Neo-polyploids in the North Atlantic region

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Abstract

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The taxonomic delimitation and distribution of three polyploid taxa endemic to the North Atlantic region are discussed: *Arenaria ciliata* L. ssp. *norvegica* (Gunn.) Fries, *Poa flexuosa* Sm. and *Papaver radicatum* Rottb. Their evolution is viewed in relation to presumed progenitors with lower chromosome number in adjacent regions, and to the geological history of the North Atlantic region.

The North Atlantic Arctic areas, situated between Eurasia and North America including Greenland, are of biogeographical significance in relation to Tertiary and Pleistocene plant evolution. Extending over several latitudinal and climatic zones (Alexandrova 1970), the Atlantic Arctic sector shows patterns of polyploid differentiation in various genera.

The present work deals with *Arenaria ciliata* ssp. *norvegica, Poa flexuosa,* and *Papaver radicatum*, all of which are endemic to the region.

The *Arenaria ciliata* L. group of taxa

The polyploid complex *Arenaria ciliata* L. has a disjunct distribution in Europe. The distribution of the Southern European taxa is shown by Favarger (1960, 1963, 1965, 1967), and of the taxa occurring further North on the present map (Fig. 1).

The concept of species and subspecies follows the practice introduced for polyploid complexes in Flora Europaea (Heywood 1960, p. 199). The nomenclature follows Favarger (1963), Nordhagen (1935), and Ostenfeld & Dahl (1917), differing in some respects from Hess et al. (1967, p 822–823) and Chater et al. (1964, p. 120).

Nordhagen (1935) enumerates the following subspecies of *A. ciliata* from Northern Europe and the Alps:

1. *hibernica* Ostenf. & Dahl, Sligo, Ireland
2. *norvegica* (Gunn.) Fries, Iceland, Scotland, Scandinavia
3. *pseudofrigida* Ostenf. & Dahl, High-Arctic areas (Fig. 2)
4. *tenella* (Kit.) Br.-Bl., Central and Eastern Alps
5. *moehringioides* J. Murr., Central European mountains (western areas)
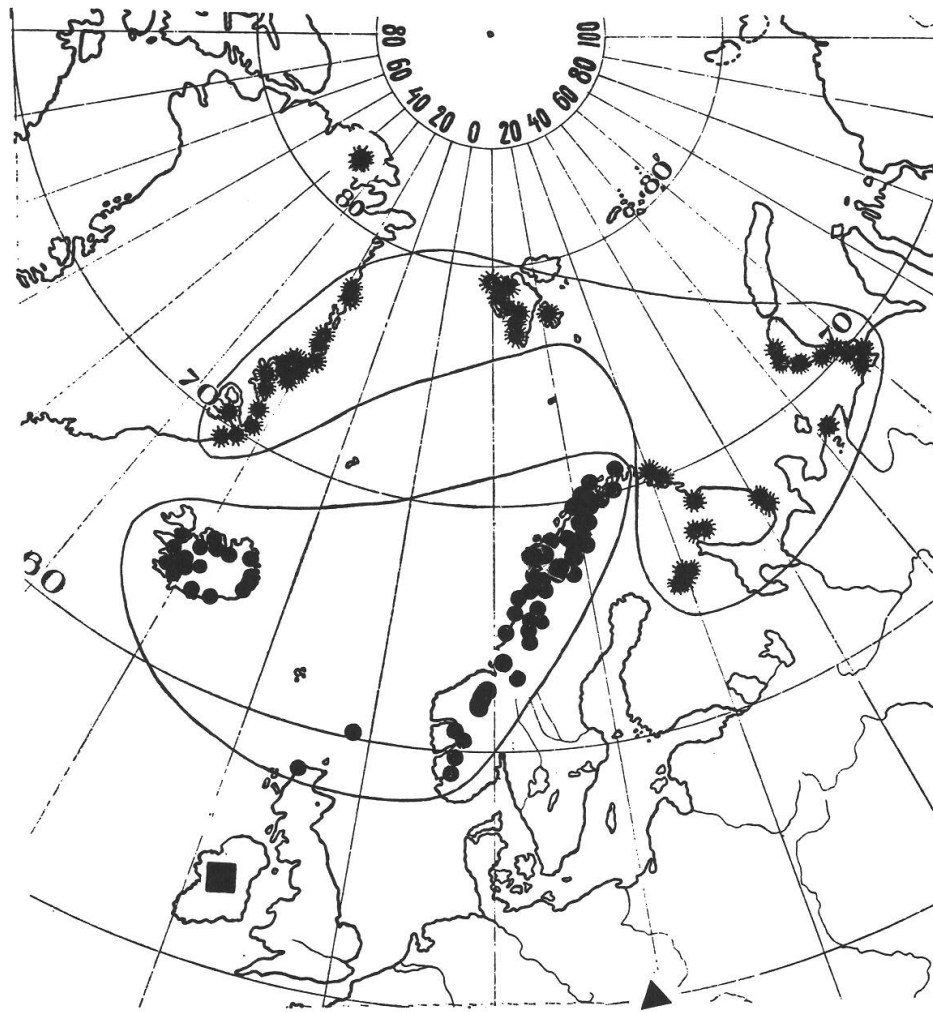6. *polycarpoides* (Roy & Fouc.) Br.-Bl., Pyrenees

Fig. 1. The distribution of the North European subspecies of *Arenaria ciliata* L. *: ssp. *pseudo-frigida* (2 n = 40). – ▲: ssp. *tatrensis* (2 n = 40). – ■: *ssp. hibernica* (2 n = 40). – ●: ssp. *norvegica* (2 n = 80). – Updated after Nordhagen (1951).

