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Teuvo Ahti: *Parmelia olivacea* and the allied non-isidiate and non-sorediate corticolous lichens in the Northern Hemisphere

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PARMELIA OLIVACEA AND THE ALLIED NON-ISIDIATE AND NON-SOREDIATE CORTICOLOUS LICHENS IN THE NORTHERN HEMISPHERE

BY

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Introduction

While collecting lichens in various parts of Canada and northern Europe I have formed the impression that the brown corticolous lichen *Parmelia olivacea* (L.) Ach. em. Nyl. is considerably more frequent in Finland, Sweden and Norway than in climatically corresponding parts of eastern North America (Ahti 1964, pp. 21, 30). In Ontario I found that the commonest form of the species was smaller in size than is usual in northern Europe, and, in addition, I encountered an undescribed species that superficially resembles *P. olivacea* (op. cit., p. 21).

In order to clarify the taxonomy and the ranges of the corticolous lichens which resemble *P. olivacea* and normally lack soredia and isidia, a large number of specimens in the following herbaria were examined (the symbols are those used by Lanjouw & Stafleu, 1964, with some additions):

Ahln	Herb. of Dr. S. Ahlner, Stockholm, Sweden.
BM	British Museum (Natural History), London, England.
CAN	National Museum of Canada, Ottawa, Ont., Canada.
(COLO	University of Colorado Museum, Boulder, Colo., U.S.A.)
Deg	Herb. of Dr. G. Degelius, Gothenburg, Sweden.
E	Royal Botanic Garden, Edinburgh, Scotland.
FH	Herb. of Cryptogamic Botany, Harvard University, Cambridge, Mass., U.S.A.
GL	Dept. of Botany, University of Glasgow, Scotland.
GLAM	Glasgow Art Gallery and Museums, Glasgow, Scotland.
H	Botanical Museum, University of Helsinki, Finland (H-Nyl = Herb. W. Nylander).
Hak	Herb. of Dr. R. Hakulinen, Hämeenlinna, Finland.
HFR	Forest Research Institute, Helsinki, Finland.
HSI	Dept. of Silviculture, University of Helsinki, Finland (Herb. G. Lång).
K	Royal Botanic Gardens, Kew, England.
Klem	Herb. of Dr. Oscar Klement, Kreuzthal-Eisenbach, Germany.
(KW	Botanical Institute of the Academy of Sciences of the Ukrainan S.S.R., Kiev, U.S.S.R.)
LE	Botanical Institute of the Academy of Sciences, Leningrad, U.S.S.R.
LINN	The Linnaean Society of London, England.
M	Botanische Staatssammlung, Munich, Germany.
MIN	Dept. of Botany, University of Minnesota, Minneapolis, Minn., U.S.A.
MSC	Michigan State University Herbarium, East Lansing, Mich., U.S.A.
Nord	Herb. of Mr. Ingvar Nordin, Uppsala, Sweden.
NY	The New York Botanical Garden, New York, N.Y., U.S.A.
O	Botanical Museum, University of Oslo, Norway.
OULU	Dept. of Botany, University of Oulu, Finland.
S	Swedish Museum of Natural History, Stockholm, Sweden (S-Vr = Herb. E. P. Vrang).
Th	Herb. of Dr. J. W. Thomson, Madison, Wis., U.S.A.
TNS	National Science Museum, Tokyo, Japan.
TUR	Dept. of Botany, University of Turku, Finland (TUR-V = Herb. E. A. Vainio).
UAC	Dept. of Botany, University of Alberta, Calgary, Alberta, Canada.
UC	Dept. of Botany, University of California, Berkeley, Cal., U.S.A.
UPS	Institute of Systematic Botany, University of Uppsala, Sweden.
US	United States National Museum, Washington, D.C., U.S.A.
W	Naturhistorisches Museum, Vienna, Austria.
WIS	Dept. of Botany, University of Wisconsin, Madison, Wis., U.S.A.

I am grateful to the curators and owners of these herbaria for loaning specimens, or for their help during my visits to them. I have not examined the material in COLO, except numerous duplicates in other herbaria, but Dr. William A. Weber kindly tested a number of specimens there with PD for me. In addition, I have examined some specimens sent by Mrs. Greta Du Rietz and Mr. Göran Eriksson, Uppsala, Sweden. I also want to thank Dr. Mariya F. Makarevich, who checked some material in KW and gave other information on the species in the U.S.S.R.

I am obliged to Dr. HARUMI OCHI for his translation of some Japanese text, to Mr. F. H. BRIGHTMAN, who revised the English of my manuscript, and to Mr. S. HOLMSTRÖM who photographed some specimens. The study is a minor part of a research project for which auxiliary personnel were engaged under a grant from the Finnish National Research Council for Science.

Parmelia olivacea (L.) Ach. has been commonly treated in a very wide sense, including both saxicolous and corticolous species with and without isidia and soredia. NYLANDER (1868, p. 346, and more completely in HUE 1886) defined *P. olivacea* s.str. as a non-isidiate and non-sorediate species and described a number of new species, which now form the core of the group that is usually called sect. *Melaenoparmelia* Hue em. Hillm. The status of this group, which may possibly deserve the rank of subgenus (cf. HALE & KUROKAWA 1964, p. 121), and its subdivision are not discussed any further here, because the chemistry of the group is still very incompletely known when compared with the other groups of *Parmelia*. It is apparent that all the species treated here do not belong to one and the same section or subsection, although they superficially resemble each other.

Among the European corticolous species of *Melaenoparmelia* that are lacking in soredia and normally without isidia also, although in some of them isidia or isidioid lobuli may occasionally be developed, only *P. olivacea*, *P. glabra* (Schaer). Nyl. and *P. laciniatula* (Flag.) Zahlbr. are generally accepted (e.g. POELT 1962). In Asia three species of the group have usually been recognized, viz. *P. olivacea*, *P. glabra*, and *P. huei* Asah. (e.g. TOMIN 1937, ASAHINA 1952).

In North America the situation is more complicated. In FINK's (1935) flora two corticolous species of the group were mentioned for the United States, namely *P. olivacea* and *P. multispora* Schneid. He also recorded *P. glabra*, but only from rocks and mosses, although the species is strictly corticolous in Europe. In BERRY's (1941) monograph the same three taxa were accepted and *P. glabra* (as *P. olivacea* var. *glabra*) was also reported from trees. In the checklist of HALE & CULBERSON (1960) *P. glabra* is absent, but *P. subolivacea* Nyl. is mentioned instead, although the latter is usually considered to be a synonym of *P. olivacea*. BERRY's (1941) paper is now completely out of date, especially with regard to *Melaenoparmelia*, and many of the distribution data of those species that are correctly treated are based on misidentifications.

In the southern hemisphere the group in question is not well represented. In New Zealand there is one species, at least, but on the other hand, *P. ushuaiensis* Zahlbr. (*P. roivainenii* Räs.), which was considered to be without isidia and soredia and very closely related to *P. olivacea* by RÄSÄNEN (1932 p. 19)

and SANTESSON (1944, p. 24), does not belong to this group at all. In fact, the type specimens of *P. ushuaiensis* (S,W) and *P. roivainenii* (H) have numerous small isidia on the upper surface, which were regarded as soredia by ZAHLBRUCKNER (1917, p. 42) in his original description.

Taxonomically important characters and key to the species

External morphology

It is possible to learn to recognize the species of the *P. olivacea* group from habit characters alone, although in some cases there are difficulties without microscopical or chemical study. Each species has a characteristic pattern of lobation and rugosity, which is not easy to describe because of the great range of variability according to the habitat and the age of the individual. The lobes may be more or less discrete, contiguous, overlapping or even panniformly layered. Their ends may be flat, concave or convex, the upper surface smooth to wavy or rugose, and the lower side smooth to reticulate. All these characters offer minor criteria for identification of the species.

The ability to produce secondary lobules in central parts of the thallus is also a useful character. In *P. subolivacea* and *P. multispora* scattered more or less cylindric lobules that could be called isidia are occasionally found even on the upper surface of the thallus. Somewhat similar marginal lobules may be present in *P. laciniatula*, *P. halei* and *P. trabeculata*. These structures do not usually seem to be associated with parasitic fungi, although such fungi may induce galls in this group, particularly in *P. olivacea*. However, non-parasitised individuals of *P. olivacea* become extremely rugulose in poor growing conditions.

Pseudocyphellae

ANDERSON & WEBER (1962) claimed that their new species *P. saximontana* is the only one in *Melaenoparmelia* that has pseudocyphellae. Indeed, such structures are not usually mentioned in handbooks as being present in this group (except in *P. aspera* Mass., which has pseudocyphellae at ends of peculiar warty isidia). On the contrary, GYELNIK (1932, p. 492) indicated in the description of his sect. *Vainioëllae*, which includes e.g. *P. olivacea*, that pseudocyphellae are absent.

Therefore, it was most surprising to find that small white to greyish pseudocyphellae are constant on the lobes as well as on the apothecial margins of *P. olivacea*. They are also present in several other species, although they are smaller and therefore less conspicuous than in *P. saximontana* and many pseudocyphellate species of the other groups of *Parmelia*. They proved to be useful taxonomic criteria in the *P. olivacea* group, as they are in other lichens.

Anatomy

This aspect was not studied very thoroughly, but as shown by ROSENDAHL (1907) and others, there are many taxonomically useful anatomical characters in *Melaenoparmelia*. However, it was clear from the material studied that the various layers in the thallus have characteristic thicknesses, although the range of variability is considerable. The measurements given in this paper are all original but are based on only a few specimens of each species.

ROSENDAHL (1907) stated that there are several species of *Melaenoparmelia* that have only one pseudoparenchymatic layer of cells in the cortex. In the present paper *P. laciniatula*, *P. huei* and *P. multispora* are representatives of this group.

Apothecia

In most of the species under discussion apothecia are very common; in fact, they are constant in »mature» individuals. Spores apparently play a major role in dispersal, since effective organs of vegetative propagation are absent or poorly developed. However, in *P. laciniatula* the apothecia are extremely rare and in *P. halei* they are less abundant than in the rest of the species. Both of these species produce small lobes that probably serve as means of vegetative dispersal. Useful though variable taxonomic characters are offered by some parts of the apothecia, e.g. its margin, which may be verrucose to smooth, and the thickness of subhymenium. In general, the disc is shiny when immature but dull when the spores are ripe.

The shape and size of the spores are very important specific characters in *Melaenoparmelia*. In the present group they are ellipsoid to globose, but in no two of the species studied here are they fully identical. In *P. multispora* and *P. trabeculata* the number per ascus is normally 16 instead of the usual 8. All the measurements given are original but are based on only 10—20 specimens in each case (in *P. halei* and *P. huei* only 5). Statistical measurements of spores in lichens would be highly desirable, but are difficult to perform in many species with the usual sectioning techniques because the distinction between mature and immature spores is not always easy.

Pycnidia

Pycnidia are visible as more or less black spots on the upper side of the thallus, being often most abundant in the centre. In some species they are constant and abundant, while in some others of very sparse occurrence. The pycnoconidia of *Melaenoparmelia* are reported (e.g. NYLANDER in HUE 1886; ROSENDAHL 1907) to be of two types: cylindrical or bifusiform (with constriction at the middle), which should be useful specific characters. However, I have found that the central constriction is at times very difficult to see, even with higher magnifications. In some cases the pycnidia seem to contain both cylindrical and bifusiform pycnoconidia. More research, preferably with an electron microscope, is required to clarify their variability, and therefore some of the data on their shape and size given here may not be fully reliable. Also the size of the pycnoconidia may be of some taxonomic importance in this group.

Chemistry

The lichen substances and other chemical components of *Melaenoparmelia* are known rather incompletely. Atranorin, gyrophoric acid, lecanoric acid, protocetraric acid, fumarprotocetraric acid, norstictic acid, stictic acid, imbricaric acid and the pigments parmelia-brown and glomellifera-brown have been recorded (ASAHINA 1951, KROG 1951, DAHL 1952, ANDERSON & WEBER 1962; the present study). In addition, there are some earlier, less reliable reports (e.g. ROSENDAHL 1907, p. 455), and in several species unidentified acids have been extracted (e.g. KROG 1951). ROSENDAHL (op. cit., p. 454) also showed that calcium oxalate is present in most species of the group, although some species (e.g. *P. olivacea*) are lacking this compound.

In the present study only the standard colour test reagents were used on a large scale. Some crystal tests were also performed but they gave unsatisfactory results in most cases. Dr. CHICITA F. CULBERSON, Dr. MASON E. HALE and Dr. SYO KUROKAWA kindly made some important chemical tests as well. The chemical components offer very useful taxonomic characters in the group and with improved knowledge their importance will undoubtedly be increased. As far as is known, in this group chemical and morphological variation are well correlated, so that it is probable that there are no distinct chemical strains.

Key to the species

1. Medulla PD + red 2
— Medulla PD — 5
2. Medulla K + yellow to red; N. American 3
— Medulla K — 4
3. Under side usually brown, distinctly reticulate and trabeculate, spores globose or subglobose, usually 16 per ascus; boreal ..... *P. trabeculata* (p. 54)
— Under side black and smooth, spores oblong, 8 per ascus; temperate Appalachian ..... *P. halei* (p. 38)
4. Loosely to closely appressed, up to 10 cm in diam., greenish-brown, dull to somewhat shiny, distinctly rugose, laminal pseudocyphellae numerous on lobe ends, mature apothecia commonly scattered and absent from the periphery of the thallus, usually 3—5 mm in diam., their margin persistent, crenulate, spores 7—9 × 12—15 μ, subhymenium 30—75 μ (the East Asian — Alaskan var. *albopunctata* approaches *P. septentrionalis* in some characters, but has the margins of the apothecia crenulate and the subhymenium thick) ..... *P. olivacea* (p. 10)
— Closely appressed, up to 5 cm in diam., shinier and darker brown, fairly smooth, laminal pseudocyphellae absent or sparse, mature apothecia more crowded, common also at the periphery of the thallus, usually 1—1.5 mm in diam., margin persistent to disappearing, essentially entire, spores 6—7 × 10—13 μ, subhymenium 15—30 μ ..... *P. septentrionalis* (p. 22)
5. Medulla C — 6
— Medulla C + red (lecanoric acid) 8
6. Apothecia very rare, lobes thin, finely laciniate along margins and densely beset with minute isidioid lobules and folioles, under side pale brown; European ..... *P. laciniatula* (p. 57)
— Apothecia usually present, lobes coarser and thicker, not densely beset with narrow lobules, under side black to dark brown; N. American 7
7. Closely to loosely appressed, rather thick, laminal pseudocyphellae sparse or absent, spores usually short ellipsoid (to globose), 8 per ascus; chiefly in arid N. America ..... *P. subolivacea* (p. 33)
— Closely appressed, thinner, laminal pseudocyphellae absent, spores globose (to short ovoid), 16 per ascus; oceanic western N. America ..... *P. multispora* (p. 50)
8. Very closely appressed, thin, dark brown, medulla white or yellow, upper side completely glabrous, spores 5—7 × 13—14 μ; eastern Asian ..... *P. huei* (p. 41)
— Loosely to closely appressed, thick, pale to dark brown, medulla white, upper side densely covered with fine short hairs (best seen on margins of young apothecia), spores 7—8 × 12—14 μ; widespread ..... *P. glabra* (p. 43)

The species

1. Parmelia olivacea (L.) Ach., em. Nyl.

Plate 1

var. ***olivacea***

P. olivacea (L.) ACHARIUS 1803, p. 213; NYLANDER 1868, p. 346. — *Lichen olivaceus* LINNAEUS 1753, p. 1143. — Type: Sweden? (LINN, no. 66 in SAVAGE 1945, p. 196; lectotype).

P. olivacea var. *subcaesia* NYLANDER in NORRLIN 1876, p. 17 (nom.nud.). — Orig. coll.: U.S.S.R. Karelia borealis: Suojärvi, Mökkö, *Salix caprea*, 1870, J.P.Norrlin (H-Nyl,H).

P. olivacea f. *caesiopruinosa* (»*caesio-pruinosa*») LYNGE 1912, p. 5. — Type: Norway. Troms: Bardu, Indset, 9.VI.1911, B. Lynge (W, isolectotype).

Concerning other infraspecific epithets and nomenclatural combinations, see ZAHLBRUCKNER (1929, pp. 97, 99, 101).

Foliose, adnate, forming circular rosettes 5 to 8 (10) cm in diameter; deeply incised, lobes 2—5 mm broad, wider and often slightly ascending and involute at ends; the centre coarsely wavy, radiately folded and also frequently heavily rugulose, dark green to brown, the lobe ends usually paler; dull to somewhat shiny; pseudocyphellae usually abundant, particularly on broad lobe ends; lower surface coal black, densely rhizinate, with a dark brown bare rim along the margins, rhizines brown to black, ca. 30—60 μ long, simple or sparsely branching.

