensis</i> (Hyl.) Jalas	-	-	-	-	-	-	-	-	NF	S	24	4	P	PP	The widespread Eurasian ssp. <i>serpyllum</i> (cf. Jalas, 1950)	
<i>Thymus rupestris</i> F.W. Schmidl ssp. <i>reluctata</i> Jalas	-	-	-	-	-	-	-	-	SS	NF	20	4	P	PP	The widespread European ssp. <i>rupestris</i> (Nordal & Jonsell, 1998)	
Total no. of north boreal, alpine and arctic taxa in each region	463	356	176	226	357	nc	nc	597	698							
Table 2 totals:																
No. endemics	3	1	0	0	5	4	10	15	22							
(% of total)	0.6	0.3	0.0	0.0	1.4	1.1	2.5	3.2	3.2							
No. single-region endemics	2	0	0	0	0	0	6	1	8							
(% of total)	0.4	0.0	0.0	0.0	0.0	0.0	0.2	1.1	1.1							
Table 1 and 2 totals:																
No. endemics	16	12	9	5	16	10	17	33	44							
(% of total)	3.5	3.4	5.1	2.2	4.5	2.8	5.5	6.3	6.3							
No. single-region endemics	8	2	3	1	0	0	6	4	13							
(% of total)	1.7	0.6	1.7	0.4	0.4	0.4	0.7	1.9	1.9							

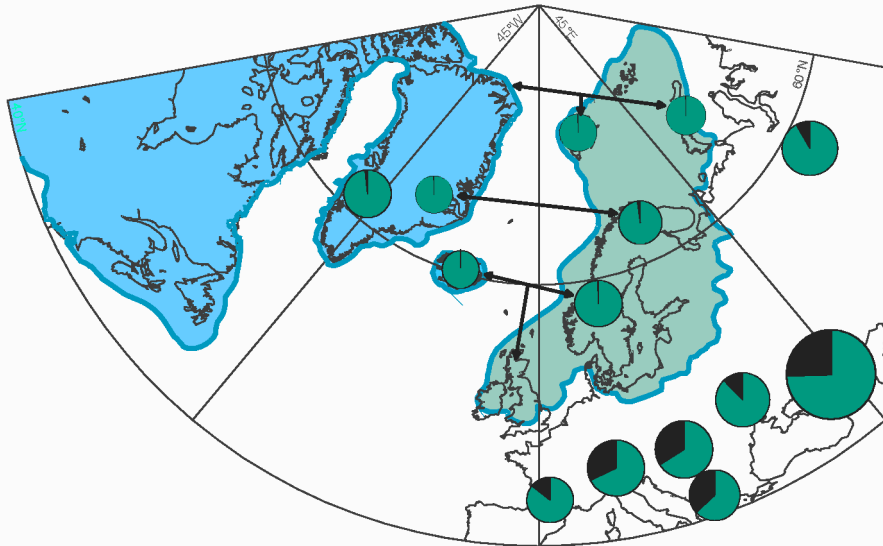


Fig. 10. Levels of current vascular plant endemism (black part of pie) in the previously glaciated North Atlantic regions (“single-region endemics”, data from Tables 1 and 2; cf. Fig. 1) and in alpine Eurasian regions situated outside the main area of glaciation (data from Myers & Giller, 1988). Pie size increases proportionally with the total number of species in each region. The lines connecting North Atlantic regions illustrate the three main patterns observed for North Atlantic endemics that are shared among two or more regions (“several-region endemics”). The alpine regions outside the main area of glaciation are (from the west) the Pyrenees (14% endemism), the Alps (32%), the Balkan Mountains (34%), the South Greek Mountains (37%), the Carpathians (12%), the Caucasus (25%), and the Ural Mountains (8%).

to define an alternative western delimitation within the vast North American Laurentide Ice Sheet. Otherwise, the entire present geographic range of the taxa accepted in this paper should be within the area glaciated at the time of the maximum extent of the ice sheets as defined in Figure 1. We have rejected several postulated endemics because they now are known to occur also outside this area (see Appendix 1).

We divided the glaciated North Atlantic area into nine regions that are geographically isolated from each other, most of them by the sea (by the inland ice in Greenland), and thus can be expected to be separated by dispersal barriers (Fig. 1; defined in Table 1). In the following, the term “*North Atlantic endemics*” will be used for the taxa accepted after the criteria stated above. Taxa restricted to a single one of the nine geographic regions will be referred to as “*single-region endemics*”, and taxa shared among two or more geographic regions will be referred to as “*several-region endemics*”.

The accepted taxa were further divided into two ecological groups. The first group consists of 43 taxa (the “*hardy endemics*”; Table 1) considered hardy enough to be potential *in situ* glacial survivors given the reconstructions of ice sheet extent (Fig. 1) and paleoclimate (see, e.g., Bennike, 1999). These taxa currently occur regularly in sites well above/beyond the current treeline or in sites with similar climatic conditions; i.e., in alpine, subarctic, or arctic sites, including coastal ones. The cur-

rent restriction of these taxa to the previously glaciated area can be explained by (1) *in situ* glacial survival, (2) postglacial immigration from periglacial areas where they subsequently went extinct (or have not yet been identified), or (3) postglacial immigration of their progenitor(s) from periglacial areas and rapid *in situ* speciation (e.g., via hybridization giving rise to a first-generation hybrid propagating asexually; via repeated hybridizations continuously giving rise to new first-generation hybrids; via hybridization and chromosome doubling giving rise to new allopolyploid species that propagate asexually or sexually; or via rapid divergent evolution at the same ploidy level, for example by ecogeographic differentiation involving strong selection or by strong genetic drift caused by small effective population sizes in predominantly asexual or self-fertilizing populations). The other group of accepted endemics comprises 34 less hardy taxa (the “*non-hardy endemics*”; Table 2), which currently are absent from such sites and therefore considered much less likely as nunatak survivors. Although this distinction admittedly is not entirely clear-cut in all cases, separate analyses after a rough division into two such groups revealed striking differences (see below).

