Det Kgl. Danske Videnskabernes Selskab.
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KØBENHAVN
HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL
BIANCO LUNOS BOGTRYKKERI
1927

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I. Introduction.

It has hitherto been generally acknowledged in the field of phytogeography (vide e. g. Warming 1888) that the geographical distribution of cryptogams is worthy of interest, yet up to now it has been greatly neglected. The object of the present essay is therefore to show that a closer study of the geographical distribution of the fungi especially associated with phanerogams, the so-called endophytic micromycetes, is not only of great value for our knowledge of the micromycetes themselves, but also of use in elucidating the migratory methods and paths of the flowering plants to which they are attached. In view of the fact that we are here entering upon a quite new and untried field, I should like to give an outline of that special part of mycogeography on which we are at present engaged, and which we might define as micromycogeography, in order to point out that all the greater fungi, such as *Agaricaceae, Lycoperdaceae, Helvellaceae* etc. are not included, no more than are the *Fungi fimicoli,* which doubtless have a very wide distribution.

It is necessary to divide the material in this way, and we must confine ourselves this time to the micromycetes living on dead or living plants in the arctic regions. Amongst other reasons because these small fungi are gathered together with the phanerogams and can easily be studied from the material brought home.

Micromycogeography, considered within these limits, is closely allied to the science of the geographical distribution of the zoo-cecidia, about which Lagerheim states in several publications (inter alia 1908 p. 340) that it is in fact of great importance in solving the question of the wanderings of the phanerogams in the post-glacial period.

II. The Ecology of Micromycetes.

The geographical distribution of micromycetes — like that of higher plants and animals — depends upon two factors. First, that the local conditions correspond to the particular needs of the species. Next, that its migratory ability and method have permitted it to find its way to the regions suitable to it.

The ecology of micromycetes has been studied very thoroughly as regards those species which affect the cultivated plants of agriculturists and gardeners. We have learnt from it that the demands made by micromycetes on their surroundings in order to thrive, vary greatly. *Phytophthora infestans,* decisively demands very moist air and 16° of heat in order to infect the leaves of potato-plants, moreover, the plants must be fully grown, it never attacks leaves which are still growing. In that respect it is directly opposed to *Sphaerotheca mors-uvae,* which only attacks the leaves and berries of *Ribes* while they are very young. *Oidium quercinum* only attacks leaves and shoots of *Quercus* and *Fagus* in July, the leaves appearing in the spring are hardly attacked at all. Lauritzen (1919) has studied the temperature necessary for the attack of certain parasites. For instance, *Puccinia graminis* does not infect wheat at less than 5° nor at more than 27°, and it prefers 12°. *Ascochyta Fagopyri* attacks *Fagopyrum* best at 15° and

Colletotrichum Lindemuthianum attacks beans at 27° in conjunction with a high degree of moisture. F. KØLPIN RAVN has pointed out (1900 p. 133) that *Helminthosporium teres* attacks *Hordeum sativum* with much greater force at low temperatures (1°—10°) than at higher temperatures, and that it cannot attack barley at all at 20°. DUFRENOY (1918) has studied the ecology of micromycetes with special regard to the height above sea-level of the growing places; he found that *Rhododendron,* for instance, was attacked by *Chrysomyxa Rhododendri* at between 1300 and 1450 m but it was not attacked so long as it grew below 1300 m. *Meum* is not attacked by *Triphragmium echinatum* so long as it grows below 1900 m and several similar cases could be pointed out.

The state of health of the host-plants themselves is a great factor in the attacks of the fungi; healthy, well-grown oaks are but little attacked, but on the weather-beaten, under-nourished oaks on the west side of the oak-woods at Hald near Viborg, and on the small, stunted oaks at Livø in the Limfjord I found an abundance of parasites and half-parasites. Conversely, vigorous leaves of *Poa* are more strongly attacked by *Erysiphe graminis* than older leaves, and the large leaves that develop on the ground-shoots of *Salix* are much more strongly attacked by *Melampsora* than normal leaves. Thus the leaves on suckers of *Populus* are chifly attacked by *Marssonina.*

We need not mention further examples in order to show the high degree in which ecological factors affect the geographical distribution of micromycetes.

The Micromycetes can only thrive where they find the proper conditions and the right host plants, and where the host-plants are susceptible to infection at the time when the parasite is capable of infecting them.

III. Host-plants.

The relations between the host-plants and the endophytic microfungi deserve special mention. Both parasites and saprophytes are connected with one or more quite definite host-plants. With regard to the genuine parasites their limits are on the whole narrower than those of the saprophytes, but both groups are connected with certain species of host-plants. The area of distribution of the fungi is never quite identical with that of the host-plants. Earlier botanical authors have concluded without evidence that host and parasite always travelled together. Axel Blytt is one of the few who has devoted a great deal of research to the conditions leading to the distribution of microfungi. He even classifies all the Norwegian parasitical fungi in exactly the same way as the phanerogams, under arctic, sub-arctic, boreal, sub-boreal, atlantic, sub-atlantic and synanthrope species. As a guide he employs the mode of immigration of the host-plants. He concludes by saying (1896 p. 13, translated): "These considerations lead us to suppose that the distribution of the parasitic fungi is governed by the same laws as those of the phanerogams".

I have arrived at exactly the opposite result. Every thorough examination of a single species shows us that it does not coincide with the distribution of the host-plant. If the endophytic microfungi always accompanied their host-plant, we ought to be able to find in each country all the endophytes known on this host. But this we never can. We need only look up Sydow's *Index Plantarum Hospitum* (Syll. XIII) which contains a list of all the micromycetes found on each individual species of phanerogams, and compare Sydow's statements with the number of species found on the same host at Spitsbergen. We shall then see that it is by no means all micromycetes that follow their host.

We mention at random:

	Spec. known to Sydow	Spec. found at Spitsbergen
On Betula nana	10	1
- Cardamine pratensis	6	1
- Dryas octopetala	20	2
- Eriophorum polystachyum	16	3
- Mertensia maritima	4	1
- Oxyria digyna	10	2
- Papaver radicatum	9	2
- Saxifraga oppositifolia	9	3
- Silene acaulis	8	6

From these figures we might be tempted to draw the conclusion that phanerogams have, generally speaking, a wider geographical distribution than endophytes, but this is by no means the case. We know of many instances to the contrary, e. g. *Cintractia caricis* is found in arctic regions on arctic species of *Carex*, but in Central Europe, on the Alps and in the United States on different species of *Carex* indigenous in these regions.