Lobes ca. 195—300 μ thick, upper cortex with many cell layers, 12—22 μ, algal layer 45—90 μ, medulla proper 105—225 μ, lower cortex 8—12 μ.

Apothecia common and often numerous in central parts of older thalli, 3—8 mm in diameter, lacking near the ends of the lobes, very short-stalked to sessile, disc dark brown, margin raised, rarely disappearing, usually distinctly crenulate and pseudocyphellate, even when immature; subhymenium (30—) 50—75 μ, pale, hymenium 50—60 μ, asci clavate, 20—25 × 45—55 μ, spores ovoid, 7—8.5 × 12—15 μ, 8 in the ascus; pycnidia always present, abundant, pycnoconidia ca. 0.5—1 × 4.5—6 μ, indistinctly bifusiform or (?) cylindrical.

Reactions: PD + red, K—, C—, KC—. According to KROG (1951) it contains an acid that is protocetraric or fumarprotocetraric acid. DAHL (1952) listed it under protocetraric acid. In a chromatogram made by Dr. S. KUROKAWA on Japanese material of *P. olivacea* var. *albopunctata* fumarprocetraric acid was demonstrated.

Exsiccati examined:

ARNOLD, Lich. exs. 1029 (H, H-Nyl, M, S, W); ARNOLD, Lich. Monac. exs. 336 (H, LE, M); DIETRICH, Crypt. Fl. balt. 84 (LE); ELENKIN, Lich. Fl. Ross. 104a (LE), 104a p. maj. p. (FH); FELLMAN, Lich. arct. 81 (H, M); FRIES, Lich. Suec. Exs. 261 (S), 261 p.p. (M, S-Vr); FUNCK, Crypt. Gew. Fichtelgeb., ed. 1, 497 (LE, W); HAVAAS, Lich. Norv. exs. 178 (H); Krypt. Exs. Vindob. 3063 (H, LE, M, MSC, S, W); MALME, Lich. Suec. Exs. 65 (H, M, S, W), 880 (H, S, WIS); NORRLIN & NYLANDER, Herb. Lich. Fenn. 28 (H, M, MSC, W); RÄSÄNEN, Lich. Fenn. Exs. 707 (H, LE, M, TUR, W); RÄSÄNEN (—HAKULINEN), Lichenoth. Fenn. 28 (M, OULU), 28 p.p. (H, Hak, TUR), 84 (H, Hak, M, OULU, TUR), 154 p.p. (Hak, M), 155 (H, M), 155 p.p. (Hak, OULU, TUR), 234 (H, Hak, M, OULU, TUR), 533 (H, Hak, M, OULU, TUR), 684 (H, Hak, M, OULU, TUR), 830 (H, Hak, M, OULU), 929 (H), 929 p.p. (Hak, M, OULU, TUR), 1029 (H, Hak, M, OULU, TUR), 1077 (H), 1077 p.p. (Hak, OULU, TUR), 1129 (H, Hak, M, OULU, TUR), 1130 (H, Hak, M, OULU, TUR); SAVICZ, Lichenoth. Ross. 16 (LE, S, Th, W), 16 p. maj. p. (H); STENHAMMAR, Lich. Suec. Exs. 69 (W); TOBOLEWSKI, Lichenoth. Polon. 72 (M); VEREITINOV & KASHMENSKIY, Shkol'n. gerb. sporov. rast. 11 (LE).

var. ***albopunctata*** (Asah.) Ahti n. comb.

P. olivacea f. *albopunctata* ASAHINA 1951, p. 194. — Type: Japan. Prov. Suruga: Ohmiyaguchi 2-gome, Mt. Fuji, July 6, 1925, Y. Asahina 51 (TNS, lectotype; H, isolectotype).

Differs from var. *olivacea* in having usually a more closely appressed and thinner thallus, and papillary outgrowths, often bearing pseudocyphellae at their ends, are frequently produced on the upper surface. However, these structures, which are more irregular than the warts of *P. aspera*, may be absent. The colour is often yellowish brown, resembling that of *P. halei*. The ends of the lobes are usually more shiny and less pseudocyphellate than those of var. *olivacea*.

Lobes 75—120 μ thick, upper cortex with many cell layers, 8—15 μ, algal layer 30—45 μ, medulla 45—75 μ, lower cortex 10—12 μ.

Apothecia common and scattered, mostly in the centre, usually 1.5—3 mm in diameter, essentially sessile, margin crenate, only slightly raised and therefore the apothecia soon becoming more or less flat; subhymenium 45—60 μ, hymenium 60 μ, asci ca. 15 × 45 μ, spores ovoid, 6—9 × 10.5—13 μ, 8 in the ascus.

Reactions as in var. *olivacea*. Fumarprotocetraric acid present (see var. *olivacea*).

Taxonomy

P. olivacea var. *olivacea* has been thoroughly described in many recent European lichen floras. Although *P. septentrionalis* has been included in *P. olivacea*, this is not obvious from the descriptions. Those in North American handbooks are usually based on clearly discordant elements. However, apart from those of HUE (1899) and ASAHINA (1952), who dealt with var. *albopunctata*, I have seen no reference in any flora to the presence of the numerous laminal pseudocyphellae on the broadened lobe ends (however, they were noted by LETTAU 1957, p. 218), which are very characteristic of *P. olivacea*, also serving to distinguish it from *P. septentrionalis*, the close relative (concerning the other differences, see under the latter species). It is common, however, that in poor growing conditions the lobes are not well-developed, making the pseudocyphellae sparse or difficult to observe. Also in var. *albopunctata* they are usually less abundant.

The eastern American and western and central Eurasian populations have a very uniform range of variability but the specimens of the Pacific coasts — e.g. Alaska, Kamchatka, and Japan — show some differences, as is commonly the case with circumpolar species. I was unable to clarify their status very definitely, because the amount of material examined was relatively small and because I have not seen this type in field. However, some observations are discussed below.

From Japan ASAHINA (1951) described *P. olivacea* f. *albopunctata*, which was said to have lobes »tenuissime albopunctate», particularly in the peripheral parts. This Japanese type had previously been recognized by HUE

(1899, p. 148). White dots (pseudocyphellae) are present in all populations of *P. olivacea*, as stated above, but I have seen several specimens from east Asia and Alaska that have white dots at the ends of distinct papillae. Such a type is not known to me from elsewhere. It is the true f. *albopunctata* and was apparently referred to *P. aspera* (= »*exasperata*») by NYLANDER (1890), which is not known from Japan (ASAHINA, 1951, 1952). The cited specimen was not found in NYLANDER's herbarium. TRASS (1963, p. 209), who collected *P. olivacea* in Kamchatka, considered his specimens to be not quite typical, as they have fairly short and narrow lobes (2—3 × 1—2 mm) which are hardly shining at all. Dr. G. DEGELIUS, who collected similar material in Japan, told me that in the field the lichen had a strange appearance and did not look like *P. olivacea*. ASAHINA (1952, p. 56, in Japanese) indicates that f. *albopunctata* has narrower and longer lobes than the type.

I agree that most of the Pacific specimens are peculiar, and that the variation is confusing. Almost all of them are very closely appressed to the substratum, even the lobe ends, the lobes are broad to narrow, very shiny to more rarely dull, and the apothecia are smaller on an average than in Europe. No differences in the spores have been reported, and I have not observed any either with certainty, since in many specimens no spores could be found. If there is only one type in the Pacific area it is at most a variety which is provisionally accepted here as var. *albopunctata*.

Among the rest of *P. olivacea* a pruinose form has been recognized. Its valid name at form level is f. *caesiopruinosa* Lynge. LYNGE (1912, 1921) stated that it is common in northern Norway (Troms and Finnmark), but is also found in southern Norway, though sparingly and poorly developed. According to him the greater frequency in the north would indicate climatic causes. This difference in abundance is also true in Sweden and Finland. Several specimens of this type have been examined also from Siberia and North America. WEBER (1962, pp. 318—322) showed that the pruinosity of many saxicolous and terricolous lichens is due to the accumulation of calcium oxalate and that its presence appears to be correlated with the occurrence of calcium carbonate in the substrate. Such correlation also exists in the case of *P. olivacea* f. *caesiopruinosa*. 41 heavily to slightly pruinose N. European (mainly Finnish) specimens, deposited in H, have been collected from the following substrates: *Sorbus aucuparia* (42 %), *Populus tremula* (22 %), *Salix* spp. (20 %), *Betula* spp. (7 %); *Alnus incana*, *Prunus padus*, *Populus balsamifera*, and stone were represented by one collection each. These data are sufficient to indicate that f. *caesiopruinosa* is chiefly found on *Sorbus*, *Populus*, and *Salix*, i.e. on trees with eutrophic to mesotrophic bark, which contains calcium and other cations in greater quantity than e.g. the bark of *Betula* (cf. BARKMAN 1958, Tables VI—VIII), the commonest substrate of epruinose *P. olivacea*. However, all

this does not explain, why heavily pruinose *P. olivacea* (and e.g. *Physcia pulverulenta*) frequently grows side by side with epruinose individuals, apparently in identical conditions. It does not explain, either, why the pruina is best developed in humid northern boreal conditions, where dust impregnation is not so heavy as it is in arid or intensively cultivated areas. Also the pruinose specimens are often more robust and thicker than usual, but this is not always the case.

Distribution

(Figs. 1, 2)

Maps: Bohemia and Moravia (SUZA 1937, p. 23).

P. olivacea is generally regarded as a circumpolar species (e.g. SUZA 1937, pp. 21—22; KLEMENT 1952; AHTI 1964), but in the present revision all the records for Iceland, the British Isles and Greenland that it has been possible to check have proved to belong to other species, mainly *P. septentrionalis*, and therefore the expression incompletely circumpolar is more appropriate. It is also uncertain so far, whether it occurs continuously through the North American continent; probably it does not. In any case, it ranges from northern Europe over Russia and Siberia to Japan, Kamchatka, and Alaska (where it is represented by var. *albopunctata*). In eastern North America most records are from the areas around Lake Superior, although it may not be very abundant there (e.g. AHTI 1964, pp. 21, 30). More isolated stations are known from the island of Newfoundland — where it is definitely rare —, Labrador, Manitoba, and northern Saskatchewan. Its rarity in New England (only recorded in the Adirondack Mts.) is surprising. Most of the recent American records under this name are in fact *P. septentrionalis*, *P. subolivacea* or *P. halei*.

Zonally *P. olivacea* is a boreal species, which may have slight oceanic tendencies reflected in abundance, though it is absent from some of the most oceanic boreal areas. In Europe it is most abundant in the northern boreal or upper oroboreal zones (concerning the meaning of the zonal terms used here, see AHTI 1964 and JALAS 1965), but still common down to the hemiboreal zone. South of it, in the temperate (boreomeridional) zones, it becomes very rare. The Asian records seem to fit to this scheme. In North America the situation is similar, with the exceptions that no records apparently come from either northern boreal or temperate zones, most of them being from southern boreal to hemiboreal forests.

In all three continents isolated more southern mountain stations are sparse. In Europe it is present in some highlands of Germany, in the Bohemian Forest and in the southern Ural Mts., but it is absent from most of the Alps (probably), the Caucasus, the Himalayas and the Rocky Mountains.

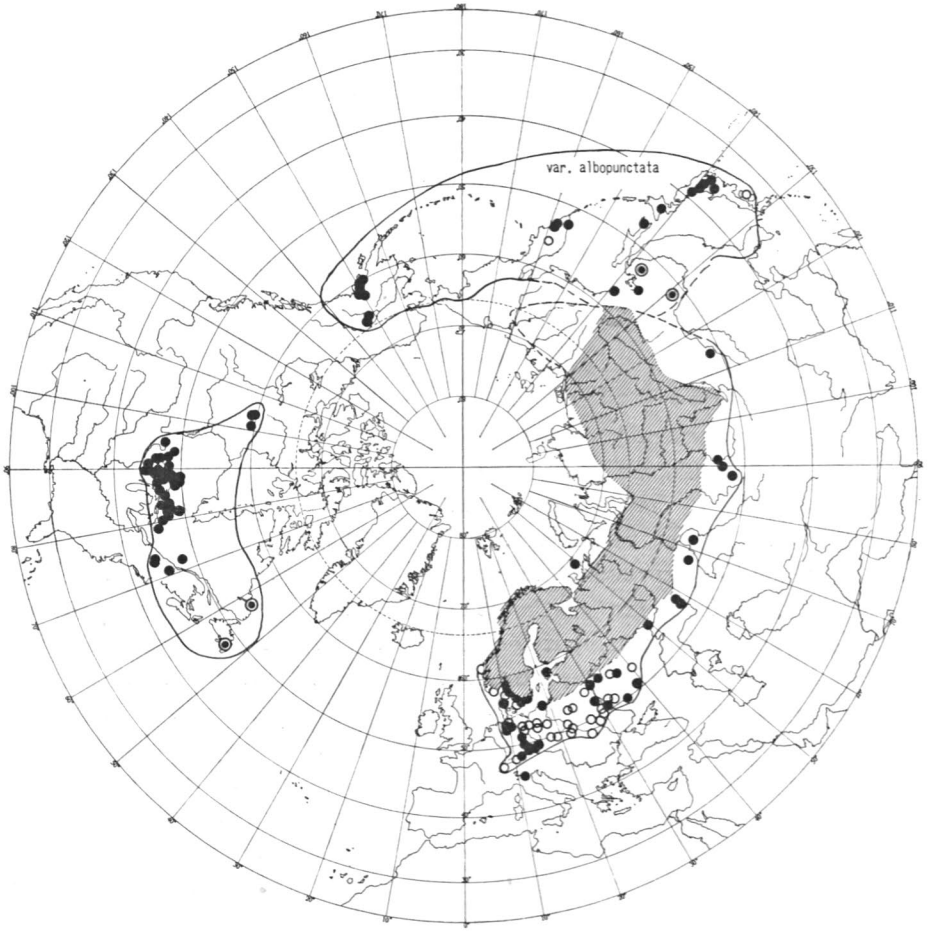

FIG. 1. Distribution of *Parmelia olivacea* (L.) Ach. The circles on the Pacific coast are var. *albopunctata* (Asah.) Ahti; the rest are var. *olivacea*. Hatching indicates continuous, more or less common occurrence.

In Bavaria and elsewhere in Germany *P. olivacea* has become very rare since the last century; most known records are from before 1900 (ERICHSEN 1939, p. 80; POELT 1962, p. 459 and *in litt.*).

The fairly recent records for Hungary (e.g. GYELNIK 1928), France (OZENDA 1948), Rumania (e.g. CRETZOIU 1941), Bulgaria (CRETZOIU 1936), and Azerbaidzhan (BARKHALOV 1957) are regarded as doubtful (probably *P. glabra*) and were omitted in the map.

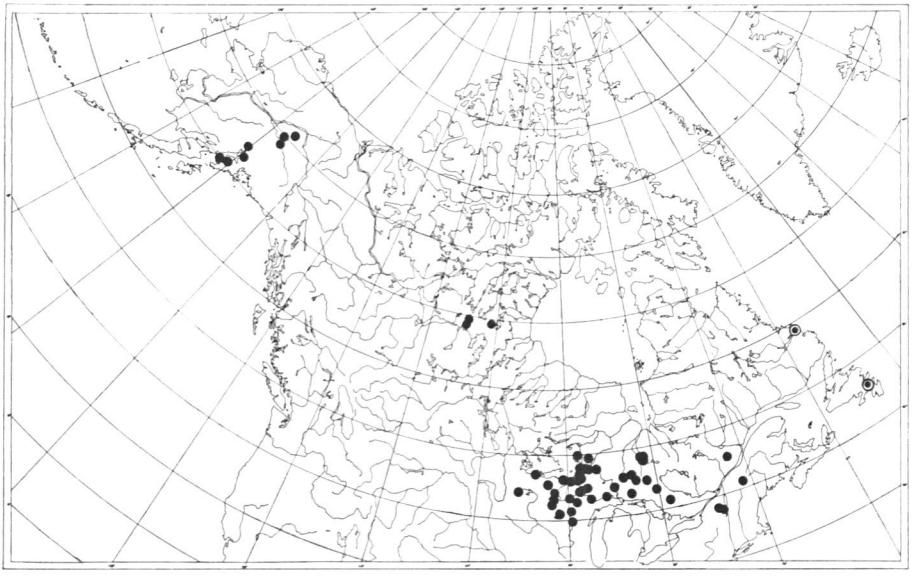

FIG. 2. Distribution of *Parmelia olivacea* (L.) Ach. in North America.

var. *olivacea*

Great Britain

[WATSON (1953) recorded this species from S. Aberdeenshire and the Clyde Is., but no specimens have been seen. The Aberdeenshire locality was apparently based on a misidentification (see p. 47) and it seems highly likely that the other was also. Several older records are based on isidiate species (CROMBIE 1881).]