Levels of endemism. — The level of endemism in the North Atlantic is very low compared to that outside the main area of glaciation (Fig. 10, Tables 1 and 2). The number of accepted single-region endemics varies from

none in Iceland and the Faroes (but these areas have endemics at the varietal level), one in Novaya Zemlya, two in East Greenland, three in Svalbard, four in the southern Scandes, six in the northern British Isles, and eight in West Greenland to 13 in northern Fennoscandia (total 37; Table 2). For seven regions, we have enumerated the total number of north boreal, alpine, and arctic plant taxa (i.e., all taxa occurring in West and East Greenland, Svalbard, and Novaya Zemlya, and taxa occurring in the north boreal, alpine, and arctic parts of Iceland and Scandinavia). The levels of single-region endemism vary from 0.0% to 1.9%. In contrast, the levels of endemism in European alpine areas outside the main area of glaciation can be above 25%, for example in the Caucasus, the Alps, the Balkan Mountains, and the mountains of southern Greece, the latter with about 37% endemism (Fig. 10; based on data summarized in Myers & Giller, 1988).

Among the total of 77 North Atlantic endemics, more than 50% (40 taxa) are several-region endemics. These endemics must either have dispersed from their site of origin or originated more than once. Even when these endemics are included, the levels of endemism are very low (2.2–6.3%). There are no North Atlantic endemics at higher taxonomic levels than species, and many taxa are only recognized at the subspecies level. The vast majority have closely related taxa within the North Atlantic area or in the European, Northwest Siberian, or northeast American surroundings. There is not a single taxonomically or geographically isolated “paleoendemic” of presumably old age; all endemics are typical “neoendemics”. Our analysis thus demonstrates that the Quaternary glaciations seriously constrained the possibilities for local plant evolution; the North Atlantic is inhabited by a typically young flora.

Geographic patterns in endemism. — A distinct pattern among the several-region endemics (Tables 1 and 2) is that there are strong connections across the North Atlantic, both in the far north (NE Greenland, Svalbard, Novaya Zemlya), in the middle (E Greenland, N Fennoscandia), and especially in the south, with many shared taxa (Iceland, N British Isles, S Scandes). This fact can be taken as evidence of considerable trans-oceanic dispersal capacity. Among the single-region endemics, there are differences among the regions not only in number but also as regards ploidy levels, reproduction, and mode of origin, in particular between northern Fennoscandia and the other regions. In some areas, especially West Greenland, the number of single-region endemics is still probably exaggerated, but we tentatively accepted several doubtful taxa because they have not yet been sufficiently studied.

The West Greenlandic single-region endemics that still are tentatively accepted are concentrated to a few

genera, whereas in two other critically revised genera (*Calamagrostis* and *Potentilla*), all postulated Greenland endemics have been merged with more widespread taxa (Greene, 1980; Elven & al., 2003). In *Puccinellia*, several Greenland endemics described by Sørensen (1953) are now regarded as conspecific with North American species, and the three remaining ones have not been fully evaluated (Soreng, pers. comm.; cf. Soreng & al., 2000–2002). In *Antennaria*, three agamotaxa closely related to the sexual *A. dioica* are still tentatively accepted, but numerous other endemics in *Antennaria* have already been rejected (e.g., by Chmielewski, 1998).

In East Greenland, the only single-region endemics (*Braya intermedia* and *Saxifraga nathorstii*) are morphologically distinct, sexual taxa, probably of recent allo-ploid origin (Ferguson, 1972; Böcher 1983). All taxa in the very depauperate flora of Franz Josef Land also occur in Svalbard. Two of the three single-region endemics in Svalbard (*Potentilla insularis* and *Saxifraga svalbardensis*) are asexuals, probably of recent hybrid origin (Brochmann & al., 1998; Hansen & al., 2000; Steen & al., 2000; Brochmann & Håpnes, 2001; Nyléhn & Hamre, 2002), and the third (*Puccinellia svalbardensis*) is possibly conspecific with a more widespread species.

In Iceland and the Faroes, we have not accepted any single-region endemics at the level of species or subspecies. Numerous local endemics have been reported from Iceland, but in the recent compilation by Kristinsson (1998), not a single one was accepted. For the northern British Isles, Stace (1997) accepted quite a few local endemics for the glaciated mountainous parts. We have not evaluated these in detail but tentatively accepted six of them.

The southern Scandes still have quite a few (33) North Atlantic endemics even if many others were rejected by us, but only four single-region endemics. These are well-defined and probably of hybrid origin. Three of them are asexual, whereas *Draba cacuminum* ssp. *cacuminum* is a sexual allo-octoploid that probably has originated *in situ* from local progenitors although it has a close northern Fennoscandian counterpart (Elven & Aarhus, 1984; Brochmann & al., 1992b).

Northern Fennoscandia is by far the richest region in terms of number of taxa (698), several-region endemics (31), and single-region endemics (13). A main reason is probably the proximity to major boreal and arctic source areas in the non-glaciated parts of northern Russia and Siberia (cf. below). In contrast to the other Atlantic regions, several of the 13 single-region endemics in northern Fennoscandia are sexual diploids or low polyploids. Five of these inhabit seashores or have close relatives on seashores (*Atriplex lapponica*, *Cochlearia officinalis* ssp. *integrifolia*, *Euphrasia bottnica*, *Puccinellia* sp., and *Salicornia dolichostachya* ssp.

pojarkovae). Two of them have no known close European relatives (*Euphrasia bottnica*, *Puccinellia* sp.). There is only one sexual allopolyploid of probable recent and local origin (*Draba cacuminum* ssp. *angusticarpa*) and one asexual taxon of hybrid origin (*Calamagrostis chalybaea*). The six remaining single-region endemics in northern Fennoscandia are probably marginal segregates of more widespread sexual groups (*Antennaria nordhageniana*, *Oxytropis deflexa* ssp. *norvegica* (closest relatives in Asia and western North America), three taxa of *Papaver*, and *Thymus serpyllum* ssp. *tanaensis*).