I. Schröter has also devoted some study to this question (1881 p. 161), he arrives at the result that parasite and host have by no means always the same distribution. And Ed. Fischer expresses the same opinion (1904 p. XXXVI) in these words: "Es ist nun aber im Weiteren sehr interessant zu constatieren, dass es auch Uredineen gibt, die auf allgemein verbreiteten, nicht nordisch-alpinen Wirthen dennoch nicht allgemein vorkommen, sondern auf die Alpen (und andere Gebirge) und den Norden beschränkt sind, also als nordisch-alpine Uredineen bezeichnet werden müssen".

I have myself pointed out that *Berberis vulgaris* is found in many tropical and sub-tropical regions without having been subject to attack by *Aecidium Berberidis* in these countries (1915 p. 752).

IV. The Migratory Methods and Paths of Micromycetes.

The second factor having an influence on the geographical distribution of micromycetes is the purely historical one. Whether they have had time to reach the localities favourable to them by the means and roads of migration at their disposal. We know of many instances amongst phanerogams in which a plant spreads widely and propagates abundantly when it has been brought by human aid to the growing-places favourable to it (e. g. *Matricaria suaveolens*). Exactly the same thing has happened in the case of many parasites, we need only recall the instance of *Phytophthora infestans* which came to Europe in 1844, *Plasmopara viticola* in 1878, *Puccinia Malvacearum* in 1869, *Puccinia Chrysanthemi* in 1895, *Sphaerotheca mors uvae* in 1900, and *Oidium quercinum* in 1907, just as *Cronartium ribicola* was carried from Europe to the United States in 1906. All these species were disseminated by their own means and with incredible rapidity over a very large area as soon as they had been carried across the Atlantic Ocean. Amongst these *Oidium quercinum* is a typical wind-spreader, while *Sphaerotheca mors uvae*, on the other hand, does not scatter its spores at all by means of the wind but only by human and animal agency. The examples given show with sufficient distinctness that many micromycetes have not yet found their way to the growing-places suitable to them.

In the instances mentioned it is the difficulty of getting across the open sea that has been too great for them.

The endophytic fungi are not able to accompany their host-plant when the latter propagates by means of pure seed. There are only extremely few species of *Ustilagineae* (*Ustilago nuda*, *Ustilago Tritici*, etc.) which are able to penetrate right into the seeds of their host-plant. We may safely take it as a general rule that the seeds of phanerogams are free from infection.

As we all know, fungi produce an enormous number of spores, and these can easily be carried at a great height by the wind and be scattered far and wide. But only the fewest species of microfungi can be dispersed in this way, viz., only those that live on generally distributed host-plants and which do not require special conditions for germination and infection. Uredo of *Puccinia graminis* can doubtless be spread over a wide area in the course of a summer by the aid of the wind, but all the species that live only on rarer host-plants can hardly be dispersed by the wind. It is a well-known fact that *Sphacelia segetum* is carried from one grass to another by the aid of insects. But otherwise the epizoic dispersal of spores of microfungi is very rare.

The micromycetes growing on arctic plants, of which we are especially thinking in this connection, are almost certainly only dispersed in one particular way, that is, by the wind carrying fragments of stems and leaves across the snow.

This is what SERNANDER (1901) calls winter-scattering, which is also a familiar method of dissemination in more southerly countries for many species of plants. It is the uppermost part of the plant with its seed, dead petals, carpels, stem-leaves etc. which is carried by the wind and heaped together until the snow melts in June. The endophytes found on the dead fragments of the plants will then be found close to the seeds, and when the latter germinate the spores of the micromycetes will be ready at the same time to attack the germinating plant. In arctic regions scattering by the wind is practically the only means of spreading known to us.

It was therefore a great satisfaction to me, after I had arrived at this explanation as the most plausible one, to see that a man who had travelled in the polar regions himself, and made particular efforts to solve this question, should arrive at the same result, namely H. G. Simmons, when he writes (1913 p. 147) after having spoken of the carrying of seed by means of ice-bergs:

"The sea ice, however, certainly is of great importance for plant migration in another way. About nine months of the year it bridges over most of the channels between the islands and lies dry, covered by hard-blown snow offering a smooth surface for the wind to sweep over and carry lighter objects for any distance. During sledge journeys I often saw small objects swept away over the snow at a rate that would have made it difficult enough to catch them even if the dogs could have been left to their own devices, and the only objects I did get hold of in a few cases, were leaves of willows. Sherard Osborn, however, who travelled whithout dogs, seems to have had better luck, as he says: "I had occasion to-day to remark a phenomenon which had often called itself to my notice, namely, the migration of the seeds of plants, for dissemination would hardly serve to express the extraordinary passage of these seeds from one part to the other of the Arctic regions. I was not botanist enough to detect the different seeds I saw, farther than merely to distinguish those of the poppy, the willow, and the saxifrage. Throughout my journey especially prior to the end of May, I constantly observed these seeds passing over the surface of the frozen floe under the influence of the wind. In the centre of the

Polar Straits, and whether far off or close to the shore, these little solitary travellers would be frisking along in their own odd way, now rolling along over a smooth space, then lurking behind some hummock until a stronger eddy of wind whisked them out; and anon flying along past us some feet above the floe"".

I have quoted SIMMONS and SHERARD OSBORN at some length because I consider it the correct explanation of the wide distribution of the circumpolar flowering plants and their adherent micromycetes.

I find that this view of the matter is further confirmed on observing what WIRÉN writes from Spitsbergen (1922 p. 369) about the scattering of seeds on these islands. He writes (translated): "Of greatest importance ,probably, to dissemination are the autumn gales, which in the abundant vegetation of the valleys of Spitsbergen have almost certainly always in the highest degree been a factor in spreading the seeds of plants. When the autumn is somewhat advanced and the ground begins to freeze in the valleys, one often sees how the violent gales carry huge clouds of sand and dust high up into the air, so that the sun is darkened and the sand and what has been carried with it is spread over the surrounding hills and valleys". GODFRED HANSEN draws about the same picture from King William's Land in Arctic America (1912 p. 65): "The snow sweeps and drives, filling up ravines, leveling everything, blotting out every single spot of black earth" and further (p. 69), "When the autumn comes the north-west wind sweeps the frost-snow along over the flat country". In the Alps, too, the winter-dissemination here described is the commonest (see POUL VOGLER 1908 p. 732).