Nordhagen (1940, 1951, 1970) and Butcher (1961) retain *A. norvegica* as a species, described from Norway by Gunnerus (Fl. Norv. 1773). Its chromosome number 2n = 80 has been reported repeatedly (Engelskjøn 1979, p. 17). Some authors give the rank of species also to *pseudofrigida* (Lid 1985, Rønning 1979). The subspecies no.5 and 6 in the enumeration above are now included in the diploid species *A. moehringioides* J. Murr. (*A. multicaulis* L. in Hess et al. op. cit.). Favarger (1963, p. 16) treats *tenella* as the nominal subspecies *A. ciliata* ssp. *ciliata*.

According to Favarger, the three cytotypes with 2 n = 80, 120, and 160, respectively, cannot be distinguished morphologically and are included in ssp. *ciliata*. However, they occupy separate areas in the Central and Eastern Alps.

Favarger (op. cit.) also discusses ssp. *tatrensis* (Zapal.) Favarger which has 2 n = 40 and ssp. *bernensis* Favarger with 2 n = 200 and 220. Zapalowics (1911) described *tatrensis* as a subspecies of *A. multicaulis*, cf. Ascherson & Graebner (1919, p. 508). Its ob-
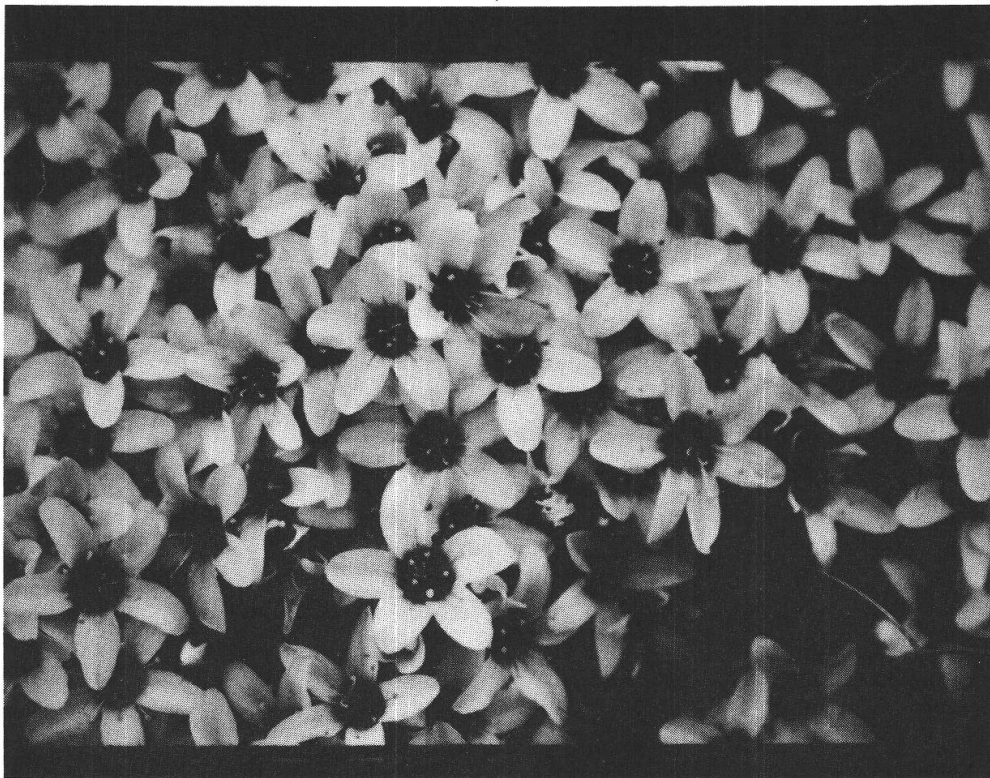
Fig. 2. *Arenaria ciliata* ssp. *pseudofrigida*. Svalbard, Spitsbergen, Ny-Ålesund. – Viktor Johansen
phot.

ovoid leaves are small, somewhat blunt, and ciliate below, and it differs from the Alpine ssp. *ciliata* in having smaller petals and seeds.

The following key is translated from Ostenfeld & Dahl (1917):

1. Stems and pedicels scabrous. Leaves obovoid, conspicuously ciliate. Petals twice the length of sepals.

   a. Leaves ciliate at least for half the length of the margin. Sepals with short hairs on the surface.   ssp. *hibernica*

   b. Leaves ciliate in the lower half of the margin. Sepals not hairy on the surface.
                                          ssp. *pseudofrigida*

2. Stems and pedicels less scabrous. Leaves ovate with few cilia below, or not ciliate, but usually with a few hairs on the margin of the short, broad petioles. Petals less than twice as long as the sepals.   ssp. *norvegica*

Ostenfeld & Dahl (op. cit.) do not give a differential diagnosis for separating these subspecies from *tenella* (ssp. *ciliata*). They only state that var. *frigida* of ssp. *tenella* differs from the Arctic *pseudofrigida* by shorter pedicels, more extended stems, more conspicuous nerves of the leaves and sepals, and more acute leaves.