Origins of the non-hardy endemics. — We consider nunatak survival of these 34 taxa unlikely given the available ice and climate reconstructions (Table 2). Trees and large shrubs such as *Alnus incana* ssp. *kolaensis* and *Salix caprea* ssp. *sphacelata*, as the most extreme examples, cannot have survived the harsh climatic conditions on nunataks. Thus, the current restriction of the non-hardy taxa to the previously glaciated area can be explained by postglacial immigration or rapid *in situ* speciation.

Most of them probably survived in periglacial areas where they subsequently went extinct because of postglacial environmental change (e.g., by the submerging of the exposed shelves south of the ice sheet, or by the drastic habitat changes occurring in southern England or in the continental European tundra). Alternatively, some of these taxa may not really be endemic but have not yet been identified in their periglacial refugia to the northeast, as shown by our rejection of many previously proposed endemics listed in the Appendix. Half of the non-hardy endemics are several-region endemics, demonstrating high dispersal ability. Notably, except in two regions, there are virtually no single-region endemics among the non-hardy ones. The exceptions are the two regions situated close to major periglacial refugia; the northern British Isles, which were directly connected to the exposed shelves and the continental southern tundra, and northern Fennoscandia, which still is directly connected to the taiga and tundra in northern Russia, suggesting immigration from these areas.

In contrast to the group of hardy endemics, the non-hardy ones comprise many (11 vs. 1) diploid taxa, some of which are regularly outcrossing, and few asexual taxa (3 vs. 12). There are no strongly documented cases of recent speciation via allopolyploidy or primary hybridization, but the three agamotaxa may be recent hybrids, and recent allopolyploidy has been suggested for a few species (e.g., *Primula scandinavica*, *P. scotica*, and *Sisyrinchium groenlandicum*; Table 2). Recent isozyme evidence suggests, however, that the two species of *Primula* may not have originated locally via allopolyploidy but are older allopolyploids which immigrated postglacially (Glover & Abbott, 1995; Hultgård & Hedrén, pers. comm.).

The hypothesis that northeastern Russia was an important source for postglacial immigration of plants, including present-day endemics, into northern Fennoscandia is supported by the occurrence of a distinct element of six taxa endemic to the area extending westwards from the Ural Mountains to the late Weichselian ice limit in Fig. 1, and 13 taxa shared between this area and the North Atlantic area of endemism as defined herein (R. Elven, unpubl. data). Twelve of the latter taxa also occur in northern Fennoscandia, some of them also reach across the Atlantic to Greenland. As in northern Fennoscandia, most of the 19 taxa in this element are sexual and diploid to low-polyloid. Among the taxa extending into the North Atlantic region are well-known disjuncts such as *Arenaria pseudofrigida* (Ostenf. & O.C. Dahl) Juz. ex Schischk. & Knorring (reaching East Greenland) and *Artemisia norvegica* Fr. (also occurring in the southern Scandes and the northern British Isles).

Several endemics probably immigrated from the area including southern England, the southern exposed shelves, and the western European continent south of the ice sheets (e.g., *Viola rupestris* ssp. *relicta*, *Cochlearia officinalis* ssp., *Salix caprea* ssp. *sphacelata*, and *Cakile maritima* ssp. *islandica*). In a recent isozyme study of *Viola rupestris*, which belongs to a section of species diverged at the tetraploid level, three fixed-heterozygous multilocus genotypes with different geographic distributions were identified (Nordal & Jonsell, 1998). One was widespread, characterizing all populations south of 65° N (ssp. *rupestris*), and two were restricted to northernmost Scandinavia (the endemic ssp. *relicta*) and the Kuusamo area in NE Finland (ssp. *rupestris*), respectively. Later, it has been shown that ssp. *relicta* also occurs on the western coast of southern Norway (Nordal & Marcussen, unpubl.), and that the few British populations of the species are isozymically quite similar to ssp. *relicta* (Jonsell & al., 2000). Thus, the species has probably immigrated to the Nordic area from three directions (SW - ssp. *relicta*, SE and NE - ssp. *rupestris*).

Origins of the hardy endemics—the putative nunatak survivors. — The current restriction of the 43 hardy endemics (Table 1) to the previously glaciated North Atlantic area can be explained as for the non-hardy ones (immigration or *in situ* speciation), or by nunatak survival. The occurrence of many (23) of these taxa in more than one region indicates considerable dispersal capacity, suggesting that they also may have been able to disperse into the area from periglacial refugia. However, in some cases, the occurrence in more than one region can be caused by multiple origins or by survival on multiple nunataks.

None of the hardy single-region endemics are diploids. Six of them are mainly asexual polyploids, all of them probably of recent hybrid origin. A well-studied

case is *Saxifraga svalbardensis* (Fig. 11). Analyses of various chloroplast and nuclear DNA markers have provided strong evidence for post-Weichselian origin of this species by hybridization between two widespread polyploids which both are common in Svalbard, *Saxifraga cernua* (Fig. 5) and *S. rivularis* (Brochmann & al., 1998; Steen & al., 2000). The virtual absence of molecular and morphological variation in this endemic and its current co-occurrence with both of its progenitor species suggest that it has originated locally a single time after the last glaciation. The 14 remaining single-region endemics are sexual polyploids, most of them predominantly self-fertilizing. The two subspecies of *Draba cacuminum*, which occur in the southern Scandes and northern Fennoscandia, respectively (Elven & Aarhus, 1984), have probably originated independently via allopolyploidy involving local populations of the hexaploid *D. norvegi-*