The importance which earlier writers (OTTO EKSTAM

1899 p. 56 and others) have in a general way attached to birds as seed-carriers over long distances, has assuredly been greatly exaggerated (see Jessen and Lind 1923 p. 36) as regards the phanerogams themselves, and is altogether negligible in the case of fungi, and we see, too, that E. Warming (1888 p. 203), where he thinks that birds have carried the seeds of flowering plants from one arctic country to another, is yet of opinion that their parasitic fungi cannot have been conveyed in the same manner but over pre-glacial land bridges (p. 206).

My investigations of the micromycetes of Spitsbergen and their occurrence in the neighbouring countries show plainly enough that the aid of birds in transporting the seeds, as well as the hypothetical land bridges, which Nathorst (1883 p. 11) and many other earlier writers have considered necessary, are quite superfluous in explaining the large number of species which Spitsbergen possesses in common with Greenland, Norway and Novaya Zemlya in spite of the great distance. In the course of the long winter prevalent in these regions fragments of plants and the endophytes living upon them may easily be carried across the ice from one country to another.

If we maintain that phanerogams, as described above, can hardly be disseminated without being accompanied by their endophytes, and that the endophytes can hardly be scattered in arctic regions except in company with their host-plants, we have only one mode of dissemination which can explain both, that is, dissemination by the wind over the ice or the frozen snow.

If heteroecious species of rust were found in arctic regions, or other species of fungi, the nature of which demanded that spores from one host-plant should be transferred to another in order to thrive, it would be a proof against my theory that the endophytes are spread together with their hosts in arctic countries. But it so happens that heteroecious rusts are particularly rare in those regions (see also RAINIO 1926 p. 258) and the only species we know from Spitsbergen is *Melampsora arctica*, the mycelium of which is perennial in the leaves and stems of *Saxifraga*. Every fragment of an infected *Saxifraga* can therefore carry the *Melampsora* with it from place to place, and where the *Saxifraga* takes root the *Melampsora* can spread new spores and attack the salices in its neighbourhood. It is no doubt for the reasons here given that we never find heteroecious species of rust without perennial mycelium in arctic regions.

The mycelium of *Ustilago inflorescentiae, Ust. violacea* and most other species of arctic *Ustilagineae* is perennial in the host and can be spread with fragments of the host-plant.

V. The Geographical Distribution of the Micromycetes of Spitsbergen.

The peculiar geographical position of Spitsbergen, equally distant from Greenland in the west, Norway in the south, and Novaya Zemlya in the east, has on earlier occasions frequently tempted naturalists to try to discover from which of these neighbouring countries the flora of Spitsbergen may possibly have immigrated.

Owing to great kindness on the part of the authorities of the botanical museums in Copenhagen and Oslo, I have had an opportunity of seeing the rich collections of herbarium plants which have been brought home by various expeditions in the course of a century. A detailed account of the species found will be published at Oslo very shortly.

Concerning the ecological conditions on Spitsbergen see SUMMERHAYES (1923) and other papers mentioned in the list of literature p. 39.

I have divided the species of micromycetes from Spitsbergen, about 200 in number, into 9 divisions, according to their geographical distribution.

Division A.

This group consists of 12 species hitherto only known from Spitsbergen, they are:

Leptosphaeria consobrina
— Equiseti
Lophodermium Svalbardense
Mycosphaerella polaris
Naevia diminuens f. prominens
Phoma sepalorum
Plenodomus Svalbardensis
Pleospora Magnusiana
— Wulfii
Pyrenopeziza Svalbardensis
Septoria polaris
Ustilago nivalis

It is quite possible, however, that these species may be found in other countries in the course of time. It must be observed, though, that *Leptosphaeria consobrina* and *Lept. Equiseti* have been described by KARSTEN in 1872 and that they have evidently not been found again elsewhere during the last fifty-five years. They are very easily recognisable, peculiar species, which it is strange no one has yet found outside these islands.

Division B.

Fungi of continuous distribution, 73 species.

Ascochyta Dianthi
— graminicola
Asteroma Cacaliae
Belonioscypha vexata
Botrytis cinerea
Cintractia Caricis
Cladosporium graminum
— herbarum
Coleroa circinans
Coniothyrium olivaceum
Coryneum foliicolum
Dendryphium fumosum

Diplodia perpusilla
Diplodina Euphrasiae
Dothidella betulina
Eriospora leucostoma
Erysiphe graminis
Fabraea Cerastiorum
Goniosporium puccinioides
Helotium herbarum
Hendersonia arundinacea
— crastophila
Isariopsis alborosella
Lachnum patens
Leptosphaeria arundinacea
— coniothyrium
— culmicola
— culmifraga
— graminum
— microscopica
Leptostroma Henningsii
Leptothyrium palustre
Lophodermium arundinaceum
— caricinum
Mastigosporium album
Melasmia Empetri
Mollisia atrata
Mycosphaerella maculiformis
— pusilla
Naevia pusilla
Peronospora Alsinearum
— parasitica
Phoma Caricis
Phoma complanata
— graminis
— herbarum
— nebulosa
Phyllachora Iunci
Physalospora Empetri
Pleospora herbarum
— Dianthi
— infectoria
— media
— scirpicola
— vagans
Puccinia Arenariae
— Saxifragae
Rhabdospora Campanulae
— pleosporoides
Rhytisma Empetri
— salicinum
Sclerotium fulvum
Septoria Melandrii
— salicicola
— Saxifragae
— Stellariae
Sphaeropezia Empetri
Sphaerotheca fuliginea
Tolyposporium Iunci
Ustilago violacea
Venturia chlorospora
— ditricha
— Petasitidis

This division chiefly includes species commonly distributed in Central Europe and U. S. A. They thrive equally well in the lowlands and on the mountains, in the arctic regions and in the south. The division therefore contains two quite different categories of species, viz.: lowland species able to thrive in glacial regions, and glacial species common in the lowlands.

Cintractia Caricis is a typical arctic-alpine species. In North-East Greenland it extends as far north as 77° (LIND 1910 p. 150) and in Tyrol and Kärnten it ascends to an elevation of 1543 to 1650 m (JAAP 1908 p. 194). SCHELLENBERG very appropriately says (1911 p. 75) of it: "ist in allen Gebieten vertreten und scheint sich den verschiedenartigsten Klimaten anzupassen". Common in European lowlands as well as in U. S. A.