Iceland

[The reports of LYNGE (1940) and DEGELIUS (1957) are mentioned under *P. septentrionalis*. If present in the country, *P. olivacea* must be very rare, which is remarkable in light of the abundance in Scandinavia (cf. discussions of DEGELIUS op. cit., pp. 18, 34, 42—44).]

Norway

Very common in forested areas except on the coasts of southern Norway, where it is much more sparse (e.g. LYNGE 1921, DEGELIUS 1934).

Sweden

Very common in northern and central parts but less common in the south and rare in Scania and on west coast (e.g. MAGNUSSON 1919). I have not seen any specimens from Gotland or Öland, either.

Finland

Common throughout the country.

Denmark

Rare. CHRISTIANSEN (1947) reported two localities for Zealand and two for Jutland. One additional record: Jutland: Viborg, leg. Branth (UPS).

Germany

Reported from a great number of localities (e.g. LETTAU 1957; GRUMMANN 1963), but very local and rare in all regions. I have seen specimens (M, S, S-Vr, a.o.) from Schleswig-Holstein, Niedersachsen (especially from the Lüneburg Heath), Brandenburg, Thuringia and Bavaria.

Switzerland

FREY (1959, pp. 216—217) reported a few localities, mainly in raised bogs, in Jura and the Bern Jura, but according to his descriptions on the habit of the specimens it is uncertain, whether any of the specimens are *P. olivacea* s.str. rather than *P. septentrionalis*.

Austria

There were no Austrian specimens in W, for instance. Most of the localities reported are referable to *P. glabra*, *P. septentrionalis* or other species. KLEMENT's (1964) record is correct: Tyrol. Fimbertal, Bodenalp, 1650 m, *Bet.*, 1963, Klement 3786 (H).

Italy

Montes Euganei, leg. ? (W). It is possible that this old specimen is mislabelled. The literature records usually mean *P. glabra*.

Czechoslovakia

According to SUZA (1937) rather common in the Bohemian Forest but elsewhere in Bohemia absent or very rare. In Moravia he reported only one station. Probably not known from Slovakia.

Poland

In the Olsztyn, Gdansk and Bialystok provinces probably scattered to rather common (e.g. LETTAU 1957, MOTYKA 1960). Absent or very rare in the south (e.g. SULMA 1935).

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Estonia

Common (e.g. RÄSÄNEN 1931; H. AASAMAA 1965, *in litt.*).

Latvia

Moricsala, *Bet.*, 1931, Linkola (H). — Probably rather common.

Lithuania

Not uncommon (e.g. MINKEVICIUS 1963).

White Russia

Scattered (e.g. TOMIN 1936) to very rare in the south. Several specimens (LE, a.o.) seen.

Ukraine

Dr. M. F. MAKAREVICH (1965, *in litt.*) has listed the literature records and the specimens under this name in KW. The older, apparently unreliable records (e.g. ELENKIN 1906, p. 148) are omitted. The specimens examined by Makarevich are mentioned here although some of them may belong to *P. septentrionalis* — also present in Ukraine — or other species. However, *P. olivacea* is not common in the country.

L'vov Dist. 15 km from Drogobych towards Striy, *Alnus* (MAKAREVICH 1947).

Volynia Dist. Shatsk area, near Pulemetsk, *Bet.*, leg. Kondrat'eva (KW).

Khmel'nitskiy Dist. Shepetovsk area, leg. Oksner (KW).

Kiev Dist. Chernobyl' area, Paryshevskaya lesnaya dacha, *Bet.*, leg. Makarevich (KW). — Kiev, Pushcha-Voditsa, leg. Oksner, Arkhimovich & Elin (KW). — Kiev-Svyatoshinsk area, Vorzel', leg. Arkhimovich (KW). — Rozvazhevsk area, Zhereva, *Bet.*, leg. Pelashenko (KW). — Verkhne-Dubechansk area, Starosel'skaya lesnaya dacha, *Bet.*, *Alnus*, leg. Makarevich (KW). Cherninskaya and Zhukinskaya lesnaya dacha, *Pinus*, leg. Oksner (KW). Near Verkhnyaya Dubechnya, *Bet.*, leg. Oksner (KW). — Near Kiev, Goloseev forest, Syrets, leg. Elin (KW).

Chernigov Dist. Gorodnyansk area, Snovsk, *Bet.*, leg. Arkhimovich (KW). — Priluki area, Levki, leg. Persidskiy (KW).

Vinnitsa Dist. Chernovtsy area, near Severinovka, Moivskoye lesnichestvo, on the Dnestr, leg. Isaeva (KW).

Kharkov Dist. Leg. Chernyaev (UPS; cf. FRIES 1855).

Chernovtsy Dist. Vyzhnitsk area, near Shepot, on R. Shepot, 980 m, *Alnus incana*, leg. Makarevich (KW; »f. *caesiopruinosa*»).

Russia

Apparently common throughout most of the republic, but absent in the very arid parts and tundras, and probably near the Pacific coast. In Europe rare south of the Moscow region but extending to Kaluga, Tula, Orel, and Tambov Districts and to Tatar A.S.S.R. and Bashkir A.S.S.R. (ELENKIN 1906, p. 149, MEREZHKOVSKIY 1920a, p. 105; numerous specimens — chiefly in LE — examined). Some southernmost records in the Ural Mts. and Siberia:

Bashkir A.S.S.R. Ufa, Shchitova, *Bet.*, 1878, Schell 13 (UPS). — Beloretsk, *Prunus padus*, 1878, Schell 95 p.p. (UPS).

Tyumen' Dist. Tyumen', Maranka, on Tura R., *Bet.*, 1914, Gorodkov (LE).

Omsk Dist. Tyukalinsk, Kitayla, *Bet.*, 1920, Gorodkov (LE).

Kemerovo Dist. Mariynsk area, *Bet.*, 1900, Sokolov (LE).

Altai Territory. Sara Koksha, *Sx*, 1931, Shishkin, Chilikina & Sumnevich 277 (LE).

Krasnoyarsk Territory. Yeniseysk, Cholkina, 1876, Brenner 112h (H). — Minusinsk area: R. Matur, Abaksha, *Bet.*, 1893, Martyanov (LE). R. Rybnaya, *Bet.*, 1907, Martyanov 187 (TUR).

Chita Dist. Aginskoye steppe, 1908, Mikhno (W).

See also var. *albopunctata*.

Canada

Saskatchewan

Higginson L., *Bet.*, 1960, Scotter 87 (WIS). — W. Oblate L., *Bet.*, 1960, Scotter 142 p.p. (WIS).

Manitoba

Kasmere L., *Bet.*, 1963, Scotter 2846 p.p., 2852 (WIS).

Ontario

Algoma Dist. Little White R., Twp 1B, *Bet.*, 1956, Cain 25893 (US). — On Lake Superior opposite to Lizard Is., 1960, Imshaug 26167 (MSC). — Lake Superior Prov. Park, Sand R., *Bet.*, 1960, Imshaug 26236 (MSC).

Cochrane Dist. Cochrane, Lillabelle L., *Alnus rugosa*, 1958, Ahti 4319 (H; as *P. aspera* in AHTI 1964 !). — NW of Cochrane, Greenwater Prov. Park, *Bet.*, 1959, Wetmore 5800 p.p., 5850 (MSC). — Gardiner, *Alnus*, 1959, Wetmore 5740, 5776b (MSC).

Nipissing Dist. L. Timagami: Kokoko L. Portage, *Bet.*, 1945, Cain 26778 (US). Gull L. Portage, *Bet.*, 1945, Cain 26557 (US). Bear I., *Bet.*, 1945, Cain 26559 (US). — Algonquin Prov. Park, headwaters of N. Madawaska R., *Bet.*, 1960, Imshaug 26767 (MSC).

Sudbury Dist. Chapleau, Racine L., *Bet.*, 1959, Wetmore 4039 (MSC). — Ivanhoe L. Prov. Park, 1959, Wetmore 6183 (MSC). — N of Gogama, *Bet.*, 1959, Wetmore 5573 (MSC).

Thunder Bay Dist. Lake Nipigon: 1884, Macoun, Can. Lich. 24 (UC). Whiteaves I., *Bet.*, 1958, Ahti 4307 (H). — Nipigon R., *Bet.*, 1884, Macoun 711 p.p. (CAN). — Geraldton, Kenogamisis L., *Bet.*, 1958, Ahti 4306 (H). — 18 mi. W of Marathon, Little Pic R., *Bet.*, 1959, Erbisch 749 (MSC). — Rossport, *Bet.*, 1958, Garton 5397 (CAN, US). — 6 mi. E of Rossport, White Sand Prov. Park, *Malus*, 1959, Erbisch 620 (MSC). — 20 mi. W of Rossport, 1959, Erbisch 812 p.p. (MSC). — Sibley Prov. Park: Silver Islet, *Bet.*, 1959, Erbisch 399 p.p. (MSC). L. Marie Louise, *Bet.*, 1959, Erbisch 407, 437a, 480 (MSC).

Timiskaming Dist. Gowganda, *Bet.*, 1959, Wetmore 5718 (MSC).

Quebec

Frontenac Co. Mégantic, *Bet.*, 1952, Masson 4301 (WIS).

Montmorency Co. (?) Laurentide Park, Grand Lac à l'Epaule, *Prunus*, 1960, Imshaug 26383 (MSC).

Newfoundland

Dist. unknown. Labrador, Capilan I., *Bet.*, 1894, Waghorne 203 (MIN). — Middle Arm, 1898, Waghorne 1123 (M).

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Minnesota

Clearwater Co. Itasca State Park, near Aiton Heights Tower, 1963, Hale 23245 p.p. (US).

Cook Co. Gunflint, 1897, Fink 395 (MIN). — Grand Portage I., *Bet.*, 1897, Fink 11 (MIN). — Harding, *Bet.*, 1901, Fink 1623 p.p. (MIN). — Susie Is., Belle Rose I., 1951, Thomson 4336 (WIS).

Koochiching Co. Rainy Lake City, *Bet.*, 1901, Fink 1167 (MIN).

Lake Co. N of Two Harbors, Encampment R., *Thuja occidentalis*, 1951, Thomson 4283 (WIS).

St. Louis Co. Near Bear Lake State Park, *Bet.*, 1963, Hale 24172 (US).

Wisconsin

Douglas Co. Dewey, *Bet.*, 1942, Thomson (WIS). — Brule R., *Bet.*, 1946, Thomson 2010 p.p., 2114 (WIS), *Amelanchier*, 1951, Gilbert (MIN).

Marathon Co. Granite Heights, 1946, Thomson 4147, 4148 (WIS).

Oneida Co. Tomahawk L., 1941, Thomson 819 (WIS).

Rusk Co. Ladysmith, 1921, Denniston (WIS).

Michigan

Houghton Co. Calumet, *Qu.*, 1957, Imshaug 20867 (MSC). — Upper entrance to Keweenaw Waterway, *Bet.*, 1958, Wetmore 1196, 1197, 1220 (MSC).

Iron Co. Kenton, Old Slate Mine, *Populus*, 1957, Imshaug 20742 (MSC).

Keweenaw Co. Isle Royale Natl. Park: 15 loc., mainly *Bet.*, one *Abies balsamea*, 1957—59, Wetmore, 17 nos. (MSC). Rock Harbor, *Bet.*, 1904, E. T. & S. A. Harper 176 p.p. (UC), 1930, Lowe 53 (S, UC). Hay Bay, *Bet.*, 1930, Lowe 756 (FH). — Keweenaw Point, West Mtn., *Bet.*, 1947, Thomson 3246 (Th, WIS).

Luce Co. Deer Park, *Bet.*, 1957, Imshaug 20325 (MSC, US), 20332a (MSC).

Marquette Co. Marquette, *Bet.*, 1906, Downing 1693 p.p. (NY), 1935, Mains (WIS).

Ontonagon Co. Porcupine Mts.: 1922, Darlington 6 p.p. (MSC). Government Peak, *Pinus strobus*, 1957, Imshaug 20656 (MSC).

New York

Essex Co. Chilson Lake, 1.200 ft, 1900, Harris (US). — 4 mi. S of North Elba, N of Heart L., 2.200 ft, *Amelanchier*, 1958, Hermann 14771 (US).

var. *albopunctata* (Asah.) Ahti

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Russia

All the Far East specimens of *P. olivacea* are listed here, although some of them could not be identified definitely as belonging to var. *albopunctata*.

Yakut A.S.S.R. Andir between Yakutsk and Aldan R., R. Mil', 1844, Middendorff (H-Nyl, UPS).

Amur Dist. Valley of R. Zeya, *Bet.*, 1908, Prokhorov & Kuzeneva 297, 303 (LE).

Kamchatka Dist. Avacha Bay, 1848, Seemann 1263 (K). — Mt. Avacha, 900 m, 1922, Hultén 4208 (UPS). — Between Petrovpavlovsk and Mt. Avacha, *Bet.*, 1920, Hultén 1060 (UPS). — Petropavlovsk, Petrovskaya, *Bet.*, 1921, Hultén 1540 (UPS), 1924, Malaise (UPS). — Bol'sheretsk, 1921, Hultén 2097 (UPS).

Khabarovsk Territory. Ayan, leg. Tiling (LE, UPS), 1855, Wright (FH; K, US, as »Ochotsk Sea»). — Udskoye, 1844, Middendorff (Deg, H, UPS). — R. Amgun valley, 1910 leg. ? (LE). — Oborskiy LPH, Durmin R., *Bet.*, *Larix*, 1939, Kolesnikov (LE; not mapped).

Sakhalin Dist. Korsakov, 1908, Faurie 284 p.p. (LE).

Japan

Hokkaido. Prov. Ishikari: Mt Ashibetsu (ASAHINA 1952).

Honshu. Pref. Yamagata: Matsuyama, foot of Mt. Asahi (op.cit.). — Pref. Fukushima: Mt. Iide, 2.500 m, 1898, Faurie 833 (BM, FH, LE, W). — Pref. Tochigi: Nikko, Mt. Mae-shirane (op.cit.). Nikko, Yumoto (op.cit.). Nikko, Sanno Pass, Kotoku, *Bet.*, 1.500 m, 1964, Degelius As-1104 (Deg. H). — Pref. Saitama: Chichibu-gun, Otaki-mura, Mt. Hakuseki, 2.036 m, *Abies veitchii*, 1949, Omura 338 (US). — Pref. Yamanashi: Mt. Fuji, near Komitake Shrine, *Alnus*, 2.370 m, 1964, Degelius As-935 (Deg, H). — Pref. Shizuoka: Mt. Fuji, Ohmiyaguchi 2-gome (ASAHINA 1952). Mt. Fuji, Ichigome, 2.225 m, 1879, Almquist (H-Nyl, S; see also ALMQUIST 1891). — Pref. Nagano: Kiso, 1914, Yasuda 23 (TUR-V).

Shikoku. Pref. Kochi (YOSHIMURA 1963).

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Alaska

Central Pacific Coast Dist. N. Cook Inlet area: O'Malley Road, 1953, Krog 147, 156 (O). Rabbit Cr. Road, 1957, Krog 1461 (O). — Kenai Pen:, Ninilchik, 1957, Krog 2298 (O). Skilak L., 1957, Krog 2601 p.p. (O). — Talkeetna Mts., Little Susitna R. S of Fishhook Cr., 1957, Krog 1462 (O).

Central Yukon River Dist. 3 mi. W of Fairbanks, NE of College, 500 ft, *Bet.*, 1954, Smith 2290 (FH, H, UC, US). — White Mts.: Lower Fossil Cr., 1953, Krog 756, 781 (O). Beaver Cr., E of Sheep Cr., 1953, Krog 3167 (O). — 20 km SW of Fairbanks, on Tanana R., *Alnus*, 1963, Viereck 7077 p.p. (WIS).