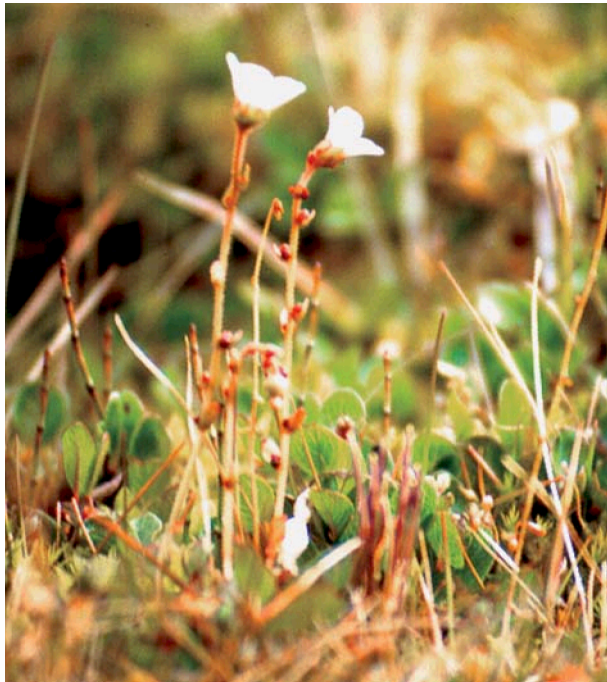


Fig. 11. The Svalbard saxifrage, *Saxifraga svalbardensis*, a mainly asexual polyploid endemic to Svalbard. Analyses of various molecular markers have provided strong evidence for post-Weichselian origin of this species by hybridization between two circumpolar species that are common in Svalbard, *Saxifraga cernua* (Fig. 5) and *S. rivularis* (Brochmann & al., 1998; Steen & al., 2000). The virtual absence of molecular variation in this morphologically and ecologically distinct endemic and its co-occurrence with both of its progenitors suggest that it has originated locally a single time after the last glaciation. The Scandinavian polyploid endemic *Saxifraga opdalensis* has originated via hybridization between local populations of the same progenitor species, but it is nevertheless morphologically distinct from *S. svalbardensis*. Photo: Arnodd Håpnes.

ca and one of the local diploid species, possibly *D. fladnizensis* (Brochmann & al., 1992b, 1993). Additivity at isozyme loci further suggested that the northern subspecies alone has originated at least twice. Isozyme data also suggested that one of the parents of *D. cacuminum*, the hexaploid several-region endemic *D. norvegica* (Table 1), itself has multiple allopolyploid origins (Brochmann & al., 1992c). All of these species of *Draba* are strongly selfing (Brochmann, 1993). Another single-region endemic that probably has originated recently via allopolyploidy is the Greenlandic *Saxifraga nathorstii*, derived from hybridization between two morphologically very different species, *S. aizoides* and *S. oppositifolia* (Ferguson, 1972; Böcher, 1983).

A single diploid was identified among the 23 hardy several-region endemics, *Silene wahlbergella*, which is a highly selfing (cleistogamous) species that probably has diverged from the circumpolar *S. uralensis* (Kurrto in Jonsell, 2001). Six taxa are asexual polyploids, among them the bulbiferous *Poa jemtlandica*. Molecular data suggest that this species has originated independently in Iceland and Scandinavia via at least two recent hybridization events between *P. alpina* and *P. flexuosa* (Brysting & al., 1997, 2000). Another bulbiferous polyploid is *Saxifraga opdalensis*, which occurs in the southern Scandes and northern Fennoscandia. Various DNA markers suggest that it originated locally in southern Norway from local populations of *S. cernua* and *S. rivularis* (Steen & al., 2000). Although the same parental species were involved in the origin of this species and *S. svalbardensis*, even with *S. rivularis* as the maternal parent in both cases, *S. svalbardensis* and *S. opdalensis* are morphologically distinct and commonly recognized as different taxonomic species. Their morphological differences probably reflect polymorphisms within one of their parental species, *S. cernua*; it is likely that two divergent lineages of this variable species were involved. The populations tentatively referred to *S. opdalensis* occurring in at least two areas in northern Fennoscandia (cf. Dahl, 1934; Rune, 1988) have not yet been analysed, but it is most likely that they have originated independently from the southern ones (Steen & al., 2000).

Many of the 43 hardy endemics may have originated directly via primary hybridization or allopolyploidy (Table 1). In several such cases, however, the allopolyploidization event has probably occurred earlier in the Quaternary, and the occurrence of these endemics must therefore be explained by Weichselian nunatak survival or immigration from periglacial refugia. In quite a few cases the endemics have probably originated by divergent evolution, only in one case at the diploid level (*Silene wahlbergella*) and more frequently within one polyploid level (Table 1). Many of these taxa are however, predominantly self-fertilizing and fixed-heterozygous, and

divergent evolution can have occurred rapidly via genetic drift because of small effective population sizes and founder episodes (which may be the case for the diploid in *Silene* and for the polyploids in *Papaver*, see below). Polyploid evolution is now known to be much more dynamic than previously envisioned (reviewed by Soltis & Soltis, 1993, 1999, 2000). In the Arctic, multiple origins of polyploids from widely distributed diploids or more low-polyploid progenitors can produce a variety of morphologically and ecologically divergent, fixed-heterozygous genotypes (e.g., Brochmann & Elven, 1992; Brochmann & al., 1992c). Additional diversity can result from subsequent hybridization between different fixed-heterozygous genotypes, even across different ploidy levels (Brochmann & al., 1992d), followed by segregation into novel fixed-heterozygous genotypes. Genetic drift induced by strong inbreeding and bottlenecking in this complex system can result in rapid geographic differentiation, which sometimes can be recognized at the taxonomic level.