Ecology

Favarger (1967) did not find morphological or ecological distinctions between the three Alpine cytotypes of ssp. *ciliata*, $2n = 80$, 120, and 160, respectively. Ssp. *ciliata* and ssp. *norvegica* are rather different in external habit and differ in geographical dis-
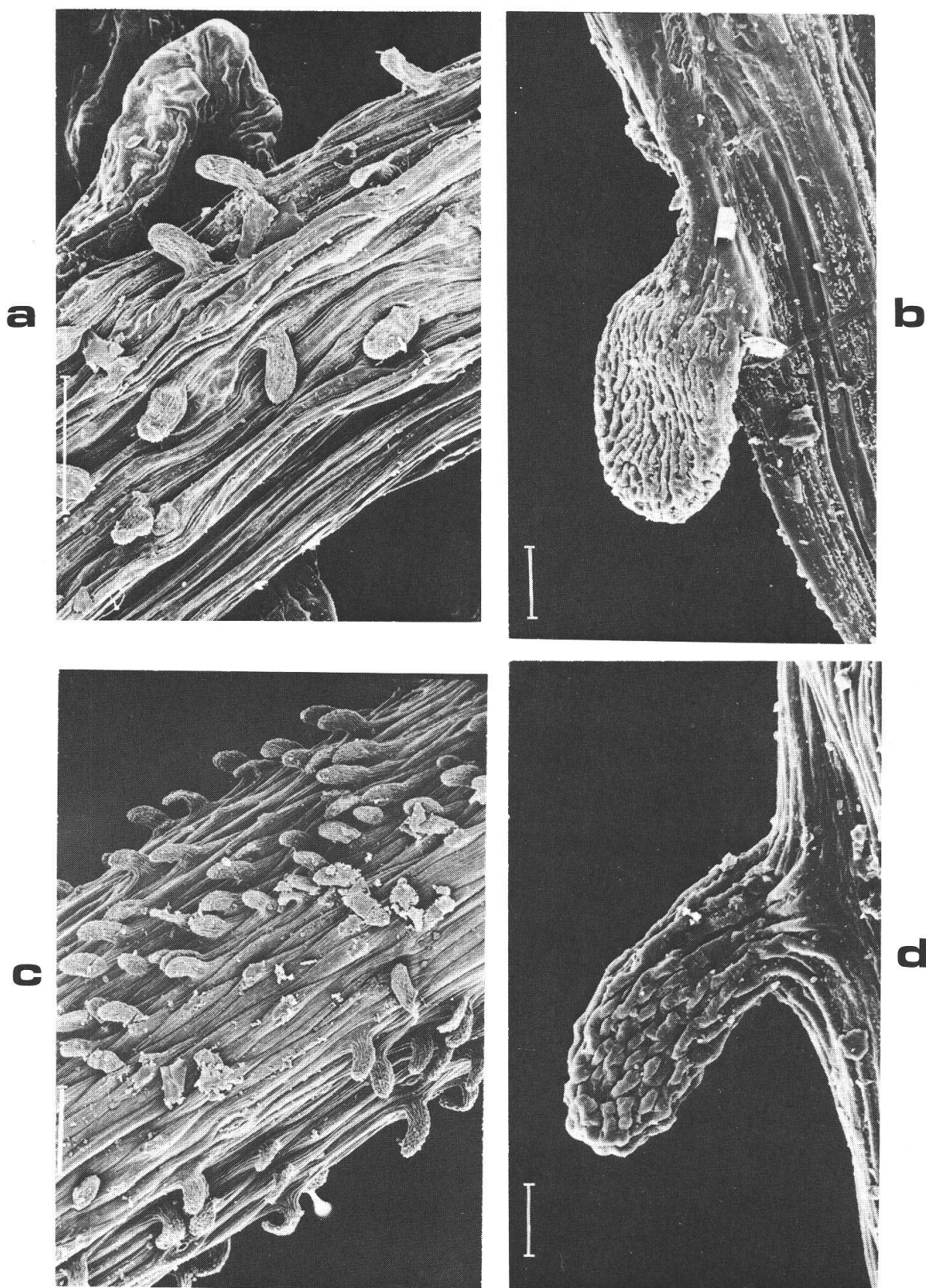
Fig. 3. *Arenaria ciliata* L. SEM pictures of hairy pedicels. a, b: ssp. *norvegica,* Southern Norway,
Opl. Vågå, between Daldokka and Øyaseter, gravelly river bank. Aug. 1951. R. Nordhagen leg.
(O). Scales 0.01 mm. – c, d. ssp. *ciliata,* voucher specimen of cytotype with 2 n = 80 (J. Bot. Neuch.
57–1040). He. Canton du Valais au pieds du mt. Gauthier, 2400 m. Juillet 1957. C. Favarger leg.
Scales 0.01 mm. E. Braaten phot.
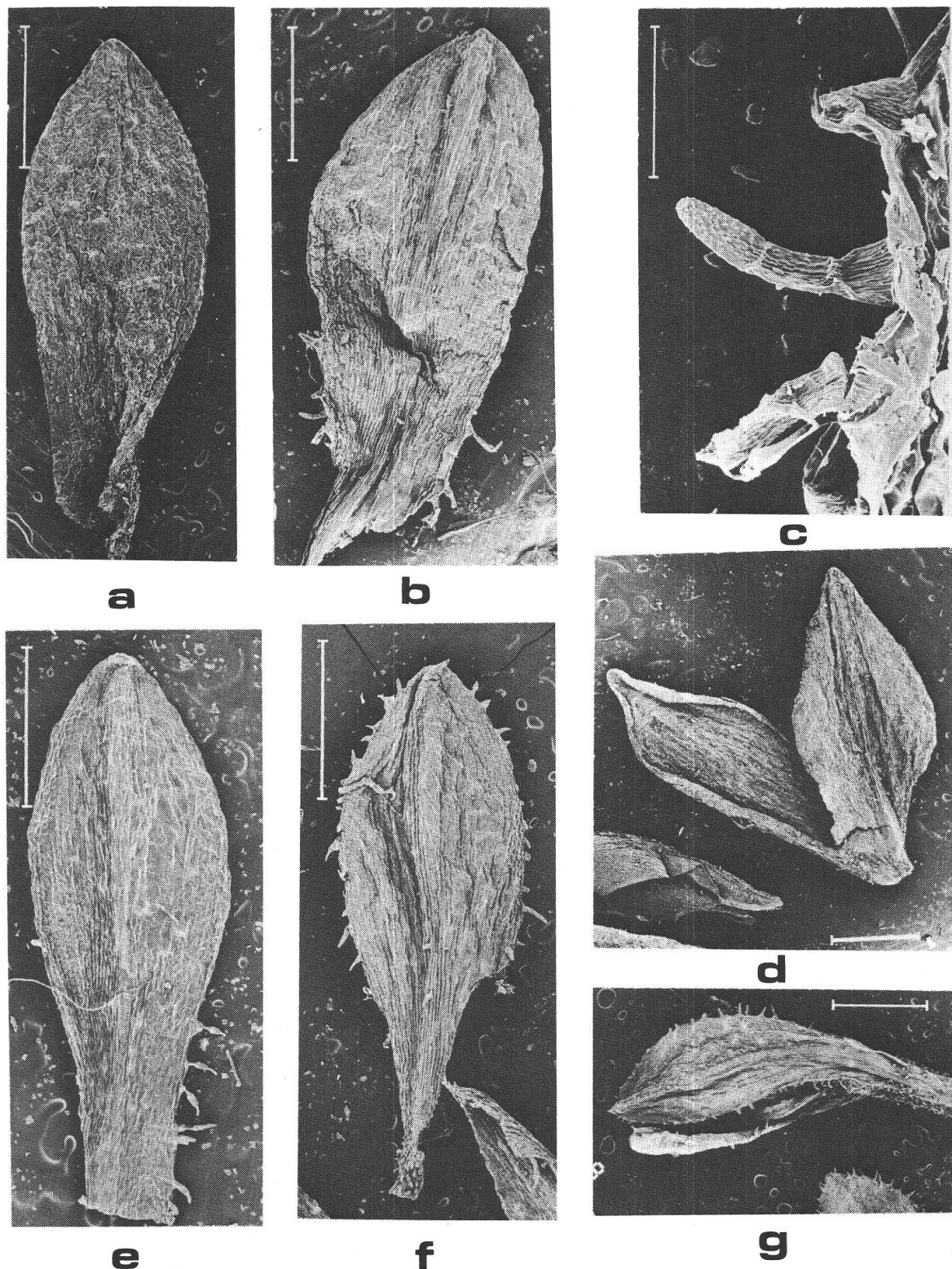
Fig. 4. a, b, c, and d: *Arenaria ciliata* ssp. *norvegica*. Southern Norway (loc. mentioned under Fig. 3a, b). a, b, and d: Leaves of the stem. – c: cilia of the margin of a leaf. – e, f, and g: ssp. *ciliata*. Leaves of the stem of voucher specimen of cytotype with 2 n = 80. e: He. Canton du Valais, Riffelberg, 2600 m. 23. 8. 1959. E. Senaud leg. (J. Bot. Neu. 59–1959). – f and g: He. Canton du Valais (No. and loc. cited under Fig. 3c, d). SEM pictures, E. Braaten phot. a–f and d–g: scales 1 mm. – c: scales: 0.1 mm.