Habitat ecology

It is a frequently stated fact that *P. olivacea* grows most abundantly on birch (particularly *Betula pubescens*, *B. verrucosa*, *B. ermanii*, and *B. papyrifera*) and is also common on *Alnus* and *Sorbus* species, although it has been noted on a great number of other trees and shrubs (e.g. ELENKIN 1906; LYNGE 1921; KUJALA 1926; RÄSÄNEN 1927; KOSKINEN 1955, p. 158; RYABKOVA 1965, p. 14). Also it sometimes grows on rocks, even being fairly common on such substrata in northern Norway (LYNGE 1921). In an eastern

Fennoscandian collection of 360 specimens (H) examined by me the frequencies of the various substrata were as follows: *Betula* spp. 43 %, *Sorbus aucuparia* 15 %, *Alnus incana* 10 %, *A. glutinosa* 8 %, *Pinus sylvestris* 5 %, barkless wood (lignum) 5 %; 17 other tree and shrub species were represented by less than 5 % each. In other areas the proportions are somewhat different, but a general feature is that towards the southern margins of its range it becomes more and more confined to birch, and particularly to birches of open swampy forests, as in northern Germany (e.g. SCHULZ 1931; ERICHSEN 1939, 1957), Bavaria (e.g. ARNOLD 1891), Switzerland (FREY 1959), Bohemia (HILITZER 1925, SUZA 1937), and Moscow district (GOLUBKOVA 1959, p. 157).

It is also well-known that *P. olivacea* prefers open habitats; according to KOSKINEN's (1955, p. 176) measurements it is semisciophilous to moderately photophilous in central Finland. HILITZER (1925, p. 41) referred it to the group of mesophilous lichens in Bohemia, which grow in moderately humid habitats. Having also a good cold-resistance, it is understandable that *P. olivacea* is found optimally developed in the thin suboceanic upper oroboreal (subalpine) mountain birch woodlands in Scandinavia, where it is the most abundant epiphytic lichen (e.g. HÄMET-AHTI 1963a).

In the Scandinavian mountain birch forests *P. olivacea* is also a good indicator of the average snow-cover, since it strictly avoids lower parts of trunks with prolonged snow-cover (FREY 1927, p. 215, NORDHAGEN 1928, p. 98, KUJALA 1929, p. 34). HÄMET-AHTI (1963a, p. 22) even compiled a map of the lower limit of *P. olivacea* in the northernmost Fennoscandia, which beautifully correlates with the expected variation in thickness of snow-cover. However, in the middle boreal forests and south of them it can be hardly used as such an indicator, since there it is usually not very abundant on lower trunks of trees, but is concentrated on upper trunks, which are better illuminated. Along the edges of fields and open peatlands and on lake shores it is also commonly found on lower parts of trees, however. RÄSÄNEN (1926) regarded *P. olivacea* as an apophyte — a plant that benefits from human activities rather than suffers from them.

Role in plant communities

BARKMAN (1954) described an epiphytic community with *P. olivacea* as dominant, as a distinct association, *Parmelietum olivaceae*. Here the status of this community and the use of *P. olivacea* as a faithful species is discussed using the concepts of the French-Swiss school but with a more ecosystematic (cf. e.g. KRAJINA 1960) approach than that of BARKMAN. Of course, the epiphytic communities may be also and perhaps more properly understood as synusial types.

BARKMAN (1954, 1958, p. 466) based *Parmelietum olivaceæ* on a few relevees from northern Sweden and Norway and supposed it to be essentially subarctic, recording it from northern and central Scandinavia, Bohemia, and probably northern Russia and northern Siberia. The Bohemian records were referred to the variant *parmeliosum furfuraceae* (BARKMAN 1958), fragments of which may be also found in the Swabian Plateau, Brandenburg, and Poland. KLEMENT (1959) has published some data on this association from Sweden and Norway, which are apparently more representative than BARKMAN's. The records of HÄMET-AHTI (1963a) on the macrolichens of mountain birches in northern Norway and Finland also give a good idea of the composition of the association. The abundant members are *Parmelia olivacea, P. sulcata, Hypogymnia physodes* (but never *H. vittata*, although this species was recorded by KLEMENT), *Parmeliopsis ambigua, P. hyperopta, Cetraria pinastri, C. sepincola, Alectoria simplicior,* and *Leptorhaphis epidermidis.*

KLEMENT (1959) suspected that the variant (or subassociation according to his usage) *parmelietosum furfuraceae* is a mixture. It is in fact based on the records of HILITZER (1925, pp. 128—129) from Bohemia. Under the *Parmelia furfuracea* association HILITZER recorded a community (op. cit., Tab. XVIIa: 29—33), which he said »may be called a *Parmelia olivacea* variant» of the association. It is dominated by *Parmelia furfuracea* and *Hypogymnia physodes* and is only found on smooth trunks of birch locally in the Šumava district of the Bohemian Forest (alt. 870—1000 m). Similar communities are also common in e.g. southern and central Finland, and in my opinion they have not much to do with the true *Parmelietum olivaceae* but clearly belong to what is called *Parmelietum furfuraceae* (e.g. KLEMENT 1955, BARKMAN 1954, 1958). In Bohemia HILITZER (1925) found *P. olivacea* also in his *Parmelia sulcata* association on oaks and birches, though very sparsely. DU RIETZ (1945) included the communities rich in *P. olivacea* in central Sweden in his union *Physodeto-sulcatetum.*

BARKMAN (1954) considered the *Parmelietum olivaceae* to be clearly continental as did also KLEMENT (1959), although all the Scandinavian birch-dominated regions are somewhat oceanic. However, HÄMET-AHTI (1963a, p. 78) stated that in northern Norway the association is common and well-developed in both oceanic and (relatively) continental true subalpine birch forests, while only near sea level in the forests which she refers to as »submaritime» is is poorly developed. A possible explanation is that the coast is unfavourable because of denser woods, thicker snow, and frequent periods with temperatures above 0°C in the winter. However, one should also note that the so-called submaritime forests were later referred by HÄMET-AHTI (1963b; see also JALAS 1965) to the middle boreal zone, which in thermal sense corresponds to central Finland, where the association is also rather poorly developed.

In any case, the *Parmelietum olivaceae* is best developed in the northern boreal and upper oroboreal areas, and the more southern occurrences of the communities dominated by *P. olivacea* seem to have slightly different compositions. Such communities or »community fragments» are common in southern Finland on upper trunks and twigs of *Betula* in various kinds of forest. By the edges of fields and in open peatlands or on the shores of lakes they are also found on *Alnus*, *Sorbus*, and *Salix*. The tree species affect the composition of such communities, resulting in subassociations in addition to the variants controlled by the macroclimate. In conclusion, all the communities with abundant *P. olivacea* are characteristic of well illuminated, rather cold and humid habitats, as was emphasized by BARKMAN (1954) and by KLEMENT (1959).

In Asia well-defined communities with *P. olivacea* as dominant have not been reported, except by OMURA (1953) in Japan (see under *P. huei*). Even on the Pacific coasts, e.g. Kamchatka and Japan, where humid pure birch woodlands are widespread (e.g. HÄMET-AHTI 1963a, pp. 2—3; 1963b, map) *P. olivacea* does not seem to attain the same abundance it has in northern Europe.

In North America I only found *P. olivacea* in small colonies, and never in any great quantity. However, the numerous records of this species from the Lake Superior region and elsewhere indicate that it may be possible to distinguish communities related to the *Parmelietum olivaceae* even there.

2. *Parmelia septentrionalis* (Lynge) Ahti n. comb.

Plate 1.

P. olivacea var. *septentrionalis* LYNGE 1912, p. 4. — *P. olivacea* f. *septentrionalis* (Lynge) LYNGE 1921, p. 156. — Type: Norway. Troms: Målselven, Likkavarre, 2.VI.1911, (J. Holmboe &) B. Lynge (O, holotype; W, isotype).
P. olivacea var. *Normannii* Lynge (in sched.; W).
P. nitida Östman (in sched.; S, UPS).

Foliose, tightly appressed to the substrate, at the periphery as well as in the centre, forming rounded rosettes 1—3.5 (5) cm in diameter; the major lobes up to 0.5 cm long and 1—3 mm broad, margins irregularly crenulate; upper surface slightly convex to plane, dark brown, rarely white pruinose, irregularly wavy, somewhat rugulose but almost smooth and shiny in the periphery; laminal pseudocyphellae rarely abundant and then chiefly along the margins of the lobes and elongate in shape; lower surface light brown to black, smooth or sparsely trabeculate, densely rhizinate, the rhizines black, 25—35 μ long, unbranched.

Lobes 80—160 μ thick, upper cortex 5—8 μ, with many cell layers, algal layer 30—60 μ, medulla proper 60—150 μ, lower cortex 9—12 μ.

Apothecia numerous, crowded (density commonly 60 per sq.cm), small, up to 1—1.5 mm in diameter, concave when young but soon becoming flat to convex, shiny,

often covering the greater part of the upper surface and also present near the lobe tips; margin thin, slightly elevated to disappearing, smooth or rarely indistinctly crenulate, pseudocyphellate; subhymenium thin, 15—30 μ, pale, hymenium 50—75 μ, light brown, asci narrowly clavate, 15 × 35—40 μ, spores simple, ovoid, (5)6—7(9) × (9)10—13(14) μ, 8 in the ascus, commonly uniseriate; pycnidia common, pycnoconidia 0.5 × 4.5 μ, straight, cylindrical.

Reactions: PD + red, K—, C—, KC—; probably contains fumarprotocetraric acid.

Exsiccati examined (all distributed as *P. olivacea*):

CUMMINGS, Dec. N. Am. Lich. 105 (BM, CAN, NY, UC, US, WIS); CUMMINGS, WILLIAMS & SEYMOUR, Lich. Bor.-Amer. 26 (H, MIN, NY, S); ELENKIN, Lich. Fl. Ross. 104a p.min.p. (FH), 104c (FH); POELT, Lich. Alpium 96 (H, M,S); RÄSÄNEN (—HAKULINEN), Lichenoth. Fenn. 28 p.p. (H, Hak, OULU, TUR), 154 p.p. (Hak, M, OULU), 155 p.p. (Hak, OULU, TUR), 929 p.p. (Hak, M, OULU, TUR), 1077 (M), 1077 p.p. (Hak, OULU, TUR); REICHENBACH & SCHUBERT, Lich. exs. 89 p. min. p. (W); Rel. Farlow. Lich. 478 (BM, K, NY, O, UC, US, W, WIS); Rel. Tuckerm. 69 p.p. (BM, FH, US); SAVICZ, Lichenoth. Ross. 16 p. min. p. (H).

Taxonomy

LYNGE's (1912) description of *P. olivacea* var. *septentrionalis* is exhaustive and essentially agrees with mine, which is based on a much larger amount of material. The most characteristic features of *P. septentrionalis* distinguishing it from *P. olivacea* are smaller size, rarity of laminal pseudocyphellae, presence of apothecia on the peripheral parts (even very small specimens of *P. septentrionalis* have apothecia, unlike *P. olivacea* which may form large sterile rosettes), density and small size of apothecia, smoothness of apothecial margin, smaller spores, and thinner subhymenium. Any of these characters may seemingly overlap those of *P. olivacea* but in the overall picture really »intermediate» specimens are very rare. The difficult specimens seem usually to be depauperate *P. olivacea*.

In both the localities known to Lynge, *P. septentrionalis* was growing side by side with *P. olivacea*, and I have frequently seen them together in the field elsewhere. I have also seen a great number of mixed gatherings in herbaria. In these cases the two species are generally easily distinguishable. I have hesitated to designate *P. septentrionalis* as a separate species rather than as a subspecies or variety of *P. olivacea*, but the occurrence of mixed stands of the two without intermediates supports the use of this category. In addition, there are a great number of different though not fully conclusive characters separating them, and their distribution and ecology are not identical. In fact, *P. subolivacea* seems to be more closely related to *P. olivacea* than *P. septentrionalis* is, in spite of the differences in spores and chemistry.

Independently of LYNGE, the late Swedish amateur lichenologist MAGNUS ÖSTMAN recognized *P. septentrionalis* perfectly well, using the name »*Parmelia nitida* n.sp.» and also some other names (see HASSELROT 1943, p. 54),

which were never validly published. A good description in Swedish was found with one of his specimens. His numerous excellent specimens of *P. septentrionalis* — often purposely collected in mixed gatherings — from Härjedalen, Sweden, leave no doubt about the distinctness of *P. olivacea* and *P. septentrionalis*. Also MALME (1910, p. 116) mentioned that in North Sweden *P. olivacea* is often darker and more shiny, suspecting that there is a distinct race.

Pruinose specimens of *P. septentrionalis* are rarer than those of *P. olivacea*. However, some examples have been collected in Finland, Siberia (several localities), and Alaska.

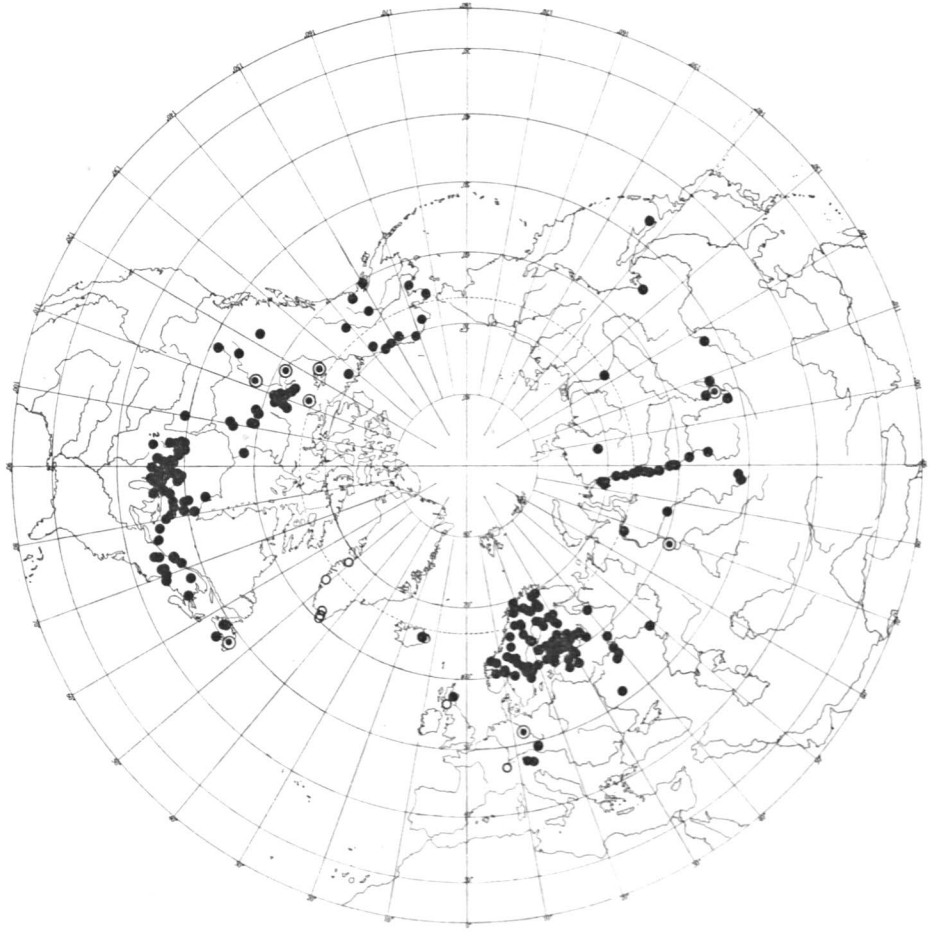

FIG. 3. Distribution of *Parmelia septentrionalis* (Lynge) Ahti.

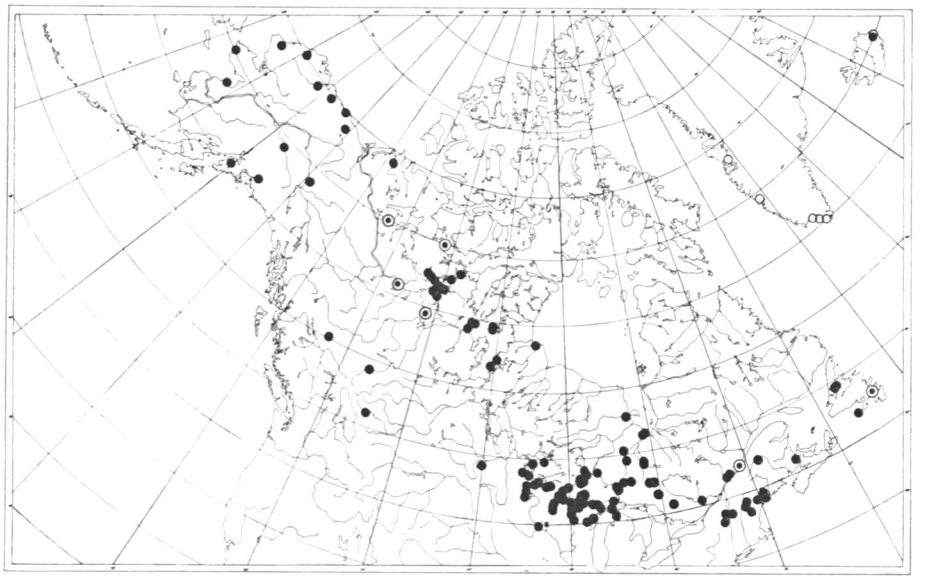

FIG. 4. Distribution of *Parmelia septentrionalis* (Lynge) Ahti in North America.