The North Atlantic poppies (*Papaver*)—a key genus in Nordic phytogeography. — The majority of the North Atlantic taxa described in *Papaver* section *Meconella* (the arctic-alpine poppies) have been considered as North European endemics since their description, mainly in the period from Lundström (1914) to Knaben (1959a, b). They are octo- and decaploid, and the decaploids *P. dahlianum* and *P. radicum* were hypothesized by Knaben (1959a, b) to be allopolyploids derived from the octoploid *P. lapponicum* and two non-Nordic diploids. The many subspecies described within *P. radicum* in Scandinavia, the Faroes, and Iceland were assumed by Knaben (1959a, b) and many others as results of divergence during long isolation (at least Weichselian) isolation in multiple nunatak and coastal refugia. Recent palynological investigations (e.g., Paus, 1988; Birks, 1994), however, rather suggest survival southwest of the North European ice sheets. Isozyme studies revealed, surprisingly, no differentiation at all among the many postulated subspecies and very little among some (until now) accepted species (*P. radicum*, *P. lapponicum*, and *P. laestadianum*, the latter now considered to be an octoploid subspecies of the otherwise decaploid *P. radicum*; see Solstad & al., 1999, in press). These data indicate that the rather subtle morphological differences among the postulated subspecies are caused by recent genetic drift in small and fluctuating populations in unstable habitats. The question on the origin of the species themselves remains. They are among the most high-ploid arctic-alpine poppies, and *P. lapponicum* and *P. radicum* probably share the majority of their original diploid genomes. Recent allopolyploid origins of the species are unlikely; there are no putative progenitors in the surrounding areas. The morphologically most

similar species at low ploidy levels are found in NE Asia and Beringia (Petrovsky, 1999; Solstad & Elven, unpubl.).

SUMMARY AND CONCLUSIONS

There is now strong geological evidence suggesting that some nunataks, ice-free uplands, and ice-free coastal shelves existed within the maximum limits of the Late Weichselian ice sheets (25,000–10,000 years ago) in the North Atlantic area (Fig. 1). However, these areas were probably so climatically harsh that only very hardy organisms could have survived (Bennike, 1999). *In situ* glacial survival of organisms such as the spruce (Kullman, 2000) and the forest herb *Melica nutans* (Tyler, 2002) is very unlikely if these reconstructions are correct. In contrast to the situation in the massive northern refugium of Beringia (Goetcheus & Birks, 2001), no fossils have so far been found in the North Atlantic area that could have provided definite evidence of continuous *in situ* existence of life before and through the time of maximum ice sheet extent (Birks, 1994). The quite extensive fossil record that now has accumulated rather suggests that migration rates were high and that colonization rapidly followed deglaciation (Alm & Birks, 1991; Birks, 1994; Bennike, 1999).

Molecular data on intraspecific differentiation are now available for many terrestrial, freshwater, and marine species in the North Atlantic. However, in the absence of fossil evidence, molecular data cannot be used for definite determination of the location of refugia, only to determine whether there are divergent lineages within a species indicating isolation in more than one glacial refugium (Taberlet, 1998). The refugia could have been situated inside the general area of the main ice sheets or outside this area, from where the organisms migrated following deglaciation. High levels of molecular diversity may indicate where refugia have been located. However, low diversity levels can be expected because of genetic drift if the refugial populations were small, and high levels of diversity can also result from secondary contact between lineages that have diverged in different refugia (cf. Petit & al., 2003).

Many plant species occur disjunctly across the Atlantic although they lack obvious mechanisms to promote long-distance dispersal, and such disjunctions have frequently been cited as strong evidence for long-term isolation between American/Greenlandic refugia and north European ones. However, molecular data have shown that populations from opposite sides of the Atlantic often have identical or very similar chloroplast haplotypes as well as nuclear multilocus genotypes (often complex, fixed-heterozygous ones in inbreeding

polyploids). Among other organisms, molecular data have unraveled a variety of different Quaternary histories representing all degrees from deep intraspecific phylogeographic splits to none at all. Such variety has even been demonstrated within individual species, for example in pond-inhabiting *Daphnia* and in a marine species (the barnacle *Semibalanus balanoides*). These findings agree with earlier comparative studies suggesting that each species or lineage has its own unique history of glacial isolations and interglacial range expansions (e.g., Taberlet & al., 1998; Fedorov, 1999; Weider & Hobæk, 2000). Thus, in many species in the North Atlantic, there are such low levels of “genetic endemism” that it is sufficient to invoke survival in a single refugium, which can have been located outside the ice sheets. For other species, two (or more) Atlantic refugia can be inferred, but the locations of these refugia are in many cases unknown because of lack of fossil data. They may have been located to the south of the American as well as to the south and/or east of the European ice sheets.

Our re-evaluation of the postulated endemics in the north boreal, alpine, and arctic flora of the North Atlantic resulted in a list of 77 accepted taxa. The degree of endemism in individual North Atlantic regions is very low (0.0–1.9%) compared to areas outside the main ice sheets (Fig. 10). There is a strong contrast between the geographic patterns of endemism in the North Atlantic area and those of more southern and partly glaciated European mountains (cf. Stehlik, 2003; Tribsch & Schönschwetter, 2003). The southern endemics are usually geographically restricted and occur in or close to areas presumed to be glacial refugia. They seem to have been quite stationary since the glaciations, probably due to vertical migration in the high mountains, and perhaps also due to rapid close-up of the surrounding vegetation after deglaciation. The North Atlantic endemics, on the other hand, are often shared among several geographically isolated regions, indicating extensive migration. Such highly dynamic patterns severely complicate inferences on location of refugia from present-day occurrences.

Given the current ice sheet and climate reconstructions, 34 of the accepted North Atlantic plant endemics are probably not hardy enough for nunatak survival. These species, such as the trees *Alnus incana* ssp. *kolaensis* and *Salix caprea* ssp. *sphacelata*, have most likely immigrated from more favourable periglacial areas (or, in some cases, evolved postglacially *in situ*). Among the 43 hardy endemics, there is not a single outcrossing diploid that could suggest long-term evolution. Most of them are asexual or self-fertilizing polyploids, and there is now strong molecular evidence for rapid evolution of some of them via *in situ* hybridization between non-endemic taxa. Others are probably pre-glacial poly-

ploids, which immigrated postglacially or survived *in situ*. Some taxa have originated via divergent evolution at a single polyploid level, possibly promoted by rapid genetic drift in mainly self-fertilizing, fixed-heterozygous progenitors with small effective population sizes.