Puccinia Saxifragae is commonly found in all arctic regions on many different species of *Saxifraga,* e. g. in Alaska (HARRIMAN 1904 p. 39), Greenland (ROSTRUP 1888 p. 533, 1894 p. 11, 1904 p. 114, 1906 p. 4, FERDINANDSEN 1908 p. 12) Iceland and the Färoes (JOHANSON 1884 p. 161, ROSTRUP 1903 p. 290 and 1901 p. 307) besides Novaya Zemlya (JØRSTAD 1923b p. 5). Common in Fennia and Norway and sometimes found in Sweden (LIRO 1908 p. 267, SCHRÖTER 1886 p. 210, ROSTRUP 1886 p. 230, JØRSTAD 1923 p. 8, BLYTT 1896 p. 54, ELIASSON 1895 p. 111 and LAGERHEIM 1909 p. 32), in Denmark and the German lowlands it is only found on *Saxifraga granulata,* but in the Alps it is again common on many species of *Saxifraga* (MAGNUS 1905 p. 61, SYDOW 1904 p. 501).

Goniosporium puccinioides is common in circumpolar regions viz.: Ellesmere Land and Greenland (ROSTRUP 1906 p. 9, 1891 p. 629, 1894 p. 30), Iceland and the Färoes (JOHANSON 1884 p. 172, ROSTRUP 1903 p. 326, 1901 p. 316), Novaya Zemlya (LIND 1924b p. 25) near Oslo (ROSTRUP 1904b p. 43), and is common in Denmark (LIND 1913 p. 516) and southwards. In Graubünden it is recorded at an altitude of 1850 m and from several places in Italy (FERRARIS 1914 p. 248).

Rhytisma salicinum is of peculiar interest because it is comparatively easy to identify on fossil leaves of *Salix*. N. HARTZ (1909 p. 228) has found it on leaves of *Salix aurita* at Stokkemarke Torvelung 120 cm deep in the turf and in interglacial deposits near Eistrup. OTTO GERTZ (1917) has found it three times in Scania: on *Salix reticulata* from a postglacial period, on *Salix aurita* and *Salix caprea* from the fir period and on *Salix caprea* from the oak period. He therefore adds: "In all probability it immigrated into Sweden together with the first polar plants as soon as the latter were enabled by the melting of the inland ice to take possession of the country".

These four species, then, differ from the arctic-alpine species mentioned below (division I) only in not having become extinct in the lowlands as the temperature rose. In other words they are in a smaller degree dependent on ecological circumstances than the species mentioned in division I.

And as with these four species, so it is with the following thirty-one species:

Cladosporium graminum
— herbarum
Coniothyrium olivaceum
Dothidella betulina
Helotium herbarum
Leptosphaeria coniothyrium
— culmifraga
— microscopica
Lophodermium arundinaceum
— caricinum
Mastigosporium album
Mollisia atrata
Peronospora Alsinearum
— parasitica
Phoma complanata
— herbarum
Phoma nebulosa
Phyllachora Iunci
Pleospora herbarum
— infectoria
— media
— vagans
Puccinia Arenariae
Rhabdospora pleosporoides
Septoria Melandrii
— salicicola
— Saxifragae
— Stellariae
Sphaerotheca fuliginea
Ustilago violacea
Venturia chlorospora.

They can all be found high up in the arctic regions, and yet they thrive equally well in the lowland of Denmark.

A second sub-section consists of the species of fungi attached to *Empetrum nigrum*; they are most likely to be found wherever the latter thrives; they are:

Melasmia Empetri	Sphaeropezia Empetri
Rhytisma Empetri	Physalospora Empetri

A third sub-section consists of the southerly species which are widely distributed in the lowlands of Central Europe but rarely found as far northwards as Spitsbergen; they are:

Ascochyta graminicola	Isariopsis alborosella
Erysiphe graminis	Leptosphaeria culmicola
Fabraea cerastiorum	Pleospora scirpicola

Of these, *Erysiphe graminis* is not exactly rare in arctic regions, but it only develops its conidial stage (*Oidium*), never its perithecia, which must be regarded as a sign that it is a southern species.

The fourth sub-section includes all the remaining species of division B. They are found in widely scattered growing-places, and several of them are so rare that it is very difficult to form an opinion as to their geographical area.

Division C.

Arctic species, found at Spitsbergen and westward. 15 species.

Diplodia Simmonsii	known	from	Ellesmere Land and North-East Greenland
Gloeosporium Roaldii	—	—	Arctic Canada
Gnomonia hyparctica	—	—	North-West Greenland

Hendersonia Arabidis	known from	West Greenland
— gigantea	— —	North-East Greenland
— Rostrupii	— —	West Greenland
— Stefanssonii	— —	Arctic Canada and Iceland
Leptosphaeria algida	— —	West Greenland
Linospora insularis	— —	Arctic Canada and Iceland
Massariopsis Wulffii	— —	North Greenland
Mycosphaerella vivipari	— —	Kingua (Arctic America)
Phacidium Polygoni	— —	West Greenland
Phyllosticta Saxifragarum	— —	Umanak (Greenland)
Pyrenophora paucitricha	— —	Arctic Canada and Greenland
Stagonospora eriophorella	— —	Alaska

Division D.

Arctic species found at Spitsbergen and eastward. 4 species.

Diplodia Bessimyanii	Novaya Zemlya
Diplodina Papaveris	— —
Leptosphaeria Weberi	— —
Mollisia graminea	— — and North-Fennia

Division E.

Circumpolar species found both at Spitsbergen and to the east and west. 15 species.

	West	East
Didymosphaeria Dryadis ..	Arctic Canada, North-East and East Greenland	Novaya Zemlya
Diplodina arctica	Arctic Canada, North Greenland 82° 28′	— —
— Pedicularidis	West Greenland	— —
Leptosphaeria caricinella ..	Arctic Canada, West, North and North-East Greenland	— —
Microthyrium arcticum	West Greenland	— —
Mycosphaerella densa......	Iceland	— —
— Ranunculi .	Greenland, Iceland	— —

	West	East
Mycosphaerella Taraxaci...	Ellesmere Land, North Greenland, Iceland	Novaya Zemlya
Naevia Stellariae	West, North and East Greenland	— —
Phoma Oudemansii	Arctic Canada	— —
Pleospora deflectens	Arctic Canada, North-East and East Greenland	— — and Arctic Russia
Pyrenophora filicina	West and North-East Greenland	Novaya Zemlya
Septoria eriophori	Greenland	— —
Sphaeronema foliicolum ...	Arctic Canada and East Greenland	— —
Synchytrium groenlandicum	West Greenland 70° and Iceland	— —

Division F.