tribution. From an ecological point of view, there is more resemblance between the diploid *A. moehringioides* and *A. ciliata* ssp. *norvegica* than between ssp. *ciliata* and ssp. *norvegica*. The former grow at low altitudes and are both calcicole, whereas ssp. *ciliata* occurs in granite massifs of the Alps (cf. Lunde 1962, Favarger 1963). In the Western Alps, however, ssp. *ciliata* descends to the subalpine belt (Favarger op. cit.).

A comparison between ssp. ciliata, the cytotype with 2 n = 80, and ssp. norvegica

The material of ssp. *ciliata* studied includes the voucher specimens on loan by courtesy of Professor C. Favarger and the Botanical Institute of the University of Neuchâtel. The plant material of ssp. *norvegica* belongs to Herb. O. Figs. 3 and 4 show SEM pictures of the two taxa. They vary in quantitative characters which are difficult to measure.

The two subspecies agree with the following specific diagnosis: Perennial herbs with leafy vegetative and flowering stems, not rooting at the nodes. Flowers pedicellate, pedicels longer than the sepals. Leaves entire, ovate-spathulate, somewhat fleshy in living plants. Hairs and cilia of the same kind. Stems and pedicels described as scabrous with downward-directed hairs. The character distinguishing them is the variation in pubescence of sepals and leaves. In ssp. *norvegica* the sepals are glabrous or with a few hairs on the surface. In ssp. *ciliata* the sepals are occasionally glabrous, as in *norvegica,* but are usually hairy.

The chief character separating ssp. *ciliata* from ssp. *norvegica* is the following:
Leaves glabrous or slightly ciliate at the margin:
1. Leaves ciliate on 1/4–2/3 of the margin or along the whole margin: ssp. *ciliata*
2. Leaves ciliate for not more than 1/3 of the margin or only with a few cilia at the base
   of the short and broad petiole: ssp. *norvegica*

According to Ascherson & Graebner (1919, p. 504) there is some variation in ssp. *ciliata*: they mention two forms of *tenella,* now ssp. *ciliata,* called f. *frigida* and f. *glabrata.* The latter, from Tal des Glenners at 2700 m, in Graubünden, Switzerland, is characterized only by leaves without cilia.

A common characteristic mentioned by Ascherson & Graebner is that "in den Achseln der am Grunde schwach verbundenen Blattpaare ein wenig-blätteriger, oft nur auf 2 kleine Blätter beschränkter Kurztrieb entspringend". A pair of such small leaves is seen on the stem in the SEM photographs (Figs. 4 d & g). They are densely ciliate, the leaves on the stems having ciliate margins.

Species related to the Arenaria ciliata group

A. gothica Fries (2 n = 100, K. Horn in Nordhagen 1951) was described from Southern Sweden as growing on moist limestone and gravel. Plants on gravelly shores of Lac de Joux in the Swiss Jura, and from limestone depressions and tracks in Yorkshire, England, are recorded under this name. Duckert-Henriod (1962) found 2 n = 100 ± 2 in the Swiss population. When Halliday (1958, 1960) found 2 n = 80 in the Yorkshire population, he treated it as a subspecies with the new name *A. norvegica* Gunn. ssp. *anglica* Halliday. However, from morphological analyses of herbarium specimens (O) Dr. Sverre Løkken (personal communication) found that *gothica* auct. angl. differs from *norvegica,* as did Butcher (1961). The two taxa differ as to life form: *A. gothica* is annual or biennial, whereas *norvegica* is perennial. Halliday described the English population as being short-lived in the natural habitats, with a single or occasionally two flowering seasons. As a rule they are very floriferous, but vegetative shoots are rare.