We conclude that the contemporary North Atlantic biota essentially were formed after immigration following the retreat of the massive Weichselian ice sheets. It is possible that some ice-free areas, such as the extensive ice-free uplands in Greenland, have supported survival of some hardy plants (e.g., *Saxifraga oppositifolia*) and animals throughout the entire Weichselian, but we found no definite evidence for this hypothesis. More studies are clearly needed of highly disjunct and hardy species such as the “east-” and “west-Arctic” ones, including contemporary populations in proposed nunatak areas. In particular, more molecular work should be carried out for species with good fossil records. So far, the evidence accumulated since Áskell and Doris Löve edited their book in 1963 suggests that endemism and disjunctions in the North Atlantic can be explained without invoking *in situ* glacial survival. However, as pointed out by Berg (1963), each species has its own unique history and represents a problem *per se*. Thus, in a strict sense, there is not one single nunatak hypothesis versus one single *tabula rasa* hypothesis to test in future work, but numerous—one for each species.

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Appendix. North boreal, alpine and arctic vascular plant taxa proposed as endemic to the glaciated parts of the North Atlantic area but rejected as such in this paper. The list includes only a selection of the very numerous taxa proposed as endemic; we have included taxa that recently or frequently have been cited as endemic in the literature. Most of the numerous taxa described and considered as endemic for Iceland by Á. & D. Löve in several papers and floras (e.g., Löve, 1970) are omitted. *Geographic regions*: GW - Greenland, West and South (SE to Lindenowfjord); GE - Greenland, East (N of Lindenowfjord); Sb - Svalbard including Bear Island and Franz Josef Land; NZ - Novaya Zemlya (excl. Vaigach); Ic - Iceland; Fa - The Faroes; BI - Northern British Isles; SS - Scandes, southern part; NF - Fennoscandia, northern part including the Kola Peninsula. *Main reasons for exclusion* (“Ex”): A - Part of actively evolving agamosperous hybrid complexes with unclear delimitation of taxa or with very numerous taxa; B - The taxon is verified to or strongly suspected to occur also outside the relevant geographic area; C - Part of intricate, insufficiently analysed species complex and may therefore also occur outside the relevant geographic area; D - Rejected as distinct taxon in this paper or in the Panarctic Flora Checklist (Elven & al., 2003), in many cases already published as conspecific with other taxa in the literature.