Arctic-subarctic species found only on Spitsbergen and in Scandinavia. 6 species.

Lizonia distincta	Fennia
Phoma Ranunculi	Fennia
Phyllachora amenti	Dovre
Pyrenophora Wichuriana	Swedish Lapmark
Ustilago hyperborea	Dovre
— picacea	Alten, Dovre, Jemtland

Division G.

Arctic-subarctic species found on Spitsbergen and westward and in Fennoscandia. 13 species.

Didymella hyperborea	Arctic Canada, Labrador, West Greenland	Swedish Lapmark, Norway 69° lat.
Exobasidium Vacc. Myrtilli f. amphigena.............	Greenland	North-Scandinavia
Leptosphaeria Andromedae	Kingua, West, North-East and East Greenland	Norwegian Lapmark, Swedish Lapmark

	West	East	South
Naevia fuscella	Arctic Canada, West and East Greenland, Iceland, Färøes	Novaya Zemlya	Dovre, Åreskutan, Mustiala
Niptera advena	Arctic Canada, North-East Greenland, Iceland	— —	Swedish Lapmark
Phoma sceptri	West Greenland, Iceland	— —	Finmarken, Dovre Russian Lapmark

Notes on lists C, D, E, F, G, H.

Owing to the tabulated form of the lists, all biographical references have been avoided and the names of the works which have been accessible to me are given below on p. 39: in spite of every care it is very probable that further information concerning the geographical distribution of the above-mentioned species may be obtainable elsewhere. But the details collected here are eloquent enough. They show that most of the arctic fungi have a wide distribution, especially in the directions east and west. They show that the flora of Spitsbergen has not come from one particular side, but must have immigrated both from the east, west and south.

Out of the c. 200 species mentioned, 147 are also found south of Spitsbergen, 146 also west of Spitsbergen and 75 species are common to Spitsbergen and Novaya Zemlya; this difference may very well be due to the regions east of Spitsbergen not yet having been sufficiently examined.

Division I.

Arctic-alpine species found in Spitsbergen and in other arctic regions, but absent in the lowlands of Central Europe, and found again in the Alps or other high mountains. 48 species.

Leptosphaeria brachyasca	West Greenland, North Greenland 83°	Dovre
Marssonina obscura	Arctic Canada	Sweden, Fennia
Massaria macrotheca	West and East Greenland, Iceland	Dovre
Metasphaeria Cassiopes	West and North Greenland 82° 48′	Tromsø
— sepalorum	Iceland	Umeå
Mycosphaerella inconspicua	Arctic Canada, Kingua, Labrador, West and East Greenland	Swedish Lapmark
— perexigua	West and East Greenland, Iceland	Dovre
Phoma Caricis	Ellesmere Land, West Greenland, Färoes	Sweden
Pleospora macrospora	Arctic Canada, West Greenland	Alten and Swedish Lapmark
Septoria punctoidea	Ellesmere Land, Greenland, Iceland	Dovre

Division H.

Arctic-subarctic species found both in Scandinavia and west and east of Spitsbergen. 9 species.

	West	East	South
Crumenula pusiola	Greenland and Iceland	Novaya Zemlya	Fennia, Norwegian Finmark
Entyloma ambiens	Arctic Canada	— —	Tromsø, Umeå
Leptosphaeria insignis	Arctic Canada	— —	Denmark (once)
Leptothyrium arcticum	common in all	arctic regions	Fennia
Mollisia graminis	common	Novaya Zemlya	Fennia
Mycophaerella Wichuriana	Arctic Canada, Ellesmere Land, West, North and East Greenland, Iceland, Färoes	— —	Finmark, Dovre Swedish Lapmark, Jemtland

	West	East	Fennoscandia	The Alps
Belonidium juncisedum	Adirondack, West, North and East Greenland, Iceland		Fennia, Magerø, Polaure	Tyrolese Alps
Bostrychonema alpestre	Alaska, Greenland, Iceland Färøes		Common in the north of Norway and Sweden	Very common in the Alps
Clathrospora Elynae	Arctic Canada, Greenland, Iceland			Sellajoch 2100 m Furchapass 2450 m Simplon 2020 m Albulapass 2313 m
Clathrospora pentamera	Utah, Alaska, Arctic Canada, Ellesmere Land, Greenland, Iceland, Färøes		Dovre, Tofte 61° 30′ Kitofka and Tyrvää	Italy and Pamir
Clathrospora punctiformis	North Greenland, Iceland			Prague.
Didymella glacialis	Arctic Canada, Labrador, West Greenland		Swedish Lapmark, Norway 69°	Tyrol, Taschachferner 2010 m
Helotiella erythrostigma	East Greenland, Iceland			Krain 1300 m
Heteropatella umbilicata	Arctic Canada, Ellesmere Land, Greenland, Iceland, Färøes	Novaya Zemlya	Finmarken, Dovre, Umeå	Helvetia and French Alps

	West	East	Fennoscandia	The Alps
Hypospila rhytismoides	Arctic Canada, Labrador, Greenland, Iceland	Novaya Zemlya, Siberia	Dovre, Swedish Lapmark	Scotland, Bavarian Alps, Engadine, Krain, Italy
Leptosphaeria silenes acaulis	Unalaska, Ellesmere Land, Labrador, West, North and East Greenland, Iceland	Novaya Zemlya	Common in North-Scandin. also Dovre, Hardanger	Tyrolese Alps 2600 m, Krain, Northern Italy
Massaria eucarpa	West and East Greenland			Kaukasus
Melampsora arctica	U. S. A., Arctic Canada, all arctic regions	common	Common in North Scandinavia	Common in Helvetian Alps
Mycosphaerella confinis	Arctic Canada, Kingua, West and East Greenland	Novaya Zemlya	Fennia, Dovre	Mount Nanos in Kärnten
Mycosphaerella eriophila	Alaska, Arctic Canada, Greenland, Iceland			Mountains of Helvetia and Germany
Mycosphaerella minor	Arctic Canada, West Greenland, Iceland, Färøes		Kola, Dovre	
Mycosphaerella Pedicularidis	Arctic Canada, Kingua, West Greenland	Novaya Zemlya	Dovre	Bernina 1720 m
Mycosphaerella Polygonorum	Arctic Canada, Ellesmere Land. West and East Greenland. Iceland			Caucasus, France
Mycosphaerella Tassiana	Common in all	arctic	and subarctic regions.	Silecia, Common in Helvetia and Italy. Pamir 2600 m Kopavnik Mountains.