Distribution

(Figs. 3, 4.)

As far as I know, the two localities reported by LYNGE (1912, 1921) from Norway and one mentioned by RASSADINA (1938) from Altai Mts. are the only ones published under the epithet *septentrionalis*. POELT, who took up *P. olivacea* var. *septentrionalis* in his recent keys for the European macrolichens (1962), has suspected, quite correctly (in herb., M) that some Canadian specimens should be referred to this taxon. In fact, *P. septentrionalis* is widespread and often common in boreal areas of the northern hemisphere. In northern Europe it has been collected relatively little, apparently because of the abundance of the similar *P. olivacea*, but in eastern North America, where the latter species is less abundant, it is comparatively well represented in herbaria.

P. septentrionalis is completely circumpolar, ranging continuously over northern Eurasia and North America and occurring also in Scotland, Iceland and (probably) Greenland. No records are available from Japan. In the interior parts of the continents it may be commoner than on the coasts. It hardly extends beyond the hemiboreal zone in the south, and may be most abundant in the northern boreal regions. A very few isolated mountain stations are known: e.g. the Alps in the Tyrol, the Bohemian Forest in Czecho-

slovakia, and the Rocky Mountains in southern Alberta, although the latter may not in fact be isolated.

The specimens examined (a great number of them are to be found under *P. olivacea* in herbaria, being mixtures of *P. olivacea* and *P. septentrionalis*):

Great Britain

Moray (*v.c. 95*). Aviemore, 700 ft, *Bet.*, 1955, Laundon 1169 (BM).

Argyll Main (*v.c. 98*). Loch Awe, N. Port Sonachan, *Alnus* (LAMB 1942, p. 323, as *P. olivacea:* not verified).

Iceland

S. Múlasysla. Hallormsstadaskogur, *Bet.*, 1956, Degelius (Deg.). LYNGE (1940) reported *P. olivacea* from the same place and from Húsavík. Very rare in the country (cf. DEGELIUS 1957).

Norway

Hedmark. Tynset, 1913, Östman (O).

Oppland. Brandbu, 1908, Lynge (Th). — Dovre: Toftemoen, 1870, Zetterstedt (UPS). — Gausdal: sanatorium, 1883, Brenner 9850 (H). — Gudbrandsdalen, leg. Blytt (UPS).

Buskerud. Hol: Geilo, *Bet.*, 1947, Degelius (Deg).

Möre and *Romsdal.* Norddal: Grönningsäter, 1947, Magnusson 20589 (UPS).

Troms. Målselven: Likkavarre, *Alnus incana*, 1911 Holmboe & Lynge (O, W); by the church, on rocks, 1911, Lynge (S-Vr). — Tromsö, *Sx*, 1931, Degelius (Deg).

Sweden

Östergötland. Kvarsebo, 1910, Hulting (UPS).

Närke. St. Mellösa: Ytterby, Kungsstenen, 1891, Hellbom (UPS).

Uppland. Balingsta: Ölsta, Sävaån, *Prunus padus*, 1962, Greta Du Rietz (Herb. Greta Du Rietz). — Bromma: Johannelund, *Populus tremula*, 1911, Du Rietz (UPS). — Brännkyrka, *Bet.*, 1910, Hülphers (S-Vr). — Funbo: Broby, *Bet.*, 1960, Nordin (Nord). — Sollentuna: Rotebro, *Sorbus aucuparia*, 1942, Santesson (S).

Västmanland. Kila: Jumsebosjön, *Bet.*, *Sorbus aucuparia*, 1961, Nordin 227a (Nord). Kåttbo, *Bet.*, 1965, Nordin 2892 p.p. (Nord, UPS). — Sala: the mine, *Bet.*, 1942, Degelius (Deg).

Värmland. Sunne: Åmberg, 1910, Hülphers (S).

Gästrikland. Ovansjö: Gardsjön, *Alnus incana*, 1933, Ahlner (Ahln).

Dalarna. Rättvik: Sjuberg, *Alnus incana*, 1931, Vrang 216 (S).

Hälsingland. Ängersjö: Ängersjö, *Sorbus aucuparia*, *Bet.*, rails, 1895 and 1897, Östman (H, OULU, S). Öjingsvallen, *Sorbus*, 1903, Östman (S). Orrnäset, *Populus tremula*, 1900, Östman (S).

Härjedalen. Linsäll: Linsäll, *Sx*, 1912, Franzén (S). — Tännäs: ca. 20 loc., chiefly in Funäsdalen, Ljusnedal and Bruksvallarna (cf. HASSELROT 1943, pp. 18—22, 54), mostly on *Sx*, 1912—13, Östman (mainly S; Deg, Th). — Älvros: Kolsätt, Suavallen, *Sorbus*, 1903, Östman (S). Högen, *Bet.*, 1904, Östman (S).

Jämtland. Näskott: Taxelven 1907, Faxén (S). — Rödön: W Ytterån, Badhusudden, *Alnus incana*, 1939, Faxén (UPS).

Åsele Lappmark. Vilhelmina: Klimpen, 1926, Degelius (UPS).

Västerbotten. Holmsund: Umeå uthamn, *Alnus incana*, 1965, Nordin 2858a p.p. (Nord). — Norsjö: Norsjö, *Sorbus*, 1932, Schröler 94 (UPS). Rengård, *Sx*, 1932, Schröler 93 (UPS) — Umeå: Ålidbacksområdet, *Populus tremula*, 1965, Nordin 2850a p.p. (Nord).

Norrbotten. Övertorneå: Mikkola island, *Populus tremula*, 1930, Degelius (Deg).

Pite Lappmark. Arjeplog: Vuoggatjålmejaure, E side, *Bet.*, 1935, Arwidsson (S).

Lule Lappmark. Gällivare: Stora Luleälv, Petsasts, *Sorbus aucuparia*, 1962, G. Eriksson 214 (Herb. G. Eriksson). — Jokkmokk: Lilla Luleälv, Blackälven, Taurejuädno, Snärak, *Alnus incana*, 1962, G. Eriksson 198a (Herb. G. Eriksson).

Torne Lappmark. Jukkasjärvi: Abisko, Kårsavagge, 1961, Thomson 9966 p.p. (MSC).

Finland

Alandia. Finström: Amnäs, *Fraxinus excelsior*, 1913, Warén (TUR).

Regio aboënsis. Lieto: Uotila, *Bet.*, 1963, Kärenlampi (TUR). — Turku: Hirvensalo, *Juniperus communis*, 1935, Laurila (TUR).

Nylandia. Askola: Monninkylä, Sikomäki, *Bet.*, 1940, Tynni (H). — Espoo: Röylä, *Alnus incana*, 1965, Ahti 17031 (H). — Helsinki: Mellunkylä, *Sx phylicifolia*, 1965, Ahti 17037 (H). Vartioharju, Broända, *Sx phylicifolia*, 1965, Ahti 17064 (H). — Kirkkonummi (Kyrkslätt): Lövholmen, *Bet.*, 1864, Kullhem (H). Masala, Sundet, *Alnus glutinosa*, 1940, Häyrén (H). — Tuusula: Maantiekylä, *Bet.*, *Sx caprea*, *S. phylicifolia*, 1965, Ahti 17028, 17029, 17032 (H).

Karelia australis. Vehkalahti: Pyhältö, *Sorbus auc.*, 1947, Fagerström (H).

Satakunta. Sine loco, 1859, Malmgren (H).

Tavastia australis. Hollola: Häyhti, 1872, Lang (TUR-V). Hersala, *Bet.*, 1873, Lang (TUR-V). — Jokioinen: *Alnus incana*, 1910, Salmenlinna (H). — Lammi: Evo, *Alnus incana*, 1874, Norrlin (H). — Luhanka: Lempää, *Malus*, 1908, Sola? (H). — Padasjoki: *Pinus*, 1872, Lang (TUR-V).

Savonia australis. Savonlinna: Suuri Simanansaari, *Sx*, 1965, Isoviita (H). — Taipalsaari: Karhunpää, *Sx myrsinifolia*, 1965, Vitikainen (H). — Valkeala: Saarento, *Sx pentandra*, 1940, A. Ulvinen (H).

Ostrobottnia australis. Alavus: Niinimaa, Patama, *Sorbus auc.*, 1946, Leppälä, RÄSÄNEN, Lichenoth. Fenn. 154 p.p. (Hak, M, OULU). — Karijoki: Peni NW, 1946, Railonsala (TUR). — Lapväärti: Slätmosa; Holmosa; Peni — Lapväärti; Pyhävuori; Perus; Torngrund; *Sx myrsinifolia*, *S. aurita*, *Bet.*, *Alnus incana*, 1946 and 1953, Railonsala (mainly TUR; Hak, OULU). — Tiukka: *Bet.*, 1946, Railonsala (TUR).

Tavastia borealis. Saarijärvi: Mahlu, *Prunus padus*, 1935, Koskinen (H).

Savonia borealis. Kuopio: Savilahti, *Alnus incana*, 1905, Linkola (H). Huuhanmäki, *Alnus incana*, 1907, Linkola (H). Kolmisoppi, *Alnus incana*, 1933, Lumiala (H). Puijonrinne, *Alnus incana* and *Prunus padus*, 1946, M. Sovinen, RÄSÄNEN, Lichenoth. Fenn. 28 p.p. (H, Hak, OULU, TUR).

Karelia borealis. Ilomantsi: Patrikka, *Bet.*, 1937, Ahlner (Ahln).

Ostrobottnia kajanensis. Kuhmo: Koskenmäki, *Sorbus aucuparia*, 1956, Railonsala (H, Hak), HAKULINEN, Lichenoth. Fenn. 1077 (M), 1077 p.p. (Hak, OULU, TUR). — Ristijärvi: Mustavaara, Laitala, *Sorbus aucuparia*, 1956, Railonsala, HAKULINEN, Lichenoth. Fenn. 929 p.p. (Hak, M, OULU, TUR).

Ostrobottnia borealis. Ii: Räynä, 1864, Brenner (H). — Kemi: *Sorbus aucuparia*, 1912, Häyrén (H). — Oulu: Tuira, 1927, Lindström (OULU). — Simo: *Prunus padus* and *Alnus incana*, 1915 and 1916, Räsänen (H). Tiurasenkrunni, 1920, Räsänen (TUR).

Kuusamo. Kuusamo: Kuusamo, Toranginjärvi, *Bet.*, *Sx*, 1965, Ahti 20153, 20154 (H).

Lapponia enontekiensis. Enontekiö: Toskaljärvi SE, *Sx*, 1947, Huuskonen (OULU). Urtasvankka, Urtasjärvi, *Sx*, 1955, Huuskonen (TUR). Karesuvanto, Sakkaravaara, *Bet.*, 1957, Huuskonen (OULU). Naimakka, *Bet.*, 1964, Eurola (OULU).

Lapponia inarensis. Inari: Laanila, Laanioja, *Bet.*, 1931, Kari (TUR). Ukonjärvi, *Bet.*, 1951, A. & R. Hakulinen 1503b (Hak.) — Utsjoki: Karigasniemi, *Bet.*, 1951, Degelius (Deg). Kevo, mouth of Tšarsjoki, *Sx phylicifolia*, 1965, Ahti & Poelt (Herb. J. Poelt).

Prov. unknown. »Lapponia tornensis», 1856, E. Nylander (H).

Germany

Sine loco, REICHENBACH & SCHUBERT: Lich. exs. 89 p. min. p. (W); leg. Auerswald (LE).

Switzerland

At least some of the localities of *P.* »*olivacea*» listed by FREY (1959) may belong here see under *P. olivacea*).

Austria

C a r i n t h i a. Sine loco, *Bet.*, leg. ? (W; very old specimen).

T y r o l. Stubaier Alpen: above Steinach, 1.250 m, *Bet.*, 1958, Steiner, POELT, Lich. Alpium 96 (H, M, S); 1.100 m, *Fraxinus*, 1964, Klement 9768 (Klem).

Czechoslovakia

B o h e m i a. Bohemian Forest, Šumava, Kvilda, *Bet.*, 1924, Hilitzer (UPS).

U. S. S. R.

Estonia

Tartu, 1958, Aasamaa 3 p.p. (Th).

Ukraine

S u m y D i s t. Shpilevka, 1903, Nosovich (LE).

Russia

M u r m a n s k D i s t. Salla, E end of L. Korvasjärvi, *Alnus incana*, 1937, Lehtonen & Pankakoski (H).

K a r e l i a n A.S.S.R. Konchezero, 1928, Polyanskiy 42 (LE). — Sortavala, Kotiluoto, *Bet.*, 1926, Kari (TUR). — Vieljärvi: Pihtilahti, *Sx phylicifolia*, 1943, Railonsala (TUR); Pihtilahti, Leppäselkä, *Juniperus, Alnus incana*, 1943, Railonsala (TUR); Pihtilahti, Harsava, *Sorbus aucuparia*, 1942, Railonsala (TUR); Kukkajärvi, *Sorbus aucuparia*, 1942, Railonsala (TUR); Jyrkilä, Jyrkilänsaari, *Prunus padus*, 1944, Railonsala (TUR); Klessoila, *Alnus incana*, 1944, Railonsala (TUR).

A r k h a n g e l s k D i s t. Obozerskaya Sta., *Bet.*, 1914, Anufriev 11 (LE).

L e n i n g r a d D i s t. Lakhta, *Bet.*, 1919, Savich (LE), 1903, Elenkin, ELENKIN: Lich. Fl. Ross. 104a p.p. (FH). — Sablino: *Bet.*, 1926, Nikolskiy (FH, LE); Chertovo, 1907, Vereitinov (LE). — Petrodvorets, *Tilia*, 1920, Ganeshin (LE). — Luga, *Crataegus*, 1925, Ganeshin (LE). — Kozlovka, *Bet.*, 1925, Rajllo, SAVICZ: Lichenoth. Ross. 16 p. min. p. (H, not mapped). — Minova, *Malus*, 1943, Räsänen (H). — Antrea (Kamennogorsk), *Bet.*, 1920, Porkka (TUR). — Narva R., 1907, Romenskiy & Savich (LE).

V o l o g d a D i s t. Vologda, Pribyrkovo (?), *Bet.*, 1927, Dostoynova (LE).

Y a r o s l a v l D i s t. Komarovo, 1903, Elenkin (LE).

M o s c o w D i s t. Leg. Czermack (LE). — Markovo, 1903, Elenkin (LE). — Lyubertsy, 1903, Elenkin, ELENKIN: Lich. Fl. Ross. 104c (FH).

V l a d i m i r D i s t. Kirzhach, R. Kirzhach, *Alnus glutinosa*, 1911, Kuznetsov (LE).

T a t a r A.S.S.R. Kazan, Nemetskaya Shveitsariya, 1883, Krylov (LE); Lebyazhye L., 1883, Krylov (LE).

T y u m e n' D i s t. Salekhard (Obdorsk), *Bet. nana* in tundra, 1914, Gorodkov (LE). — Kalimskiy on the Ob, *Pinus cembra*, 1876, Brenner 565i (S). — Artamanoyova, 1876, Brenner 577g (S). — Selekina, 1876, Brenner 621b (S).

K r a s n o y a r s k T e r r i t o r y. Along the Yenisey R. (all collected by Magnus Brenner in 1876): Potapovo, no. 687 p.p. (H); Tolstoy nos, marker on a grave, nos. 685u, 1800 p.p. (S); Dudinka, no. 1184b (S); Nikandrovskiy ostrov, *Alnus viridis*, nos. 1796d, 1848c (S), 1826d (H), 1843b (S, UPS); Tatyanova, no. 488e (S); Malo-Briochovskiy ostrov, *Alnus viridis*, no. 1810a (S); Nikulino, *Abies sibirica*, nos. 189a (S), 189b (H); Ust'-Kureyka, nos. 4811 p.p. (S), 1343 p.p. (H); Turukhansk, no. 1303a (S); Chulkovo, *Alnus viridis*, no. 270d (S); Plakhino, no. 771b (S); 9 verst S of Plakhino, nos. 774i p.p. (H), 774j (S), *Bet.*, 763b (S); Vorogova, *Alnus*, no. 1716c (S); Anisovo, no. 224h p.p. (S); Podporozhenskaya derevnya, *Bet.*, no. 72c (S); Podkamennaya Tunguska, *Alnus viridis*, no. 249f (S), *Abies sibirica*, no. 1708k p.p. (S); Novosaleskaya, *Bet.*, nos. 1294e p.p. (S), 1294f p.p. (UPS); 61 verst N of Yeniseysk, *Prunus padus*, no. 1034b (S); Yeniseysk,

nos. 114a, 142e, (S); Yeniseysk, Cholkina, no. 165 p.p. (S); Vershininskoe, *Alnus viridis*, no. 54h (FH); Krasnoyarsk, *Crataegus*, nos. 66a (S), 66b (H). — Headwaters of Khatanga R., Boganida R., *Alnus*, 1843, Middendorff (LE). — Pozeka, *Bet.*, *Alnus*, leg. Kostmanov (TUR-V). — R. Tandaka, *Bet.*, 1908, Kubischov (LE; not mapped).