Nordhagen (op. cit.) separates the perennial, more robust plants of *norvegica* from the lax plants of *gothica* by their life forms. In Gotland, *A. gothica* is a summer annual, but in mild winters a few individuals live through the winter and continue to flower in spring. They fade after fruit setting.

A comparison of the life form of the polyploid *A. gothica* and the amphidiploid *Saxifraga osloënsis* Knaben (2 n = 44) is interesting. One ancestor, *S. adscendens* L. (2 n = 22), a mountain plant, is biennial. Its first summer leaf rosettes flower after winter dormancy and fade after fruit setting. When refrigerated at temperatures below zero, the rosettes are induced to flower.

The other ancestor, *S. tridactylites* L. (2 n = 22), a lowland plant, is a winter annual, but, when sown in spring, behaves as a summer annual.

Observations in the Oslo area show that *S. osloënsis* varies. It grows often side by side with *S. tridactylites* and behaves as a winter annual. In mild autumns, however, the rosettes develop flower buds before winter dormancy. In moist localities a few individuals do not fade after the first fruit setting. Late in the summer the cyme develops axillary flowers. All three species are hapaxanths, developing a single cyme. In life form *S. osloënsis* is intermediate between its two ancestors (Knaben 1954, 1961).

The life form of the polyploid *A. gothica* resembles that of *S. osloënsis.* This polyploid species may also originate from ancestors with different life forms, annual or biennial. The relationship of *A. gothica* to the *A. ciliata* complex seems questionable. Hess et al. (op. cit. p. 822) hold: „Ob die Pflanzen beider Herkünfte wirklich identisch sind, muß allerdings zytogenetisch geklärt werden. Eine voneinander unabhängige Entstehung erscheint wahrscheinlicher."

A species often discussed in relation to the *A. ciliata* group, *A. humifusa* Wg., is a distinct Greenland-American element in the North Scandinavian and Spitsbergen flora. The correct chromosome number is found to be 2 n = 44 (Engelskjøn 1979, cf. also Jørgensen et al. 1958).

Poa flexuosa Sm. (*P. laxa* Haenke ssp. *flexuosa* (Sm.) Hyl.)

P. flexuosa Smith (Fl. Brit. I, 1800) was described from Scotland. Nannfeldt (1935) studied the *P. laxa* group and showed that the strains from Scandinavia, Iceland, and Scotland are of the same taxonomic entity. Nygren (1950, 1955) focused interest on chromosome numbers and embryology. Other species in the *P. laxa* group are *P. minor* Gaud. from the Central Alps, *P. nyaradiana* Nannf. from the Transsylvanian Alps, and *P. fernaldiana* from Quebec and Newfoundland. *P. flexuosa* has the widest distribution round the North Atlantic (Fig. 5). A locality in Western Greenland: Jenssen's Nunatakker, has been included according to Gjærevoll et al. (1977).

The hexaploid number (2 n = 42) was found in Scandinavian, Icelandic, and Scottish populations of *P. flexuosa* (Nygren 1955, Clapham et al. 1962, Vestre in Engelskjøn 1979). *P. laxa* s. str. has 2 n = 28 in the Alps (Nygren op. cit.) but also triploids were found, indicating the presence of diploid strains.

Nygren found that meiosis is normal in *P. minor* and *P. laxa*, with the formation of 14 bivalents and regular distribution of 14–14 during metaphase I and anaphase I, respectively. He also found a regular pollen morphology.

Hexaploid *P. fernaldiana* is reminiscent of *P. flexuosa* as regards meiosis, differing in only one respect. In *P. flexuosa*, only bivalents and a small number of univalents were found, while in *P. fernaldiana* some PMC's also had one or two tetravalents. In *P.*
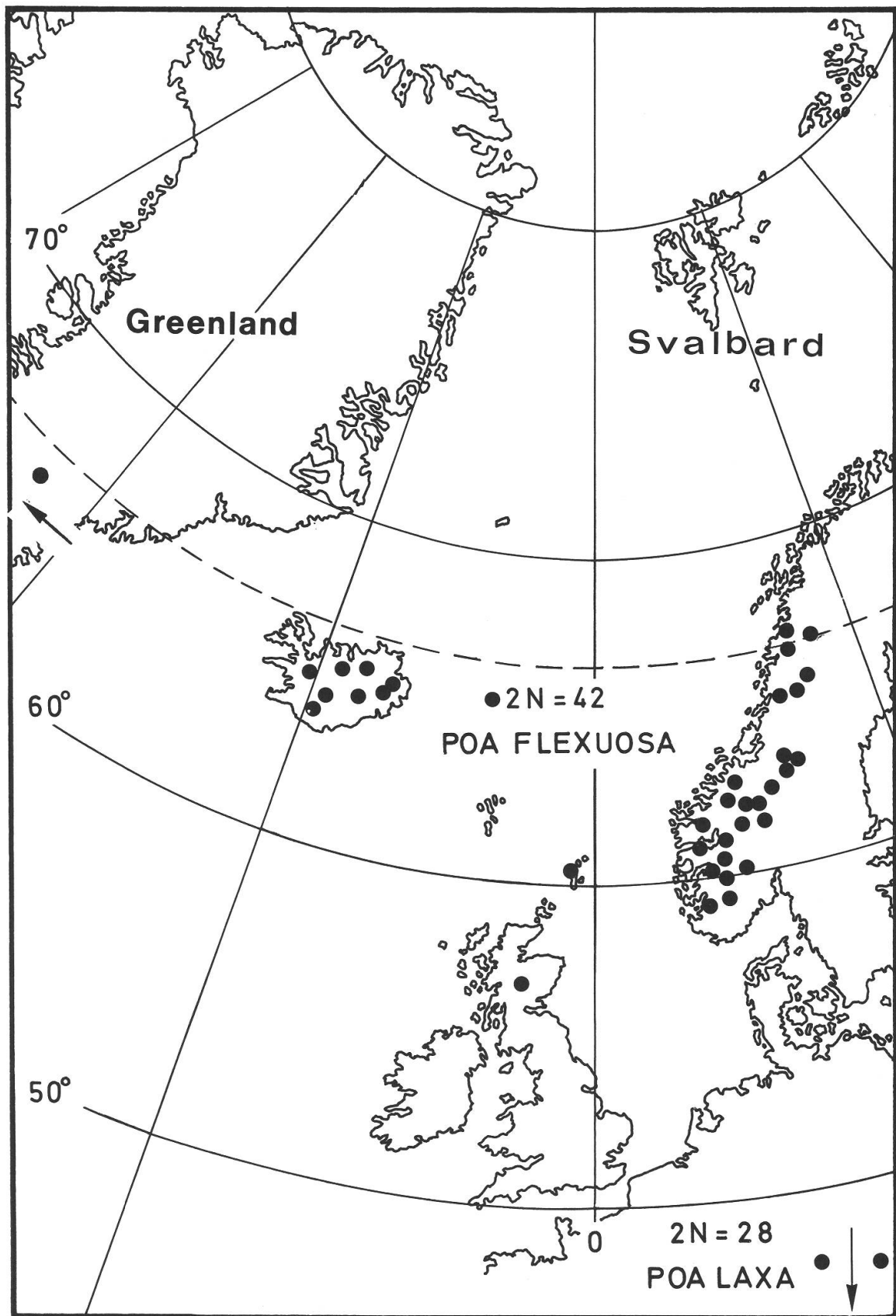
Fig. 5. Distribution map of *Poa flexuosa* Smith and *P. laxa* Haenke.