Naevia diminuens	Alaska, Greenland, Iceland, Färøes		Finmarken, Swedish Lapmark, Dovre, Åreskutan	Riesengebirge Engadine
Niptera phaea				Saxony and Brandenburg
Orbilia Primulae				Tyrol
Phialea rhodoleuca	Iceland		Sweden, Kola	Sonntagsberg (Austria)
Phoma alpina	Ellesmere Land, Umanak			North-Italy
Physalospora alpestris	East Greenland		Kaafjord, Jemtland	Helvetia and Austria
Pleospora discors	Arctic Canada, West, North, North-East Greenland, Iceland	Novaya Zemlya		Albulapass 2313 m. Mont Cenicio, Algiers.
Pleospora Iunci				Tyrol 2010 m. Sicily
Pleospora Karstenii	North Greenland 83° 2′ North-East Greenland, Iceland	Novaya Zemlya		Berninaalp 2600 m
Pseudopeziza Bistortae	Unalaska, West and East Greenland, Iceland	Novaya Zemlya	Dovre, Jemtland	Caucasus, Eiergletscher 2325 m, Gemmipasshöhe 2325 m, Zermatt Sellajoch 2100 m, Tyrol, Thuringia 800 m
Pseudophacidium degenerans	East Greenland, Iceland		Fennia, Lapland, Umeå	Engadine

	West	East	Fennoscandia	The Alps
Puccinia Cardaminis bellidifoliae	West, North-East and East Greenland	Novaya Zemlya	Norway and Sweden	
Puccinia Cochleariae				The Pyrenees
Puccinia Drabae	Greenland, Iceland	Novaya Zemlya	Fennia, Scandinavia	Albulahospiz 2313 m Asia minor 2900 m
Puccinia Iueleana			Finmarken, Hardanger, Fennia	Tyrol, Helvetia
Puccinia Oxyriae	Arctic Canada, Colorado	Fennia	From Alten to Hardanger, Kvickjock	Tyrol
Puccinia Polygoni vivipari	Common in all arctic	regions	and in Fennoscandia	Helvetia, Tyrol, Caucasus
Pyrenophora Androsaces	Kingua Fjord, North Greenland, Iceland	Novaya Zemlya		Helvetia, Tyrol 1300 m — 2313 m
Pyrenophora Cerastii	Common in all	arctic and	subarctic regions	Common in Helvetia
Pyrenophora comata	Alaska, Arctic Canada, Kingua, Ellesmere Land, West, North-East, East Greenland, Iceland	Novaya Zemlya	Finmarken, Dovre	Caucasus, Brünn.

Pyrenophora chrysospora	Alaska, Arctic Canada, Greenland, Iceland	Novaya Zemlya	Åreskutan, Dovre	Albula, Krain, Mountains of Italy
Pyrenophora helvetica	Arctic Canada	Novaya Zemlya		Berner Alps
Pyrenophora hispida	Labrador		Swedish Lapmark, Hardanger	Helvetia, Tyrol, Italy
Pyrenophora setigera			Magerø, Herjedalen	Mähren, Crestamora
Rhabdospora Drabae	Arctic Canada, Ellesmere Land, Greenland, Iceland, Färøes	Novaya Zemlya	Dovre, Jemtland	Bernina 2200 m
Schizonella melanogramma	Arctic Canada, U. S. A.		Scandinavia in several places	Riesengebirge, Helvetia and Tyrol up to 2450 m, Caucasus
Stegia subvelata				Albulapass, Interlaken 2075 m, Tyrol, Luxemburg
Ustilago Bistortarum	West and East Greenland, Iceland	Novaya Zemlya	Common in Fennia and Scandinavia	Riesengebirge, Helvetian Alps, Tyrolese Alps
Ustilago inflorescentiae	Unalaska, Ellesmere Land, Greenland, Iceland, Färøes, U. S. A.		Common in Fennia and Scandinavia	Common in the Alps from 1950 m up to 2400 m
Ustilago vinosa	Alaska, West and East Greenland, Iceland, Färøes	Novaya Zemlya	Common in Fennia and Scandinavia	Common in the Alps.

Notes on Division I.

The 48 species which I have called arctic-alpine are by no means all equally typical. Some species of *Clathrospora* and *Pyrenophora* are very common in high arctic regions, but totally absent in the subarctic regions and in the lowlands, and do not reappear until at a high altitude in the Alps. Other species, e. g. *Ustilago inflorescentiae* and *Mycosphaerella Tassiana,* can be found both in arctic and in subarctic regions, nay, even so far down in the most southerly parts of Scandinavia as Scania; they are again found on the Riesengebirge and other Central-European mountains.

Many of these species may be found on mountains in Central- and South-Scandinavia especially on the Dovre and on Åreskutan (Lagerheim 1884 b, Rostrup 1883). The botanical investigation of these localities is therefore of the greatest value to plant-geography; we must particularly urge upon collectors of micromycetes to note the altitude of the finding places.

Concerning the localities mentioned, there is hardly any doubt that the arctic-alpine species found at Dovre, Riesengebirge etc. are relicts, that is to say, that they have grown on the said spot since the glacial epoch. But many typical species of group I have also been found in Denmark viz.:

Pseudophacidium degenerans
Mycosphaerella minor
Puccinia Drabae
Puccinia Polygoni vivipari
Bostrychonema alpestre

We are, however, by no means entitled to define the area of these 5 species as continuous (division B). In the first place, the said fungi have only very rarely been found in Denmark, perhaps only once or a few times. Then, again, it is not at all surprising that plants, which are able to survive the severe cold and extraordinary drought characteristic of the arctic regions, can thrive in a temperate climate. LAGERHEIM has consequently fairly often drawn attention to what he calls arctic-alpine-maritime species, these being just the alpine species occasionally found along the shore. Moreover, a closer examination of the cases in which typical arctic or arctic-alpine species are found in Denmark, shows that these are always found close to the sea or in bogs.