Taxon	Geographic region(s)									Ex	Comment
	GW	GE	Sb	NZ	Ic	Fa	BI	SS	NF		
<i>Alchemilla</i> sect. <i>Vulgares</i> agspp.	GW	GE	Sb	-	Ic	Fa	BI	SS	NF	A	Numerous endemic agamospecies.
<i>Arnica angustifolia</i> Vahl ssp. <i>alpina</i> (L.) I.K. Ferguson	-	-	-	-	-	-	-	-	NF	A	Agamotaxon, part of circumpolar aggregate where the taxa are dubious.
<i>Athyrium flexile</i> (Newm.) Druce	-	-	-	-	-	-	BI	-	-	D	Stace (1997): “Possibly a change combination of characters rather than a taxon”.
<i>Atriplex longipes</i> Drejer ssp. <i>praecox</i> (Hülph.) Turesson	GW	-	-	-	Ic	-	BI	SS	NF	B	Probably also in NE Canada (Gustafsson in Jonsell, 2001).
<i>Betula pubescens</i> Ehrh. ssp. <i>tortuosa</i> (Ledeb.) Nyman	-	-	-	-	Ic	-	BI	SS	NF	B	Also in N and C Asia (“ <i>tortuosa</i> ” typified from Altai).
<i>Calamagrostis hyperborea</i> Lange	GW	?	-	-	-	-	-	-	-	AB	Conspecific with the agamosperous N American <i>C. inexpansa</i> A. Gray (Greene, 1980).
<i>Calamagrostis lapponica</i> (Wahlenb.) Hartm. var. <i>groenlandica</i> Lange	GW	-	-	-	-	-	-	-	-	AB	Included in the agamosperous, circumpolar <i>C. lapponica</i> (Greene, 1980).
<i>Calamagrostis poluninii</i> T.J. Sørensen	GW	?	-	-	-	-	-	-	-	AB	Merged with <i>C. purpurascens</i> R. Br. var. <i>laricina</i> Louis-Marie (Greene, 1980) as an E American-Greenland subspecies.
<i>Calamagrostis scotica</i> (Druce) Druce	-	-	-	-	-	-	BI	-	-	D	Stace (1997): “Perhaps an introgressed variant of it [<i>C. stricta</i>]”.
<i>Carex brunnescens</i> (Pers.) Poir. ssp. <i>vitis</i> (Fr.) Kalela	-	-	-	-	-	-	-	SS	NF	B	Probably also in NE Russia and perhaps in NW Siberia.
<i>Carex halophila</i> F. Nyl.	-	-	-	-	-	-	-	-	NF	BD	Part of the <i>C. recta</i> hybrid complex, probably also occurring in NE Russia and NE Canada (Cayouette & Morisset, 1985).
<i>Carex nardina</i> Fr. ssp. <i>nardina</i>	?	?	-	-	Ic	-	-	-	NF	B	Probably overlooked in N America and Greenland (Murray in Flora of North America, in press).
<i>Carex rufoa</i> Drejer	GW	GE	-	-	Ic	-	-	SS	NF	B	Also documented from NE Canada.
<i>Cerastium fontanum</i> Baumg. ssp. <i>scandicum</i> Gartner	GW	-	-	-	Ic	-	-	SS	NF	BD	Conspecific with the widespread <i>C. fontanum</i> ssp. <i>fontanum</i> , see e.g., Nilsson in Jonsell (2001).
<i>Cerastium fontanum</i> Baumg. ssp. <i>scoticum</i> Jalas & P.D. Sell	-	-	-	-	-	-	BI	-	-	C	Not properly compared with other taxa, probably doubtful
<i>Cotoneaster antoninae</i> Juz.	-	-	-	-	-	-	-	-	NF	A	Agamosperous local hybrid (<i>C. cinnabarinus</i> × <i>C. niger</i>).
<i>Dactylorhiza lapponica</i> (Laest. ex Hartm.) Soó	-	-	-	-	-	-	BI	SS	NF	B	Conspecific with C European plants.
<i>Dactylorhiza maculata</i> (L.) Soó ssp. <i>islandica</i> (Á. Löve & D. Löve) Soó	-	-	-	-	Ic	-	-	-	-	D	Excluded because of the polymorphy (still unanalyzed) throughout the range of the species.
<i>Deschampsia cespitosa</i> (L.) P. Beauv. ssp. <i>glauca</i> (Hartm.) Hartm.	-	-	-	-	-	-	-	SS	NF	B	Probably overlooked or named differently in NE Russia.
<i>Diphasiastrum complanatum</i> (L.) Holub ssp. <i>montellii</i> (Kukkonen) Kukkonen	-	-	-	-	-	-	-	SS	NF	B	Overlooked and named differently in Russia-Siberia, probably also in N America and Greenland.
<i>Epilobium laestadii</i> Kytö.	-	-	-	-	-	-	-	SS	NF	B	Russian material not investigated; recently described species.
<i>Euphrasia lapponica</i> Th.C.E. Fr.	-	-	-	-	-	-	-	SS	NF	D	Conspecific with the more widespread <i>E. salisburgensis</i> Funck (Elven, 1994).
<i>Euphrasia</i> spp.	-	-	-	-	-	-	BI	-	-	C	Six species accepted by Stace (1997): <i>E. campbelliae</i> Pugsley, <i>E. foulaensis</i> F. Towns. ex Wettst., <i>E. heslop-harrisonii</i> Pugsley, <i>E. ostefeldii</i> (Pugsley) Yeo, <i>E. marshallii</i> Pugsley, and <i>E. rotundifolia</i> Pugsley. Stace expresses, however, doubts about some of them; excluded here mainly because this group has not yet been sufficiently analysed.
<i>Festuca vivipara</i> (L.) Sm. ssp. <i>vivipara</i>	-	GE	-	-	Ic	Fa	BI	SS	NF	AB	Also reported eastwards to NW Siberia (Tzvelev, pers. comm.).
<i>Hieracium</i> agspp.	GW	GE	-	-	Ic	Fa	BI	SS	NF	A	About 2000 N European-Greenlandic agamospecies described, in several sections and as cross-section combinations, most of them as endemic.
<i>Juncus alpinoarticulatus</i> Chaix ssp. <i>alpestris</i> (Hartm.) Hämet-Ahti	-	-	-	-	?	-	?	SS	NF	D	Intraspecific taxonomy very confused and doubtful (Brooks & Clemants, 2000).
<i>Juncus gerardii</i> Loisel. ssp. <i>atrofuscus</i> (Rupr.) Printz	-	-	-	-	-	-	-	-	NF	B	Occurs certainly east of Fennoscandia, in NE Russia.
<i>Ledodendron vanhoeffeni</i> (Abrom.) Dalgaard & Fredskild	GW	-	-	-	-	-	-	-	-	D	This is the hybrid <i>Ledum palustre</i> ssp. <i>decumbens</i> × <i>Rhododendron lapponicum</i> Dalgaard & Fredskild (1993): “All plants are completely seed sterile, containing aborted seeds only”. Also found to be almost completely pollen sterile.
<i>Lotus corniculatus</i> L. var. <i>borealis</i> Hyl.	-	-	-	-	-	-	-	SS	NF	C	Not sufficiently compared with, e.g., taxa in the European Alps.
<i>Oxytropis campestris</i> (L.) DC. ssp. <i>scotica</i> Jalas	-	-	-	-	-	-	BI	SS	-	C	Not accepted by Stace (1997) for Scotland (the type region).

Appendix (continued).