Yakut A.S.S.R. Zhigansk, *Bet.*, 1901, Cajander (HSI), 1901, *Larix*, Cajander 145 (HSI), *Abies sibirica*, 1901, Cajander 172 (H).

Altai Territory. L. Teletskoye, mouth of R. Koldor, *Prunus*, 1931, Shishkin 348 (LE). — Headwaters of R. Kanas, *Bet.* shrub in alpine tundra, 1931, Rassadina 394 (LE). — Sara Koksha, *Prunus padus*, 1931, Shishkin, Chilikina & Sumnevich 236 (LE).

Irkutsk Dist. Valley of R. Tutura, mouth of R. Murtukan, *Bet.*, 1910, Kuznetsov 273 p.p. (LE). — L. Baikal, W shore: 51° 50′ N., *Rhododendron dahuricum*, 1928, Sukachev, Rassadina & Bryzzhev 27 p.p. (LE); Khargan, *Bet.*, 1928, Rassadina 211 p.p. (LE). — L. Baikal, E shore, Barguzin, Bannaya, 1928, Rassadina (LE).

Chita Dist. Nerchinsk, 1906, Stukov 22 (LE).

Khabarovsk Territory. Udskoe, 1844, Middendorff (Deg, H, UPS).

Sakhalin Dist. Korsakov, 1908, Faurie 284 p.p. (LE).

Greenland

»*P. olivacea*» is rare in the southwest (DAHL 1950) and once collected in Central West Greenland (HANSEN 1962). No specimens seen by me but since *P. olivacea* s.str. is not known from Iceland and arctic Canada and since HANSEN's (op.cit., p. 36) note (»only a single and rather small, but richly fertile, specimen was found on a twig») probably refers to *P. septentrionalis*, all the Greenland localities have been mapped under the latter species (as open rings).[1]

Canada

Northwest Territories

Mackenzie Dist. Great Bear L., 1826, Richardson 92 p.p. (K), sine no. (M). — Anderson R., Hook L., *Sx*, 1964, Lambert 49 (WIS). — Great Slave Lake area: 1826, Richardson 36 (FH), 92 (NY), sine no. (BM, M). Et Then I., 1951, Lindsey 13 p.p. (CAN). Fort Reliance, *Bet.*, 1962, Thomson & Larsen 11262, 11707 (WIS). Artillery L., Timber Bay, *Bet.*, 1962, Thomson & Larsen 11413 (WIS). Ross L., *Bet.*, 1961, Scotter 3798 (WIS), Ahti 10267 (H). W. Desperation L., *Bet.*, 1961, Scotter 1663 (WIS). Taltson R., *Bet.*, 1962, Scotter 2367 (WIS). E. Rutledge L., *Larix*, 1962, Scotter 2262 (WIS). Gagnon L., *Bet.*, 1962 Scotter 2208a (WIS). Thekulthili L. *Bet.*, *Alnus*, *Sx*, 1962, Scotter 2492, 2498, 2536 (WIS). — Coppermine R., »Sandstone Rapids», *Picea glauca*, 1915, Johansen (CAN).

Yukon

Hunker Creek and Bonanza Creek, *Bet.*, *Alnus*, 1902, Macoun 27 p.p. (CAN, FH).

British Columbia

Sine loco, 1875, Macoun, Fl. Canad. 2704 p.p. (K). — Blackwater R., 1875, Macoun 713 (= 44, 56) (CAN).

Alberta

Athabaska R., 1888, Macoun 715 (CAN). — SW of Whitecourt, *Bet.*, 1961, Nyland 88 (WIS). — 12 mi. S of Morley, Jumping Pound Creek, 4.100 ft, 1963, Simpson 17 (UAC).

Saskatchewan

Higginson L., *Bet.*, 1960, Scotter 87 (WIS). — N.W. Offset L., *Bet.*, 1960, Scotter 132 (WIS). — W. Oblate L., *Bet.*, 1960, Scotter 142 p.p. (WIS).

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[1] I have recently examined the Greenland specimens (8) of *P. »olivacea»* in Botanical Museum, University of Copenhagen, and found that all of them clearly belong to *P. septentrionalis*.

Manitoba

Fort Churchill, *Sx*, 1950, Thomson 3847 (CAN), 3902 (CAN, Th, WIS), *Bet.*, 1954, Beckett M-32 (US, WIS). — Lynn Lake, 1958, Doorrman (WIS). — MacBride L., *Bet.*, 1955, Ritchie 1202 (WIS). — Turtle Mts., 2.200 ft., *Bet.*, 1962, Looman 621206 (WIS). — Cochrane R., *Alnus, Sx, Bet.*, 1963, Scotter 2766, 2767, 2776, 2778 (WIS). — Kasmere L., *Alnus, Bet.*, 1963, Scotter 2831, 2846 (WIS).

Ontario

Algoma Dist. Lake Superior Prov. Park: S of Baldhead R., 1960, Imshaug 26088 (MSC). 1 mi. S of Agawa R., *Abies balsamea*, 1958, Imshaug 21816 (MSC).

Carleton Co. Ottawa: 1894, Macoun, Can. Lich. 24 (K). Rideau Park, 1897, Macoun 723 p.p. (CAN).

Cochrane Dist. Cochrane, Lillabelle L., *Alnus rugosa*, 1958, Ahti 4311 (H). — Gardiner, *Alnus* and *Sx*, 1959, Wetmore 5775, 5786 (MSC). — Moosonee: Shipsands I.; on Moose R. opposite to Moosonee; airport, *Sx* and *Alnus*, 1959, Wetmore 5885, 5890, 5917 (MSC), 5970 p.p. (H). — Martison L., *Sx bebbiana*, 1958, Ahti 4316 (H). — Mattice, *Sx*, 1958, Lepage 14094 (WIS).

Kenora Dist. Attawapiskat, *Larix laricina*, 1958, Ahti 4312 (H). — Dryden, *Alnus*, 1956, Cain 25891 (US). — 35 mi. SE of Kenora, Ethelma L., *Bet.*, 1957, Cain 26401 (US).

Nipissing Dist. Algonquin Prov. Park, Deer L. Trail, *Abies balsamea*, 1960, Imshaug 27197 (MSC). — L. Timagami, Bear I., *Sx*, 1938, Cain 18725 (UPS).

Sudbury Dist. Ivanhoe L. Prov. Park, *Alnus*, 1959, Wetmore 6138 (MSC). — Chapleau, Racine L., *Alnus*, 1959 Wetmore 4038 (MSC).

Thunder Bay Dist. Nipigon R., *Alnus*, 1884, Macoun 711 p.p. (CAN). — Sibley Prov. Park, Silver Islet, *Populus balsamifera*, 1959, Garton 5961 (CAN, US), *Malus* and *Bet.*, 1959, Erbisch 399 p.p. (MSC). — Isle St. Ignace, St. Ignace Har., *Prunus pensylvanica*, 1958, Ahti 4297 (H). — 18 mi. W of Marathon, Little Pic R., 1959, Erbisch 777 (MSC). — E of Nipigon, 1959, Erbisch 859 (MSC).

Timiskaming Dist. 4 mi. W of Elk Lake, *Sx*, 1959, Wetmore 5524 (MSC). — Gowganda, *Sorbus*, 1959, Wetmore 5726 (MSC).

Dist. unknown. Millsville, *Larix*, 1897, Macoun, Can. Lich. 293 (CAN).

Quebec

Champlain Co. S.-Timothée, *Fagus* and *Picea glauca*, 1954, Masson 6767, 6863, 6873 (WIS). — S.-Roch-de-Méhinac, *Sx*, 1954, Masson 6915 (WIS).

Montmorency Co. (?) Ste-Anne-des-Monts R., 1882, Macoun 707 (CAN).

Portneuf Co. Hervey-Jonction (Chemin Masketsy), 1954, Masson 6717, 6718 (WIS).

New Brunswick

Westmorland Co. Canaan Forks, 1887, Macoun 714 (CAN).

Newfoundland

Humber East Dist. NE end of Birchy L., *Prunus*, 1956, Ahti 5881 (H). — Cormack, *Alnus rugosa*, 1956, Ahti 5943 (H).

Dist. unknown. Northern Arm, 1894, Waghorne 19 (M).

St. Pierre and Miquelon

Miquelon, *Bet.*, 1883, Delamare (M).

U. S. A.

Alaska

Arctic Coast Dist. Umiat, *Alnus*, 1958, Thomson & Shushan 6250 (M, US WIS), 6274 (US, WIS). — S of Wainwright, Kaolak R., *Sx*, 1958, Shushan & Maher 5249 (WIS), 5306 (S, US, WIS). — Valley of the Okpilak R., at Okpilak L.: *Sx*, 1957,

Cantlon & Gillis 57-2051 (MSC), *Bet.*, 1958, Cantlon & Malcolm 58-234 (MSC). Near Mt. Michelson, *Sx*, 1958, Thomson & Shushan 9166 (US, WIS), 11564 (WIS). — Valley of Mancha Creek and Firth R., *Sx* and *Alnus*, 1958, Sharp 6517a, 6530 (WIS). — 15 mi. upstream from Cape Sabine, Pitmegea R., *Bet. nana* and *Sx*, 1958, Thomson 5200, 5370 (WIS). — Sagavanirktok R., Franklin Bluffs, *Bet.*, 1958, Thomson, Shushan & Koranda 9123 (WIS).

Bering Sea Dist. St. Michael, Whale Is., 1899, Setchell (FH, UC).

Central Pacific Coast Dist. Richardson Hwy, Mile 45, 1957, Krog 2600 (O). — Kenai Pen.: Salamatof, 1957, Krog 2299 (O). Skilak L., 1957, Krog 2601a (O).

Central Yukon River Dist. 20 km SW of Fairbanks, on Tanana R., *Alnus*, 1963, Viereck 7077 p.p. (WIS).

Minnesota

Beltrami Co. Bemidji, 1900, Fink 513 (MIN). — Red Lake, *Larix*, 1900, Fink 991 (MIN).

Cook Co. Tofte, 1897, Fink 585, 591 (MIN). — Grand Marais, *Abies balsamea*, *Alnus*, 1902, Fink 5152, 5160 (MIN).

Hennepin Co. Minneapolis (?), 1896, Fink (?) 131 (MIN).

Hubbard Co. 2 mi. E of L. George, *Fraxinus*, leg. Hale 22958 (US).

Koochiching Co. Koochiching, 1901, Fink 889 p.p. (MIN). — 3 mi. NE of Margie, leg. Hale 22113 (US).

Lake Co. Beaver Bay, 1897, Fink 712 (MIN). — Ely, 1948, Thomson 2706 (WIS).

Lake of the Woods Co. Baudette, *Abies balsamea*, 1901, Fink 56 (MIN).

Roseau Co. Warroad, 1901, Fink 141 (MIN).

St. Louis Co. Vermilion Lake, 1886, Arthur 80 (MIN). — Harding, *Bet.*, 1901, Fink 1623 p.p. (MIN). — Tower, 1901, Fink 1688 (MIN).

Co. unknown. 1896, Fink (NY). — Superior Natl. Forest, 1930, Denniston (WIS).

Wisconsin

Ashland Co. Oak Island, 1901, Fink 492 (MIN).

Douglas Co. Dewey, *Bet.*, 1942, Thomson (WIS). — E of Superior: 1942, Thomson 4155 (Th). Wisconsin Point, 1942, Thomson 1355 (Th). — Brule R.: *Amelanchier*, 1951, Gilbert (Deg, MIN), *Bet.*, 1951, Thomson 2010 p.p. (WIS). Near St. Croix L., 1942, Thomson 1125 (Th). Ranger Sta., *Prunus*, 1946, Thomson 2114 (Ahln).

Lincoln Co. 8.5 mi. NE of Merrill, *Acer*, 1946, Thomson 2436 (WIS). — NE corner, *Acer*, 1946, Thomson 2444 (UPS, WIS).

Marinette Co. Thunder Mtn., Thunder R., 1937, Thomson 920 (Th).

Vilas Co. Sayner: *Alnus*, 1941, Thomson 850 (Th, WIS). Stella L., 1938, Thomson (FH, Th, WIS).

Washburn Co. Sarona, *Larix*, 1939, Evans (Th, WIS).

Co. unknown (not mapped). Valley of the Wisconsin R.: near Lac Vieux Desert, 1893, Cheney 69 (Th, WIS). Linwood Ferry, 1894, Cheney 35-86 (WIS).

Michigan

Alger Co. Lake Au Train, 1959, Erbisch 939b (MSC).

Baraga Co. Covington, *Abies balsamea*, 1957, Imshaug 20822 (MSC).

Emmet Co. Cecil Bay, 1954, Comper (WIS).

Houghton Co. Calumet, *Qu.*, 1957, Imshaug 20867 p.p. (MSC). — Baltic, 1958, Wetmore 1390 (MSC). — Upper entrance to Keweenaw Waterway, *Bet.*, *Prunus*, 1958, Wetmore 1209, 1220 p.p., (MSC). — Rice Lake, *Thuja occidentalis*, *Alnus*, 1958, Wetmore 1271, 1273, 1301, 1314 (MSC).

Iron Co. Kenton, Old Slate Mine, *Populus*, 1957, Imshaug 20742 (MSC).

Keweenaw Co. Isle Royale Natl. Park: 9 loc., *Bet.*, *Thuja*, *Alnus*, *Sorbus*, 1959, Wetmore, 10 nos. (MSC). Rock Harbour, 1904, E. T. & S. A. Harper 176 p.p. (UC).

Luce Co. Upper Tahquamenon Falls, *Acer*, 1957, Imshaug 19880 (MSC).

Mackinac Co. Naubinway, *Larix*, 1956, Hale 11078 (US).

Marquette Co. Marquette, *Populus*, 1906, Downing 1693 p.p. (NY). — 4 mi. NW of Marquette, *Acer saccharum*, 1960, Hermann 16066 (US).

Menominee Co. S of Cedar R., Green Bay, 1957, Imshaug 20269 (MSC).
Ontonagon Co. Porcupine Mts., 1922, Darlington 6 p.p. (MSC).
Schoolcraft Co. Between Manistique and Munising, *Qu.*, 1957, Imshaug 20182 (MSC).

Maine

Aroostook Co. St. Francis, *Prunus*, 1893, Cummings & Teller, CUMMINGS: Dec. N. Amer. Lich. 105 (BM, CAN, NY, UC, US, WIS), CUMMINGS et al.: Lich. Bor-Amer. 26 (H, MIN, NY, S).
Kennebec Co. Albion, *Qu. rubra*, 1922, Parlin 7667 (FH).
Knox Co. Rockport, summit of Bear Hill, *Bet.*, 1911, Merrill (FH). — Warren, 1922, Fassett 322 (WIS).
Oxford Co. Buckfield, *Acer*, 1924, Parlin 7329 (FH).
Waldo Co. Freedom, *Prunus*, 1922, Parlin 7204 (FH).

New York

Essex Co. Chilson Lake, 1.200 ft, 1899, Harris (NY).
Saratoga Co. Alnus, 1882, Burt 13 (FH).
Co. unknown. 1873, Clinton (US).

Vermont

Rutland Co. Brandon, *Acer*, 1911, Dutton 528 (FH).

New Hampshire

Carroll Co. Chocorua, 1911, Farlow, Rel. Farlow. Lich. 478 (BM, K, NY, O, UC, US, W, WIS), *Larix*, 1911, Farlow (FH), *Malus*, 1910, Farlow (FH).
Coos Co. Summit of Mt. Washington, *Bet.*, 1894, Farlow ? (FH).
Grafton Co. North Woodstock, 1884, Cummings 10 (UC).
Co. unknown. White Mts., leg. Willey 39 (MIN), 1885, Farlow 425 (FH), leg. Tuckerman, Rel. Tuckerm. 69 p.p. (BM, FH, US). — Shelburne, 1894, Farlow (BM, FH), Duggar (WIS), Barber (WIS).