It is also conceivable that they were pseudo-relicts, that is, that they grew here immediately after the glacial epoch, then became extinct for a long period, and now again may have immigrated or been conveyed here by some means or other. In deciding on this often very difficult question the micromycetes are of great assistance. In this connection I am thinking especially of *Draba incana* which is found on the coast at Hirtshals in a single place, and *Polygonum viviparum* growing by the Limfjord. Both of these arctic phanerogams are very rare in Denmark and indeed foreign to our lowlands. We might easily be tempted to define them as pseudo-relicts, perhaps brought hither as seed by a bird. But as the said *Draba* happens to be infected with *Puccinia Drabae* and the *Polygonum* with *Puccinia Polygoni vivipari*, just as they are on Spitsbergen, the possibility that the host should first have found its way hither, and then, that the spores of the fungus should have travelled the long distance without missing these few isolated host-plants seems nearly quite untenable.

The arctic-alpine microfungi that we find at Spitsbergen and again on the mountains are completely alike and are frequently found on the same species of host-plant e. g. on *Dryas*, *Oxyria* or *Polygonum viviparum*, *Betula nana*, *Silene acaulis* etc. It follows from this that the same fungus has kept unchanged during the c. 15000 years that have elapsed since the glacial period, and that they could already then be found on the same host-plants. Some species must be of even much greater age e. g. *Mycosphaerella Tassiana*, *Clathrospora pentamera* and *Pleospora herbarum* which are found in Pamir, *Puccinia Cochleariae* which is found in the Pyrenees and *Puccinia Drabae* found in Asia Minor.

The reason that I have on the present occasion restricted myself to comparing the micromycetic flora of Spitsbergen with that of the European Alps, and only in very few instances followed the same species to the mountains of Asia or America is by no means that it would not have been very useful, but that we lack information of the micromycetes of these remote high altitudes and also that at present it has been impossible for me to obtain available information of this matter. It is known from the literature (e. g. Engler 1879) that a large number of phanerogams that we know from Spitsbergen, thrive just as well in the high mountains of Siberia and the Himalayas; *Papaver radicatum* is to be found in the high altitudes of the mountains of Afghanistan and numerous species in the Rocky Mountains (Theo. Holm 1922 p. 68). Some day when we arrive at the point when we know the micromycetes that grow on *Dryas*, *Papaver radicatum*, *Ranunculus sulphureus*, *Stellaria longipes*, *Cassiope tetragona*, *Salix spp.*, *Betula nana* and *Juncus spp.* in all the widely separated localities of these plants, it will be easier than it is now to trace the migration roads of these species. Just as the water of the Gulf Stream can be recognised as distinct from the surrounding water of the ocean not only by its temperature but also by the fruits that the stream carries with it, so also it will be possible to recognise *Dryas octopetala* from certain growing-places from *Dryas octopetala* from other growing-places only by the micromycetes that follow it.

But if we do reach this point, it will also be seen that some micromycetes do not continue to follow their host in its entire distribution, and that other micromycetes, e. g. the *Pyrenophora* and *Clathrospora* species, follow the community of plants to which they belong without adhering to any single species of phanerogams.

VI. Conclusions.

Of the 195 endophytic micromycetes at present known to us from Spitsbergen, we have seen that

Division	A, 12	species,	have hitherto only been found at Spitsbergen.
—	B, 73	— ,	have a continuous distribution.
—	C, 15	— ,	are only found at Spitsbergen and westward.
—	D, 4	— ,	are only found at Spitsbergen and eastward.
—	E, 15	— ,	are found both at Spitsbergen and westward and eastward.
—	F, 6	— ,	are found both at Spitsbergen and southward.
—	G, 13	— ,	are found both at Spitsbergen and southward and westward.
—	H, 9	— ,	are found both at Spitsbergen and southward, westward and eastward.
—	I, 48	— ,	are arctic-alpine.

This grouping of the species shows that the microfungi have immigrated into Spitsbergen by several different ways. And the number of species in each group shows us something of how many species have come from the east, south or west, even though these figures depend to a great extent on how accurately the flora of these neighbouring countries has been examined.

The comparatively large number of micromycetes which Spitsbergen has in common with the high mountains of Europe (36 species of Division B + 48 species of I) are decidedly of most interest to us. Their characteristic feature is that they occur in very widely separated areas, partly in the arctic regions, partly in the glacial regions of the Alps and sometimes on other summits and highlands in Scandinavia and other countries.

These features, common to the Alps and Spitsbergen, have been most clearly pointed out and most simply explained by A. G. Nathorst, and the idea itself has therefore been called the Nathorstian Hypothesis (Brockmann-Jerosch 1919 p. 38). Briefly stated it is based on the assumption that during the great glacial epoch the land ice pushed southward so far that only a narrow tract of land was left between it and the alpine glaciers (now the region between Leipzig and Munich) and the vegetation existing there then followed the receding ice northwards and southwards respectively, until it reached its present place (Nathorst 1883 b p. 270 and p. 275); at the same time, while the temperature rose in Central Europe, other plant communities took its place. Heer writes (1884 p. 25): "Es lag daher die Vermutung nahe, dass zur Gletscherzeit die arctische Flora nach Süden vorgeschoben worden und so in unsere Gegend gekommen sei, wo sie, als das Klima wieder milder geworden, in unsern Alpen eine für sie passende Wohnstätte gefunden habe". This leads HEER to raise the question whence the glacial flora, which in the post-glacial period accompanied the ice both northwards and southwards, originally came. It would seem that at present we are not able to give any definite answer. Most probably the Dryas Community is made up of many components of different origins. It would doubtless be a task well worth undertaking to study this very uniform plant community in all its widely separated areas, from the arctic regions to the high altitudes of the Himalayas. But research of this kind only becomes of value when the micromycetes (and other cryptogams) that belong to the community, are included.

The Dryas Community is by its very nature a very uniform one, bound up as it is, with quite definite exterior conditions of living. We notice that the Caucasus (WORONOW 1923) has 10 species of micromycetes (and no doubt more) in common with Spitsbergen, viz.:

Dothidella betulina
Helotium herbarum
Leptosphaeria culmifraga
Massaria eucarpa
Mycosphaerella Polygonorum
Pseudopeziza Bistortae
Puccinia Polygoni vivipari
Pyrenophora comata
Schizonella melanogramma
Sphaeropezia Empetri

We see from this that a number, perhaps even a large number of the arctic-alpine species that we find in Spitsbergen, have come from the Caucasus.