flexuosa, 110 PMC's were analysed from three different strains, while in *P. fernaldiana* only ten PMC's could be completely analysed. In *P. fernaldiana,* 62.2% of morphologically well preserved pollen was found as compared to 48% in *P. flexuosa* (from a total of 47 plants tested).

Development of the EMC follows the same scheme (Nygren op. cit.) in all four species. The two hexaploid species also have high seed setting and normal sexual reproduction, not apomictic as in several other *Poa* complexes.

Evolution

The finding in nature of a triploid strain of *Poa laxa* shows that natural diploids probably occur. The meiotic irregularities in the hexaploid *P. fernaldiana* and *P. flexuosa* agree with an autoploid origin, although we know that not quite "successful" amphidiploids may show meiotic irregularities of the same kind. However, both *P. flexuosa* and *P. fernaldiana* are morphologically closely related to *P. laxa,* and an origin from intraspecific hybridization seems likely.

P. flexuosa occurs on the highest mountains in Scandinavia, ascending to 2300 m in Central Southern Norway (Lid 1985). Its absence from the Arctic proper as well as from most of Northern Norway is noteworthy. The northernmost population in Sørfold, Northern Norway, extends to just north of the Arctic circle. It should be considered whether or not the restriction may be due to short-day photoperiodic adaptation.

Papaver radicatum Rottb.

The *Papaver* species of section *Scapiflora* are the only representatives of the genus in the mountains and Arctic areas of the Northern Hemisphere (Fig. 6).

The *Alpinum* group comprises the taxa in the mountains of Central and Southern Europe and all representatives appear to be diploid with 2 n = 14. The *Nudicaule* group occurs in Eastern Siberia and the Central Asiatic mountains. Here also, 2 n = 14 seems

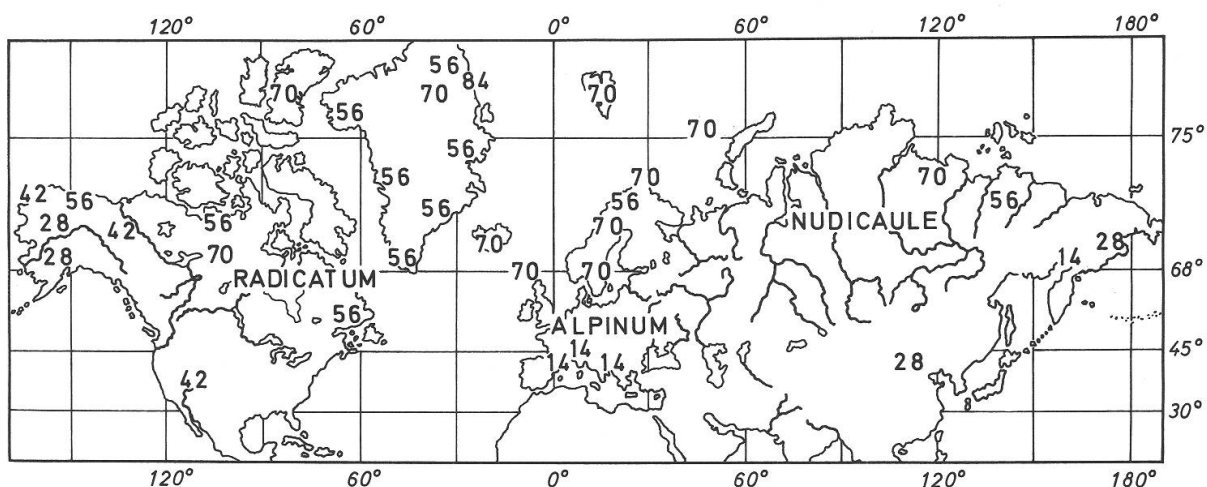Fig. 6. Map of the distribution of the three groups of the Scapiflora *Papaver* species: The Alpinum group, the Nudicaule group, and the Radicatum group. The numbers 14–84 indicate the distribution of the different cytotypes.

to be the prevailing chromosome number, but 2 n = 28 is also recorded, viz. in *P. rubro-aurantiacum* (Fisch.) Lundstr. from Shansi in China (Horn 1938, Knaben 1959). Higher polyploid levels may be present (Mesićek & Sojak 1969). – All *Scapiflora* taxa can be crossed and viable F₁ hybrids obtained. However, the diploid hybrid *P. alpinum coll.* × *nudicaule* displays a very irregular meiosis, indicating major differences in chromosome structure and genetic remoteness (cp. Fabergé 1942, 1943, 1944).