Habitat ecology

The majority of the specimens of *P. septentrionalis* have been collected from alders (especially *Alnus incana, A. rugosa, A. crispa* s. lat., and *A. viridis* s. lat.) and willows (especially *Salix pentandra, S. caprea, S. bebbiana, S. phylicifolia, S. myrsinifolia*), but it also grows on a variety of other trees and shrubs such as *Sorbus* spp., *Larix laricina, Betula* spp., *Prunus pensylvanica,* and *Abies balsamea.* In most cases it seems to occur as scattered individuals or in small patches. I have observed it forming more extensive cover on thin twigs of *Salix* and *Larix.* However, it is much less strong in competition with other lichens than *P. olivacea* and unlike the latter, it can hardly be designated as a dominant member of any widespread epiphytic community. It is commonly overgrown by e.g. *Hypogymnia physodes, Parmelia sulcata* or *P. olivacea.*

In the surroundings of Helsinki *P. septentrionalis* has been found to be most abundant in extensive alluvial willow stands, particularly on older twigs of *Salix phylicifolia.* It is usually associated with *P. olivacea,* which is

commonly more abundant, and *Cetraria sepincola*. It is noteworthy that it is very rare on the birches present in the same stands.

In general, *P. septentrionalis* seems to prefer less acid bark and more open and moist habitats than *P. olivacea*.

3. *Parmelia subolivacea* Nyl.

Plate 2B.

P. subolivacea NYLANDER in HASSE 1897, p. 445. — Type: U.S.A. California. Los Angeles Co., on *Quercus*, May 1894, H. E. Hasse (H-Nyl no. 34657, holotype). Concerning the typification see below.

Foliose, appressed, more rarely somewhat ascending at the margins, forming irregular rosettes ca. 4—7 cm in diameter; lobes 2—3 mm broad, shallowly divided, with rounded ends; upper surface dark brown to olive brown, not uncommonly white pruinose, dull or somewhat shining near the ends of the lobes, slightly to heavily irregularly wrinkled; scattered isidioid verrucae may be present on old individuals; laminal pseudocyphellae absent or scarce; lower surface smooth, blackish-brown in centre, light brown at margins, densely rhizinate and sometimes slightly trabeculate, rhizinae simple, usually 60—70 μ long, black to light brown, commonly reaching the very margins.

Lobes ca. 160 μ thick, upper cortex 15—25 μ, with several cell layers, algal layer 30—35 μ, medulla proper 120—150 μ, lower cortex 20—30 μ.

Apothecia common and frequently abundant, mainly in the centre but also at the periphery, 3—5 mm in diameter, very short-stalked, disc dark to pale brown; margin usually thin, crenate to smooth, pseudocyphellate, subhymenium 45—60 μ, hyaline, hymenium 45—50 μ, pale brown, asci cylindrical, 12—15 μ × 35—45 μ, spores short ellipsoid to globose, (4.5)6—8(9) × (6)7—10(11) μ, ratio breadth/length commonly 4:5, with fairly thick (1—1.5 μ) membrane, 8 in the ascus; pycnidia abundant, pycnoconidia 1 × 7—9 μ, acicular to subbifusiform.

Reactions: PD—, K—, C—, KC—. No acids identified.

Exsiccati examined: Crypt. exs. Mus. Vindob. 4016, as *P. olivacea* (H, K, LE, M, MSC, NY, S, US); F. E. & E. S. CLEMENTS, Crypt. Format. Color. 104, as *P. olivacea* (MIN, NY, US); HALE, Lich. Amer. Exs. 44, as *P. olivacea* (CAN, M, MSC, S, Th, UC, US); PLITT, Lich. Exs. herb. Hasse rel. 16 p. min. p., as *P. olivacea* (O, S).

Taxonomy

Although described as early as in 1897 *P. subolivacea* has been very rarely recognized by later authors. HALE & CULBERSON (1960) mentioned it, but few specimens so named were seen in the herbaria. The majority of them were found under *P. olivacea*. This is due to the similarity in habit of *P. subolivacea* and *P. olivacea*, to the fact that *P. subolivacea* has never been adequately described and perhaps to the confusion in typification of this species.

The only locality of *P. subolivacea* mentioned with the original description (HASSE 1897) is »on rocks, San Gabriel Mountains at 1500 meters alt. July 1894». However, such a specimen was found neither in NYLANDER's (H) nor

in HASSE's (NY and other herbaria) collections under *P. subolivacea*. It is quite obvious that the specimen regarded as the type by me (see above) is the only specimen so identified by NYLANDER (the measurements of the spores in the description and on the label are in full agreement) and HASSE errs in stating the type locality to be on rocks, probably referring to another, saxicolous specimen from the same area which was collected two months later. This kind of confusion is possible, because HASSE collected a large amount of lichen material near Los Angeles, especially San Gabriel Mts., in the course of several years.

P. subolivacea may most easily be distinguished from *P. olivacea* by the negative PD reaction, but the differences in the spores and the scarcity of pseudocyphellae, besides the ecology, distribution and some less easily defined morphological characters, decisively support its status as a separate species.

Distribution

(Fig. 5)

The range of *P. subolivacea* is clearly confined to western North America, and especially to the arid forest regions. It may be absent from the highly oceanic coastal areas, although in central and southern California it comes close to the coast. However, most records of this species are from New Mexico, Arizona, Colorado, and California, which is apparently also due to its higher frequency in those areas. It is almost certain that it will be found in Mexico, since it is common near the Mexican border in Arizona.

The specimens examined:

C a n a d a

British Columbia

»Brackendale», *Alnus*, 1916, Macoun 453 (CAN). — Lillooet, 1916, Macoun (FH).

Alberta

Kananaskis, 1885, Macoun 708 (CAN). — Morley, 1885, Macoun 710 (CAN). — Jumping Pound Creek: 1897, Macoun 640 (= 719) (CAN). 13 mi. S of Morley, 5.300 ft, decid. trees, 1963, Holeton 22 (UAC). — W of Calgary, 3 mi. WNW of Ghost Reservoir Dam, Jamieson Creek Valley, *Sx*, 1963, Bird 9142 (UAC).

Saskatchewan

Cypress Hills Park, 3.700 ft, *Picea glauca*, 1959, Looman 591201 (WIS).

U. S. A.

Washington

K l i c k i t a t C o. Goldendale, 1909, Foster 1163 p.p. (FH).

W h i t m a n C o. Pullman, 2.500 ft, *Crataegus douglasii*, 1948, W. B. & V. G. Cooke 24849 (NY, FH), 24850 (NY, WIS). — Kamiak Butte, 3500 ft, 1932, Herre (Th).

C o. u n k n o w n. Gary (?), 1901, Beattie 33 (FH).

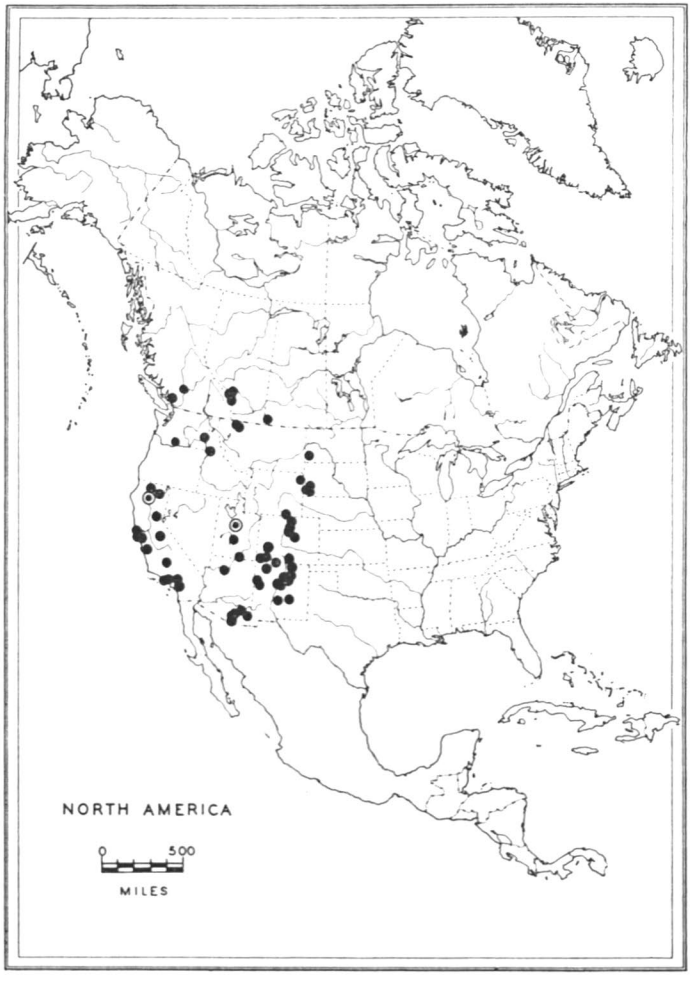

FIG. 5. Distribution of *Parmelia subolivacea* Nyl.

Idaho

Idaho Co. 7.5 mi. S of Stites, 1.500 ft, *Prunus virginiana*, 1962, Stickney 1025A (WIS).

Montana

Glacier Co. Glacier Natl. Park: Appekunny Creek Trail, 5.000 ft, 1950, Imshaug 5796 (MSC); Cracker L. Trail, 5.200 ft, *Pseudotsuga*, 1950, Imshaug 5859 (MSC). — 18 mi. W of Browning, conifers, 1962, Juneau 2 (WIS).

North Dakota

Billings Co. Th. Roosevelt Natl. Mem. Park, *Fraxinus pensylvanica*, *Prunus virginiana*, 1959, Dix 52, 103, 106 (WIS).

South Dakota

Custer Co. 11 mi. E of Custer, Custer State Park, 4.300 ft, *Qu.*, 1960, Wetmore 7587 (H). — 7 mi. NW of Hot Springs, 4.550 ft, *Pinus ponderosa*, 1961, Wetmore 10873 p.p. (H; with *Parmelia ulophyllodes*).

Pennington Co. Rapid City, 1891, Williams (NY).

California

Kern Co. 10 mi. N of Caliente, *Qu.*, 1962, Tavares & Brinson 1177 p.p. (UC).

Lassen Co. 9 mi. NW of Nubieber, Sugar Pine Mtn., *Abies concolor*, 1942, Miller (UC).

Los Angeles Co. Qu., 1894, Hasse (H-Nyl). — San Gabriel Mts., 1.300 m, 1897, Hasse (UC), 1906, Hasse 2153 p.p. (FH). — Santa Monica Mts., *Juglans californica*, 1902, Hasse (HSI). — San Antonio Mts.: Ontario Peak, 8.200 ft, *Abies concolor*, 1917, Johnston 3225 (FH). San Antonio Canyon, *Qu. chrysolepis*, 1918, Johnston 3181 (FH).

Marin Co. Mt. Tamalpais, *Qu.*, 1962, Thiers 9108 (WIS).

Mariposa Co. Yosemite Valley, 1896, Hasse, PLITT: Lich. exs. herb. Hasse rel. 16 p.p. (O, S).

Monterey Co. Hastings Natural History Reservation: *Qu.*, 1962, Tavares 856 p.p., 872 (UC); Carmel Valley, 1951, Zane (UC).

Nevada Co. 5 mi. N of Nevada City, 1961, Storer (UC).

Riverside Co. San Jacinto Mts., *Pinus ponderosa*, 1903, Hasse (H).

San Bernardino Co. San Bernardino Mts., leg. Parish, Herb. Hasse 185a (NY).

San Mateo Co. Devil's Canyon, 2.300 ft, *Qu.*, 1930, Herre (UPS).

Santa Clara Co. Santa Cruz Mts., Black Mtn., 1.600 ft, *Qu. wislizenii*, 1904, Herre 426 (103) p.p. (NY), Plitt 156 (HSI).

Shasta Co. Goose Valley, leg. Baker (UC).

Siskiyou Co. Mt. Shasta, Hotlum Sta., N side of Shastina, 5.500 ft, *Cercocarpus ledifolius*, 1941, Cooke 15750 (UC).

Utah

Kane Co. Navajo L., 8.500 ft, *Picea*, 1951, Flowers (Klem).

Sevier Co. Fish L., 9.000 ft, 1894, Jones 3755 p.p., s.n. *Theloschitis parietina* (BM).

Co. unknown. »Wasatch», 1869, Watson 1490 (NY, US).

Wyoming

Albany Co. Centennial Valley, 1897, Nelson 3346 (NY).

Crook Co. 22 mi. N of Sundance, Beaverdam Creek, 4.600 ft, *Pinus ponderosa*, 1960, Wetmore 9924 (H).

Colorado

Archuleta Co. Chromo, 8.000 ft, 1955, Shushan S9911 (MSC).

Boulder Co. Boulder, 1921, Merrill 22, 102b (FH), 1954, Hale, HALE: Lich. Amer. Exs. 44 (CAN, M, MSC, S, Th, UC, US). — SW of Boulder, Green Mtn., 7.000 ft, *Pseudotsuga*, 1954, Weber S2190 (UC, WIS), 1955, Shushan & Weber S4834 (CAN, FH, S, UPS), Crypt. Exs. Vindob. 4016 (H, K, LE, M, MSC, NY, S, US). — Boulder Canyon, above Boulder Falls, 7.500 ft., *Jamesia americana*, 1957, Viereck 1908 (LE). — W of Boulder, between Flagstaff Mtn. and Green Mtn., 6.000 ft, *Acer glabrum*, 1959, Weber S18553 (LE, NY).

Clear Creek Co. Mt. Evans, 10.950 ft, »fir», 1952, Imshaug 11148, 11180 (MSC).

El Paso Co. Palmer Lake, *Qu.*, 1928, Laidig 1, 12 (FH). — 0.5 mi. W of Palmer Lake, 7.500 ft, *Pseudotsuga*, 1954, Shushan S4054 (TUR).

Huerfano Co. 8 mi. S of La Veta, along Huajatolla Creek, *Pseudotsuga* — *Abies concolor* forest, 8.800 ft, 1955, Shushan S5956 (Hak, US), S5956A (NY, S, US).

La Plata Co. Hermosa, 1899, Baker, Pl. Southern Colo. 105 p.p. (with *Xanthoria* sp.; BM).

Larimer Co. Big Thompson R. Canyon, 3 mi. W of Loveland, 5.500—7.000 ft, 1959, Fahrenbruch S24577 (US).

Montezuma Co. Mesa Verde Natl. Park, Spruce Canyon, 6.400 ft, *Pinus edulis*, 1954, Weber S2334 (UPS).

Montrose Co. Naturita, 6.000 ft, *Pinus edulis*, 1914, Payson (FH). — Black Canyon of the Gunnison Natl. Monument, 8.400 ft, *Pinus edulis*, 1952, Imshaug 11359 (MSC), 8.000 ft, *Juniperus*, 1952, Imshaug 10884 (MSC).

Co. unknown. Minnehaha, 2.600 m, *Pseudotsuga*, 1904, F. E. & E. S. CLEMENTS, Crypt. Format. Colo. 104 (MIN, NY, US).

Arizona

Cochise Co. Chiricahua Mts., W of Portal, trail from Rustler's Park to Fly's Peak, 8.500—10.000 ft, 1957, Weber & Shushan S14108 (UPS, US).

Coconino Co. Grand Canyon Natl. Park: Aspen Canyon, 1944, Haring 1 (Th); Pete Berry's Pasture, 8.000 ft, 1944, Haring 2 (Th); Yavapai Point, *Amelanchier*, 1944, Haring 18 (Th).

Graham Co. Pinaleno Mts., Moonstime Canyon, 8.500 ft, *Alnus oblongifolia*, 1943, Darrow 1840 (Th).

Pima Co. Santa Catalina Mts.: Mt. Lemmon, 9.150 ft, *Abies arizonica*, 1944, Darrow 1752 (Th). Tucson, 8.000 ft, *Pseudotsuga*, 1952, Imshaug 12756 (MSC).

Santa Cruz Co. Santa Rita Mts.: 9.200 ft, *Pinus strobiformis*, 1943, Darrow 1653 (UC). Madera Canyon, 5.800 ft, 1952, Imshaug 12926 (MSC).

New Mexico

Bernalillo Co. Near Albuquerque: Sandia Crest, 10.600 ft, *Pinus*, 1952, Imshaug 12680 (MSC), 9.200 ft, »fir», 1952, Imshaug 12694 (MSC). — 17 mi. E of Albuquerque, W side of Sandia Range, 8.000—9.000 ft, 1955, Higgins S4911 (CAN).

Colfax Co. Ute Park, 2.200—2.900 m, *Cercocarpus montanus, Abies concolor, Pinus edulis, Qu.*, 1916, Standley 13661, 13812,, 13384, 14748 (FH, US).

Lincoln Co. El Capitan Mts., 7.000—7.500 ft, *Qu. undulata*, 1900, F. S. & E. S. Earle 215 (NY).

McKinley Co. 22 mi. S of Gallup, 1938, Hubricht B1140 (FH), B1141b (H).