Taxon	Geographic region(s)								Ex	Comment	
	GW	GE	Sb	NZ	Ic	Fa	BI	SS			NF
<i>Papaver radiculatum</i> Rottb., various subspecies	-	-	-	-	Ic	Fa	-	SS	NF	D	Thirteen Nordic subspecies accepted by Nilsson in Jonsell (2001). With one exception (the octoploid ssp. <i>laestadianum</i>), these subspecies were considered by Solstad & al. (1999, in press) based on genetic data as taxonomically insignificant, with their minor morphological differences probably resulting from recent genetic drift in semi-isolated and mainly inbreeding populations.
<i>Pedicularis dasyantha</i> (Trautv.) Hadac	-	-	Sb	NZ	-	-	-	-	-	B	Often stated as a Svalbard - Novaya Zemlya endemic but very similar and probably conspecific (or con-subspecific) with plants in Polar Ural - Yugorskiy Poluostrov and Taimyr.
<i>Pilosella</i> agspp.	-	-	-	-	Ic	-	BI	SS	NF	A	A complex of sexual (non-arctic and non-endemic) species and an overstory of partly and/or fully agamospermous microspecies.
<i>Pinus sylvestris</i> L. ssp. <i>scotica</i> (P.K. Schott) E.F. Warb.	-	-	-	-	-	-	BI	-	-	D	Rejected as distinct taxon in this paper; not fully accepted by Stace (1997).
<i>Poa arctica</i> R. Br., four subspecies	-	-	-	-	-	-	-	SS	NF	A	Taxonomically insignificant marginal populations (two in S Norway, " <i>elongata</i> " and " <i>depauperata</i> ", and two in N Scandinavia, " <i>microglumis</i> " and " <i>tromsensis</i> "; see Nannfeldt, 1940) of a variable circumpolar species.
<i>Potentilla lyngei</i> Jurtz. & Soják ssp. <i>spissa</i> Soják ined.	-	GE	-	-	-	-	-	-	-	CD	Proposed as an endemic subspecies but virtually unknown, perhaps part of a larger Greenlandic - North American complex (cf. Yurtsev, 1984).
<i>Potentilla nubilans</i> Soják ined.	-	GE	-	-	-	-	-	-	-	A	Known from one site only. Stated by Soják and Yurtsev (pers. comm.) to be a hybridogenous species (<i>P. chamissonis</i> × <i>P. hyparctica</i>), but not documented to be more than a primary, or a taxonomically insignificant and agamospermous, hybrid.
<i>Potentilla ranunculus</i> Lange	GW	GE	-	-	-	-	-	-	-	D	Regarded by Soják (pers. comm.) as a synonym for the Cordilleran <i>P. glaucophylla</i> Lehm., which American authors again regard as a synonym for the more widely distributed American <i>P. diversifolia</i> .
<i>Potentilla rubella</i> T.J. Sørensen	GW	-	-	-	-	-	-	-	-	AB	A probably hybridogenous and agamospermous "species" derived from <i>P. hyparctica</i> × <i>P. stipularis</i> , arisen independently in several areas in N and NE Asia.
<i>Potentilla vahliana</i> Lehm.	GW	-	-	-	-	-	-	-	-	B	Proposed by Soják & Yurtsev (pers. comm.) to be a W Greenlandic endemic, but most authors (including us) regard it as conspecific with a N Canadian taxon.
<i>Primula nutans</i> Georgi ssp. <i>finmarchia</i> (Jacq.) Á. Löve & D. Löve	-	-	-	-	-	-	-	-	NF	B	Occurs in NE Russia east of Fennoscandia (Tolmachev & Yurtsev, 1980).
<i>Ranunculus acris</i> L. var. <i>villosus</i> (Drabble) S.M. Coles	-	-	-	-	Ic	Fa	BI	SS	NF	C	Possibly a good endemic NW European taxon (Nurmi in Jonsell, 2001), but part of intricate, insufficiently analysed complex.
<i>Ranunculus auricomus</i> L. (incl. <i>R. monophyllos</i> Ovez.) agspp.	GW	GE	Sb	NZ	Ic	Fa	BI	SS	NF	A	More than 400 described and named N European and Greenlandic agamospecies, most of them endemic. Among them is <i>R. wilanderi</i> (Nath.) Á. & D. Löve from Svalbard, considered as distinct by, e.g., Löve & Löve (1975), but not by Ericsson in Jonsell (2001).
<i>Rumex acetosa</i> L. ssp. <i>islandicus</i> (Á. Löve) Ö. Nilsson	-	-	-	?	Ic	Fa	-	?	?	C	Considered by Nilsson in Jonsell (2001) as endemic to Iceland and the Faroes, but similar plants occur in several other northern areas.
<i>Rumex acetosella</i> L. ssp. <i>arenicola</i> Y. Mäkinen ex Elven	GW	GE	-	?	Ic	-	-	SS	NF	B	Overlooked in other areas, e.g., E Canada.
<i>Sagina boydii</i> F.B. White	-	-	-	-	-	-	BI	-	-	C	A mystery, see also Stace (1997).
<i>Salix myrsinifolia</i> Salisb. ssp. <i>borealis</i> (Fr.) Hyl.	-	-	-	-	-	-	-	SS	NF	B	Not recognized by Skvortsov (1968) in Russia, but probably overlooked.
<i>Salix myrsinifolia</i> Salisb. ssp. <i>kolaensis</i> (Schljakov) Elven	-	-	-	-	-	-	-	SS	NF	B	Not recognized by Skvortsov (1968) in Russia, but probably overlooked east of the Kola Peninsula.
<i>Saxifraga paniculata</i> Mill. ssp. <i>laestadii</i> (Neum.) Karlsson	-	-	-	-	-	-	-	-	NF	D	Excluded because of the polymorphy (still unanalysed) throughout the range of the species
<i>Saxifraga stellaris</i> L. ssp. <i>stellaris</i>	GW	GE	-	-	Ic	Fa	BI	SS	NF	B	Occurs also in NE Canada.
<i>Stellaria longipes</i> Goldie var. <i>humilis</i> Fenzl	-	-	-	-	-	-	-	SS	-	C	Taxonomically insignificant; marginal and isolated populations of the very polymorphic arctic circumpolar <i>S. longipes</i> s. lat.
<i>Stellaria femica</i> (Murb.) Perfil.	-	-	-	-	-	-	-	-	NF	B	Now documented (Elven & al., 2003) also from NE Russia and NW Siberia.
<i>Taraxacum</i> agspp.	GW	GE	Sb	NZ	Ic	Fa	BI	SS	NF	A	400–500 agamospecies described from the relevant area, most of them as endemic, in several sections. One species in sect. <i>Arctica</i> accepted (Table 1), and there are some putative endemics in sect. <i>Borealia</i> that may be acceptable after a thorough analysis. The majority of taxa are in sect. <i>Spectabilia</i> (with c. 100 species described from Iceland alone) and sect. <i>Taraxacum</i> (sect. <i>Ruderalia</i> , with several hundred).
<i>Thalictrum simplex</i> L. ssp. <i>boreale</i> (F. Nyl.) Á. Löve & D. Löve	-	-	-	-	-	-	-	SS	NF	B	The materials from NE Russia, east of N Fennoscandia, have recently been identified by O. Rebristaya (pers. comm.) as ssp. <i>boreale</i> .
<i>Urtica dioica</i> L. ssp. <i>sondenii</i> (Simmons) Hyl.	-	-	-	-	-	-	-	SS	NF	B	Overlooked in NE Russia and Siberia, and perhaps in NW North America.