The *Radicatum* group is the only one occurring in Northern Europe and North America. The species of this group display a series of polyploid chromosome numbers, 2 n = 14, 28, 42, 56, 70, and 84 (Fig. 6).

The species with lower chromosome number, *P. macounii* Greene (including *P. alaskanum* Hultén) with 2 n = 28* and *P. hultenii* Knaben with 2 n = 42, are only found in the Western Arctic. In Canada, Greenland, Iceland, and Scandinavia North to Svalbard and in Northern Siberia, only polyploid species with 2 n = 56 and 2 n = 70 are known.

P. lapponicum (Tolm.) Nordh. with 2 n = 56, has possibly a present-day circumpolar distribution, though perhaps is lacking in Eastern Siberia.

My experimental studies (Knaben 1959 a, b, 1979), especially of the *P. radicatum* and the *P. lapponicum* races, include analyses of hybrid specimens raised from intra- and interracial crosses. Population samples of all 14 of the *P. radicatum* races were analysed, and several of the races of *P. lapponicum* from Northern Norway, Greenland, and Canada were cultivated. The cytological study revealed that the large morphological variation in the two polyploid species is correlated with a large degree of differentiation in chromosome structure. As regards the 14 races of *P. radicatum,* comparative studies show that there are more differences in morphology and chromosome structure separating the races than there are differences separating the populations constituting them. Furthermore, the Norwegian races of *P. radicatum* differ between themselves as much as they differ from the Iceland races.

The differentiation into distinct races based on chromosome structure and morphology within both *P. radicatum* and *P. lapponicum* seems to be very old.

During the preparation of the manuscript on the typification of *P. radicatum* Rottb. (Knaben & Hylander 1970), we discussed the most appropriate taxonomic rank of the races – variety or subspecies – and chose the rank of subspecies. The difficulty was that on the basis of distinctive morphology, the three races in Iceland and the three in Scandinavia had previously been given the rank of species, with an additional five subspecies. To change the rank of the races to that of variety would result in confusion (Knaben, review in preparation).

Discussion

The similar distribution of the three polyploid species treated, *Papaver radicatum, Poa fle·uosa,* and *Arenaria ciliata* ssp. *norvegica,* all three endemic in the North Atlantic region, is noteworthy, the more so because their presumed ancestors with lower chromosome numbers still occur in neighbouring territories, some of them in restricted areas, with considerable distances between them.

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* There is a misprint in Knaben (1959 a, p. 22). Line 3 from below in Table 2 reads 2 n = 42. Horn (1938) found 2 n = 28 from St. Paul Inlet.

The occurrences in the areas mentioned, as described in the previous chapters, are known from chromosome counts (Jørgensen et al. 1958, Engelskjøn 1979) and from herbarium studies of material on loan from botanical museums (B, C, O, S).

With regard to *Papaver radicatum* I consider it an amphidiploid derived from the hybrid *P. alpinum* sensu lato × *P. lapponicum,* formed somewhere in the North Atlantic region. It is known that *Scapiflora* species once had a wider distribution in the area than they have today. The studies of the history of the British vegetation (cf. Chandler 1921, Pennington 1963) show that during the last Ice Age *Scapiflora* species, not native in Britain now, belonged to the tundra flora in ice-free areas in Southern England. In glacial deposits from the Weichselian period in the Cam valley, Cambridge, macrofossils (seeds) of a *Scapiflora* species were found in good condition together with macrofossils of other Alpine or Arctic species which do not grow in Britain today, e.g of *Arenaria biflora* and *Potentilla nivalis,* which are now High-Alpine species, of *P. nivea,* Arctic-Alpine, and of *Ranunculus hyperboreus* which is Arctic. The seeds of *Papaver,* found in the Cam deposits, were identified as *P. alpinum.* However, SEM pictures of seeds of species of all three *Scapiflora* groups show that they do not differ in morphology (Knaben unpublished). The seeds in the glacial deposits could just as well belong to a polyploid as to a diploid *Scapiflora* species.

The presumed ancestors of *P. radicatum* today occur in neighbouring territories, the diploid *P. alpinum* in the Alps and the octoploid *P. lapponicum* in Greenland and East of the Norwegian Sea in northernmost Scandinavia.

P. lapponicum, as well as the decaploid *P. keelei* Pors. and *P. dahlianum* Nordh., must in part originate from species with lower chromosome numbers in the Bering Strait area. This area might be named Hultén's centre of evolution of Arctic plant species (cp. Hultén 1937). Migration of *P. lapponicum* must have taken place from the Bering Strait area to the European Arctic, but it is noteworthy that in the High Arctic it occurs only in northernmost Greenland.

The character distinguishing *P. dahlianum* and *P. radicatum* from each other is the morphology of the capsules, which is ovate-elliptic in *P. radicatum,* obovoid in *P. dahlianum.* Usually, the capsules in *P. lapponicum* are obovoid, broadest below the stigma disc. In this respect *P. radicatum* resembles the Alpinum group, in which the capsule is ovate-elliptic. The capsule in the Siberian *P. nudicaule* with $2 n = 14$ is obovoid, indicating that this species and *P. lapponicum* are the progenitors of *P. dahlianum.* The hybrid specimens from the cross *P. dahlianum* × *radicatum* in my experiments display a very irregular meiosis, indicating profound genetic differences and different origin. Their areas are situated in different parts of the Arctic, with different geological history. It is noteworthy that the high-arctic *P. dahlianum* has the same distribution area as *Arenaria ciliata* ssp. *pseudofrigida* (Figs. 1 & 7).

The North European hexaploid *Poa flexuosa* has its presumed ancestors with lower chromosome numbers in the Alps. The third polyploid, *Arenaria ciliata* ssp. *norvegica,* has its possible progenitors in Central Europe, perhaps also in the Alps (*A. moehringioides*). It is difficult to imagine that ssp. *pseudofrigida* is one of its ancestors, because it belongs to a north-eastern flora element, as discussed by Hadač 1963.