HEER enumerates 37 species of flowering plants (1884 p. 110) common to Switzerland and Spitsbergen. Now, if the cryptogamic flora of Switzerland had been as thoroughly examined as that of Spitsbergen now is, and there is, by the way, not much lacking in this, we should be able, with far more certainty, to trace the ways of migration of each of these flowering plants separately.

When once the elementary components of the Dryas Community have found each other, they travel together slowly and steadily. The very circumstance that we find it accompanied by the same micromycetes on the highest peaks of the Alps and at Spitsbergen, shows that the society of plants now so widely separated must have been united before. Single seeds of *Dryas* or *Silene acaulis* may very well have been carried this long distance in the course of ages, and the spores of fungi can very well be carried a long way by the wind, but there is too slight a probability that these single spores should just chance to fall on the one host plant on which they can alone thrive. Axel Blytt has expressed the same opinion before (1896 p. 13), and I entirely agree with him on this point.

The arctic-alpine species must assuredly have been the first immigrants into Spitsbergen; as mentioned above they would follow close upon the ice-border as it gradually receded northwards and the flora would travel after it, step by step. All the species mentioned have once grown in the country situated between the land originally free of ice and Spitsbergen, and consequently we find *Rhytisma salicinum* (see above p. 17) in the deeper layers of soil together with the remains of other polar plants. Some species, to which their ecology permitted it, stayed behind in the same regions and may still be found there (division B), while others have been totally exterminated in the intermediate country, being supplanted by more warmth-loving species (division I).

Besides the actual arctic-alpine species there are a number of species which Spitsbergen has in common with the most northerly parts of Norway, especially division F, but also some of division G and H. It is most probable then, that these species immigrated into Scandinavia from the east by way of Russia and Finland, perhaps during an interglacial period, and that they then accompanied the arctic-alpine species to Spitsbergen.

On the other hand, it is not impossible that they have been carried across the ice from Spitsbergen to Norway by the wind.

The circumpolar species of the divisions C, D, E, G and H have undoubtedly immigrated into Spitsbergen during the post-glacial period. Most of them are widely distributed in the east and west but are not found in Scandinavia or other European countries. Their distribution shows that it is easy for these species to pass from country to country even when there are great oceans between.

Nathorst thought (1883 p. 11) that all the plants in Spitsbergen must have immigrated by way of a land bridge from Scandinavia and Novaya Zemlya. He considered an immigration from the west to be impossible. He writes about this (1883 b p. 448): "Ein Austausch mit Grönland (mit Ausnahme vielleicht irgend eines ganz zufälligen) hat dagegen während der quartären Zeit nicht stattgefunden".

I have arrived at another result, namely, that a large number of species of micromycetes is common to North-East Greenland and Spitsbergen. Of all the 195 micromycetes of Spitsbergen 146 are common to Spitsbergen and Greenland (and other western regions). Of these common species many have been found also in more southerly countries and may therefore be supposed to have immigrated separately into Spitsbergen and into Greenland, but 15 species of division C have never been found in more southerly regions, nor have 15 species of division E.

The bridge by which the circumpolar species has passed over is the ice which covers the seas during most winters and did so especially during the colder periods of the earth. The phanerogams, together with their endophytes, have been carried by the wind from country to country, as described above (p. 9).

In quite the same way divisions D, E and H show that a brisk exchange of plants has taken place between Spitsbergen and Novaya Zemlya.

When we have attained to a greater knowledge of these species we shall be able to fill out the divisions C, D, E, F, G and H so much that the ways by which the species named have travelled will become clearer. All these circumpolar species have undoubtedly come up to the arctic regions from the Ural, the Rocky Mountains or from other high mountains; they were possibly carried thither during some glacial period or other, and having once reached the arctic regions it would be easy for them to travel over the ice in an easterly or westerly direction.

In the main outlines the present studies show rather plainly the paths by which the micromycetes must have reached Spitsbergen. On the other hand it is almost impossible as yet to make any statement about their paths in the preglacial periods. Only it is easy enough to see from the material under consideration that they must have travelled over very long distances and during long periods of time, as we find the same genera represented at Spitsbergen and in the same blending, as in the whole of Europe, Asia and America: *Pleospora* and *Phoma*, *Entyloma* and *Ustilago*, *Melampsora* and *Puccinia* and so on. It must be an exceedingly long time since these genera split up into the species now known, as we find them intermingled wherever we look for them in the new world as well as the old one, in arctic as well as in antarctic regions.

Amongst the species that we know from Spitsbergen at least three species are found again in Pamir (Rostrup 1917, p. 218), viz., *Pleospora herbarum*, *Mycosphaerella Tassiana* and *Clathrospora pentamera*.

If any of the genera which have been dealt with ought to occupy a special position in this respect, it would be the genus *Pyrenophora*, no less than ten species are found at Spitsbergen, and several of these are conspicuously common in that region. None of these ten species are found in Denmark or elsewhere in the European lowlands, they are typically arctic or arctic-alpine species. *Pyrenophora helvetica* and *Pyr. Androsaces* are not found even in the northernmost parts of Scandinavia, they are only found at Spitsbergen and in the highest Alps; most of them are widely distributed in arctic and sub-arctic regions. *Pyrenophora Wichuriana* and *Pyr. filicina* are not found in the Alps; conversely some species are known in the Alps which are not found in the arctic regions.

It is, however, possible that the hairs which clothe the perithecia are of some physiological importance to these fungi and cause them to be so much more common in glacial regions than in those of a warmer temperature.

We cannot conclude this study of the geographical distribution of the micromycetes and their bearing on our knowledge of the geographical distribution of the phanerogams, without a reminder that the view that some few species might be of polyphyletic origin — a view that is not yet quite abandoned (see e. g. Theo. Holm 1923 p. 18) — depends in a decisive degree on whether these species, which are found in remote, isolated finding-places, are not attacked by the same endophytes. It is not so difficult, after all, to imagine the possibility that uniform conditions would be able to form homogeneous species in several places. It would be much more difficult, however, to imagine that these uniform conditions would also form the selfsame endophytes in widely separated growing-places.

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