Since the symposium on the North Atlantic biota and their history was held in Reykjavík in 1962 (cf. Løve & Løve 1963) new evidence has accumulated on the geological history of the North Atlantic region, from new marine geophysical methods (Eldholm & Thiede 1980, Thiede & Eldholm 1983, Eldholm et al. 1984).
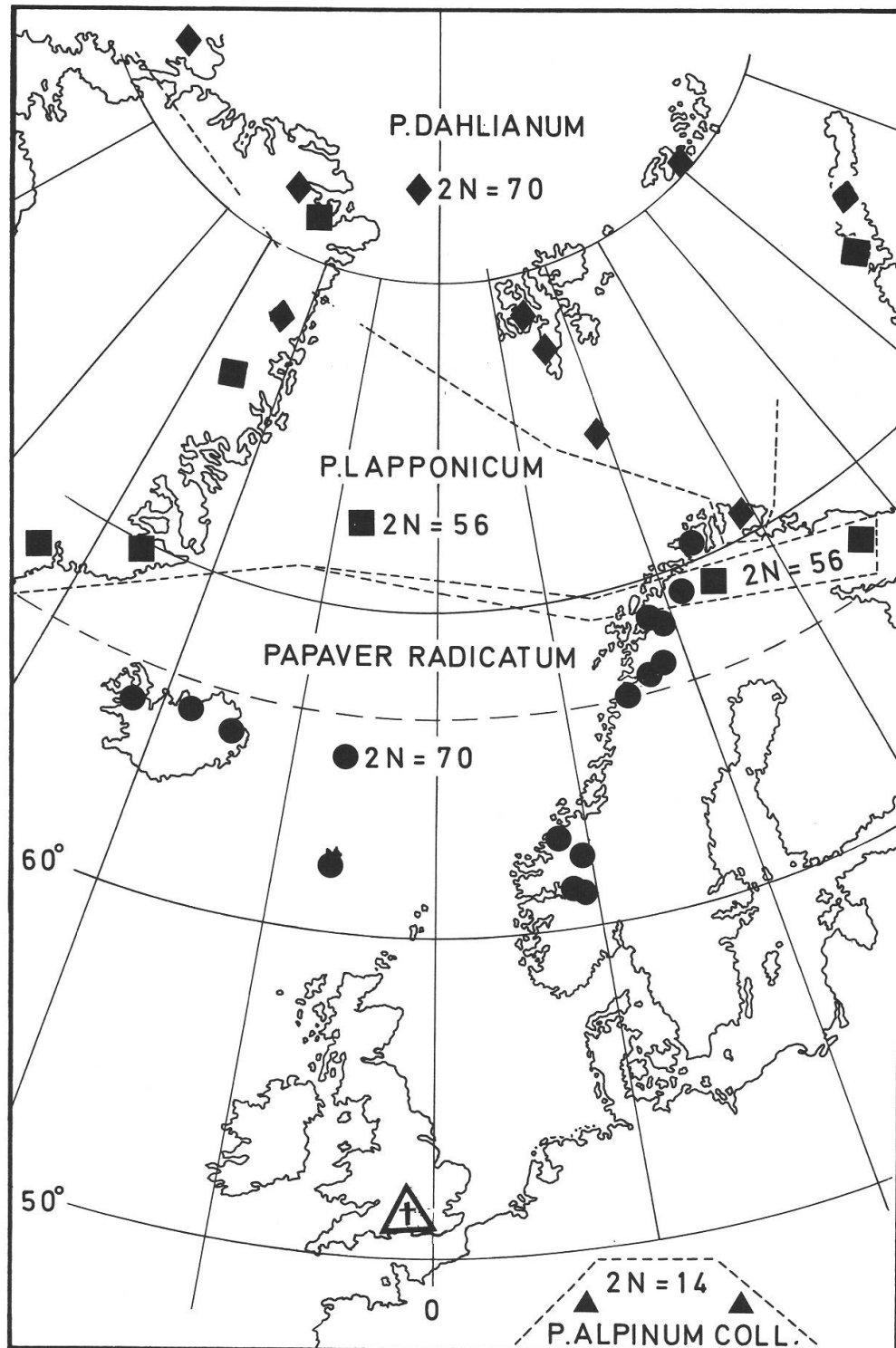
Fig. 7. Map of the distribution of Scapiflora *Papaver* species occurring in Northern Europe and adjacent Greenland.

The areas of the three polyploid species are situated on land which developed during the Tertiary and which was subject to Quaternary glaciations. The opening of the North Atlantic Ocean commenced in the early Tertiary, about 58 Ma, leading to the gradual separation of Europe and Greenland. The plate-tectonic evolution and volcanic events also resulted in the formation of the Greenland-Iceland-Faeroe-Scotland bridge. The Faeroe-Iceland bridge and the Denmark Strait area subsided below sea level during the Miocene. Greenland and Spitsbergen were more closely connected than today, and the Barents Sea area was in part submerged.

The history and development of Iceland is in itself a problem, as this island was continuously built up and eroded by volcanic activity during the Tertiary and Quaternary.

Owing to the gradual temperature decrease from the middle Eocene, the former archipelagoes and marginal areas of the North Atlantic Ocean may have served as evolution centres for polyploid taxa, like the three treated here. The Denmark Strait between Iceland and Greenland appears to be an important phytogeographical boundary, little exchange of biota having taken place during the Quaternary.

Accordingly, we have good reasons for defining a separate North Atlantic phytogeographical element comprising a restricted number of species of Tertiary origin which have undergone subsequent differentiation and area restriction during the Pleistocene glaciations and interglacials. Examples of other polyploid species with similar, restricted distributions are *Carex rufina* Drej. (Hultén 1958), *Primula scandinavica* Bruun, and *P. scotica* Hooker (cf. Knaben 1982).

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