Rio Arriba Co. 3 mi. NE of Regina, W side of San Pedro Mts., 7.200 ft, 1955, Shushan S9860 (NY), S9680 (US).

San Miguel Co. Las Vegas: *Pinus edulis*, 1929, Arsène 20045 (FH, US). Sandia Mtn., 3.226 m, 1929, Brouard 20009 (UPS). Hermit's Peak, 10.000 ft, *Pinus*, 1952, Imshaug 9907 (MSC), Burro Canyon, 8.400 ft, »fir», 1952, Imshaug 10004 (MSC). El Porvenir Creek, 7.700 ft, »fir». 1952, Imshaug 10148 (MSC). — 2.5 mi. W of Sands, 6.500 ft, 1957, Shushan S11110 (US).

Santa Fe Co. Near Santa Fe: Little Tesuque Creek, 8.500 ft, »fir», 1952, Imshaug 12439, 12441 (MSC). Holy Ghost Canyon Ridge, 10.200 ft, »fir», 1952, Imshaug 12557 (MSC). Aspen Basin, 10.100 ft, 1952, Imshaug 12621 (MSC).

Socorro Co. 47 mi. W of Tularosa, San Andres Mts., Rhodes Pass, 1938, Hubricht B999 (FH).

Valencia Co. 16 mi. S of El Morro, 1938, Hubricht B1105 (FH).

Habitat ecology

P. subolivacea grows abundantly on a great variety of trees, as stated (under *P. olivacea*) for California by HERRE (1946) and others, and for Arizona by DARROW (1950, p. 494) and WEBER (1963, p. 22). Unlike the other species treated in this paper it is common on conifers, e.g. on *Pseudotsuga menziesii, Abies concolor, Pinus edulis, P. ponderosa, P. strobiformis.* However, it also grows on deciduous trees, including *Quercus, Prunus, Alnus, Cercocarpus,*

and *Salix*. It seems to be most abundant in warm and dry, open forests, such as oak woodlands, and the *Pinus ponderosa* — *Pseudotsuga* forests in the mountains of Arizona (DARROW 1950, pp. 486—487), especially on smaller twigs.

4. *Parmelia halei* Ahti n. sp.

Plate 2A.

Type: U.S.A. Maine. Aroostook Co.: St. Francis, »on various trees», 1893 Clara E. Cummings & Emma A. Teller, CUMMINGS et al.: Lich. Bor-Amer. 26, s. n. *Parmelia olivacea* (H, holotype; FH, M, NY, US, isotypes). — Etymology: The name is given in honour of Dr. MASON E. HALE, JR., a distinguished American student of *Parmelia*.

Thallus foliaceus, viridibrunneus, orbicularis, adnatus, usque ad 10 cm latus, lobatus; lobis 1—4 mm latis, apicibus rotundatis, nitidulis; centrum versus opacus, verruculosus, saepe lobulis secundariis panniformiter dense obtectus, isidiis genuinis sorediisque destitutus, pseudocyphellis sparsissimis; subtus niger marginibus brunneis, rhizinis concoloribus, sat levis; apotheciis 3—5 mm latis, sparsis, distincte curte stipitatis, margine incurvo, verrucoso, pseudocyphellato; subhymenio 45—55 μ, hymenio 60—70 μ crasso, ascis octosporis, clavatis, 25—30 μ latis, 45—60 μ longis, sporis ellipsoideis, simplicibus, 9—9.5 × 17—19 μ; pycnidiis sparsis, pycnoconidiis circa 0.5—1 × 5—7 μ, cylindraceis, rectis.

Reactiones: PD+rubens, K+flavescens vel rubescens, C—, KC—, acidum fumarprotocetraricum et atranorinum continens.

Foliose, usually closely appressed, forming roundish or irregular rosettes commonly 10 cm in diameter; lobes yellowish to greenish brown, 1—4 mm broad, commonly layered at centre, margins small-lobulate, smooth and nitidous at ends, minutely rugulose and dull in centre, laminal pseudocyphellae absent or very sparse; lower surface coal black with dark brown marginal rim, shiny, densely rhizinate, rhizines black to brown, ca. 25—30 μ long, sparsely branched or simple.

Lobes 160 μ thick, upper cortex 20—25 μ, with many cell layers, algal layer 40—55 μ, medulla 80—100 μ, lower cortex 20 μ.

Apothecia common in central parts of old thalli but rarely numerous, 3—5 mm in diameter, strongly concave, distinctly short-stalked, disc reddish-brown, margin raised, involute, crenulate and abundantly pseudocyphellate; subhymenium 45—55 μ, pale, hymenium 60—70 μ, asci clavate, ca. 25—30 × 45—60 μ, spores ovoid, simple, 9—9.5 × 17—19 μ, 8 in the ascus; pycnidia not abundant, pycnoconidia ca. 0.5—1 × 5—7 μ, straight, cylindrical.

Reactions: PD+ red (usually instantly), K + yellow to reddish (slowly), C—, KC—. Contains atranorin and fumarprotocetraric acid (confirmed by Dr. M. E. HALE with chromatography).

Exsiccati examined: CUMMINGS, WILLIAMS & SEYMOUR, Lich. Bor-Amer. 26, as *P. olivacea* (H, M, US), 26 p.p. (FH, NY); Rel. Tuckerm. 69 (S, Th, W), 69 p.p., as *P. olivacea* (FH, UC, US).

Taxonomy

The most useful diagnostic characters of *P. halei* are the pale brown colour, large closely appressed thallus, ability to produce tiny lateral lobules, big spores, rarity of pseudocyphellae and the reaction K + yellow.

In no case had I any difficulties in identifying this species by habit only. It is undoubtedly a distinct species rather than an intraspecific taxon of *P. olivacea*.

Distribution

(Fig. 6)

P. halei is only known from the Appalachian and adjacent temperate hardwood forests from Quebec and New Brunswick down to North Carolina. It has been collected particularly frequently in the Great Smoky Mountains. Even elsewhere it is probably commoner than the material available to me

FIG. 6. Distribution of *Parmelia halei* Ahti.

suggests. A disjunct station is on east shore of Lake Superior, in the hemiboreal zone. Essentially, however, it seems to belong to the so-called Appalachian element.

The specimens examined:

Canada

Ontario

Algoma Dist. 1 mi. N of Agawa R., *Acer*, 1958, Imshaug 21849 (MSC).

Quebec

Champlain Co. S.-Thècle, *Ulmus, Bet. lutea*, 1954, Masson 6618, 6619 (WIS).
Lévis Co. S.-Henri, *Acer*, 1956, Masson & Gagnon 7366 (WIS). — S.-Jean-Chrysostome, *Acer*, 1958, Masson & Gagnon 8887 (WIS).
Montmorency Co. Montmorency R., *Abies balsamea*, 1905, Macoun 3660 (= 20: CAN, FH), 3661 (= 21; CAN).

New Brunswick

Albert Co. Fundy Natl. Park, Strainer Trail, 1960, Imshaug 26618 (MSC).

U. S. A.

Maine

Aroostook Co. St. Francis, 1893, Cummings & Teller, CUMMINGS et al.: Lich. Bor. Amer. 26 (H, M, US), 26 p.p. (FH, NY).
Knox Co. Camden: 1903, Merrill (FH). Mt. Megunticook, 1903, Merrill (FH). Mt. Battie, *Picea*, 1924, Merrill (FH). — On Penobscot Bay, *Bet.*, 1904, Merrill (CAN). — South Thomaston, 1909 and 1912, Merrill (FH). — Warren, Mt. Pleasant, *Qu. coccinea*, 1921, Merrill (FH).
Oxford Co. Sumner, *Fagus*, 1940, Parlin 14425 (Th).
Piscataquis Co. Mt. Katahdin (»Ktaadn»), 1856, Blake (NY).

New York

Essex Co. Newcomb, 1922, House (FH). — Mt. McIntyre, *Acer, Fagus, Bet.*, 1963, Thomson 11116, 11120, 11134 (WIS).
Hamilton Co. (?) Trail to Panther L., 1904, Harris 15 (FH).

Vermont

Chittenden Co. Mt. Mansfield, Underhill, 4.000 ft, 1922, Dutton 1655 (FH).
Co. unknown (not mapped). Elephant's Head, *Abies balsamea*, 1883, Faxon (WIS). — Idlewild, 1884, Faxon (S).

New Hampshire

Carroll. Co. Chocorua, 1904, leg. ? (FH).
Coos Co. Mt. Washington, leg. Pringle 345 (FH), leg. Willey (US).
Grafton Co. Woodstock, Loon Pond Mtn., 1892, Cummings (FH).
Co. unknown (not mapped). »White Mts.»: leg. Tuckerman (BM); *Abies balsamea*, leg. Tuckerman (FH, NY, S, US, W), Rel. Tuckerm. 69 (S, Th, W), 69 p.p. (FH, UC, US); 1872, Faxon 545 (NY), 1874 Faxon (FH). — Ellis R. Camp, 1889, »U.S.C.» 50 (NY). — Shelburne, 1894, Farlow (FH, W).

Massachusetts

Berkshire Co. Mt. Greylock, 3.491 ft, *Acer*, 1958, Imshaug 24105 (MSC).
Middlesex Co. Waltham, 1905, Gerritson (FH).

Connecticut

Litchfield Co. West Goshen, 1890, Underwood 663 (NY).

West Virginia

Pendleton Co. Panther Knob, *Qu. rubra*, 1957, Hale 14314 (US). — Spruce Knob, 1957, Gillespie 15455 (US).

Tennessee

Carter Co. Border of Mitchell Co., N.C., Roan Mtn., 6.000 ft, 1958, Imshaug 22201 (MSC).

Sevier Co. Mt. Le Conte, Myrtle Point, 1.970 m, *Sorbus americana*, 1939, Degelius (Deg. H, US). — Near Newfound Gap, 1.575 m, *Bet. lutea*, 1939, Degelius (Deg). — Border of Swain Co., N.C., Newfound Gap, 5.100—5.200 ft, *Ulmus*, 1958, Imshaug 22443 (MSC).

North Carolina

Avery Co. Grandfather Mtn., 5.964 ft, *Fraxinus*, 1958, Imshaug 22291 (MSC).

Jackson Co. Whiteside Mtn., 4.900 ft, *Qu.*, 1956, Sierk SNC 1 (WIS).

Swain Co. Forney Ridge, 1.760 m, *Carpinus carolinianus*, 1939, Degelius (Deg, H, US).

Yancey Co. Mt. Mitchell, 6.684 ft, *Fraxinus*, 1958, Imshaug 22352 (MSC).

Co. unknown. »Great Smoky Mts.», 1934, Schallert 974 (W).

Habitat ecology

I have not seen *P. halei* in the field, but according to herbarium labels it usually grows on deciduous trees of the genera *Fraxinus, Quercus, Acer, Fagus*, and even on *Abies balsamea* and *A. fraseri*, often in deep shade (see e.g. DEGELIUS 1941, p. 64, s.n. *P. olivacea*). Thus the ecological requirements are very different from those of *P. olivacea* s.str.

5. *Parmelia huei* Asah.

Plate 3A.

P. huei ASAHINA 1951, p. 194. — Type: Japan. Prov. Kai: Lakeside of Yamanaka, 1938, Y. Asahina 1017 (TNS, lectotype; H, isolectotype).

P. olivacea var. *corrugata* HUE 1899, p. 149. — Type: Japan. Prov. Mutsu: Aomori, 1897, R. P. Faurie 407 (W, isotype).

Foliose, closely appressed to the substratum, forming circular rosettes up to 10 cm in diameter; deeply incised, lobes 2—5 mm broad, appressed or very slightly ascending at the ends, very shiny, smooth; the centre heavily rugulose (papillate, lobulate and ridged), dark to light brown, dull; laminal pseudocyphellae fairly abundant; medulla white to yellow; lower surface black to dark brown, rhizinate up to the very margins, rhizines black to brown, ca. 20—25 μ long, simple.

Lobes ca. 80—110 μ thick, upper cortex 8 μ, one-layered, algal layer 30—45 μ, medulla proper 45—60 μ, lower cortex 8—12 μ.

Apothecia common and numerous in the centre, up to 8 mm broad, sessile, disc reddish-brown, margin persistent, smooth to slightly verrucose, pseudocyphellate; sub-

hymenium 40—50 μ, hymenium 55 μ, asci clavate, spores oblong, 5—7 × 13—14 μ, 8 in the ascus; pycnidia sparse, pycnoconidia ca. 0.5 × 9 μ, straight, cylindrical.

Reactions: PD—, K—, C + red, KC—; contains lecanoric acid and occasionally a yellow pigment (ASAHINA 1951, 1952).

Taxonomy

P. huei has much closer habit resemblances to *P. olivacea*, especially to its Japanese type (var. *albopunctata*), than it has to *P. glabra*, although the latter contains the same lichen acid. I do not hesitate to regard it as a valid species. ASAHINA (1951) compared it to *P. glabratula* Lamy (= »*fuliginosa*»), which may indeed be somewhat similar. The description of the apothecia of *P. olivacea* var. *corrugata* Hue published by MOREAU & MOREAU (1951) is almost certainly based on specimens belonging to *P. glabra*.

Distribution

(Fig. 7)

ASAHINA (1951, 1952) reported *P. huei* for Hokkaido and Honshu in Japan, and also (1952, p. 58, in Japanese) for the Kurile Islands, U.S.S.R. Earlier, TOMIN (1926a, 1937) mentioned *P. glabra* for the adjacent mainland, southern Ussuri, stating (1926a) that the specimens were atypical for *P. glabra*, reacting C + red and having spores 8—9 × 14—15 μ. It is most probably *P. huei*.

P. huei is apparently confined to East Asian temperate and hemiboreal, oceanic areas.

The specimens examined:

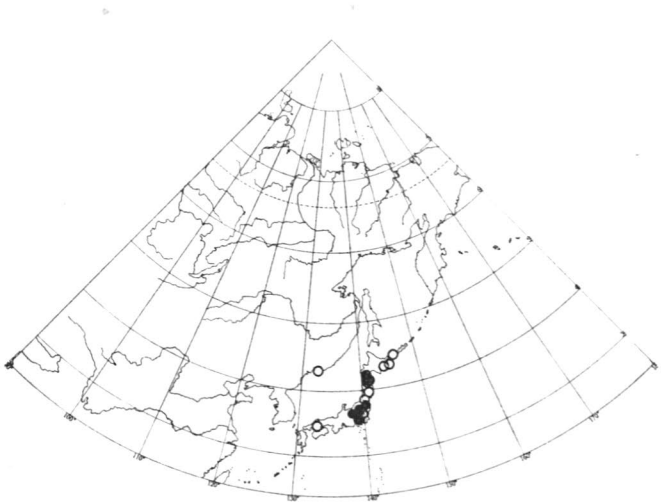

FIG. 7. Distribution of *Parmelia huei* Asah.

U. S. S. R.

Russia

P r i m o r' e T e r r i t o r y. S. Ussuri, valley of the river Likhachevka, *Abies holophylla* (TOMIN 1926a, as *P. glabra*).

S a k h a l i n D i s t. Kuril Is.: Kunashir I., *Abies* (ASAHINA 1952).

Japan

H o k k a i d o. Prov. Kushiro: Akkeshi (ASAHINA 1952). — Prov. Nemuro: Nemuro, *Sx* (op.cit.). — Prov. Oshima: Hakodate, 1855, Wright (FH; BM, K, US, W, as »Japan»), 1896, Faurie 14 (BM, FH).

H o n s h u. Pref. Aomori: Mena, Higashidori-mura, *Morus bombycis*, 1955, Kuwano & Gohara, Kurokawa 550352, 550353 (TNS). Tanabu, Uchida, *Alnus japonica*, 1955, Kurokawa 550301 (TNS); see also KUROKAWA (1956, 1957). Aomori, 1898, Faurie 407 (W), 1899, Faurie 1028 (BM, FH), 1902, Faurie 5267 (BM, FH, LE). Ominato (ASAHINA 1952). — Pref. Iwate: Morioka (op.cit.). Esashi-gun, Asai, Mt. Maeda (op.cit.). — Pref. Yamagata, *Acer mono* (NAKANISHI 1962). — Pref. Fukushima: Mt. Bandai, 1.200 m, 1898, Faurie 931 (LE). Minami-aizu-gun (ASAHINA 1952). Mt. Iide, *Fagus crenata* (OMURA 1953, as *P. olivacea*, uncertain). — Pref. Gumma: Mt. Akagi, 1913, Tsunoda 176 (W). Mt. Nabewadi (ASAHINA 1952). Oze Basin (op.cit.). — Pref. Nagano: Suga-daira, 1950, Kurokawa 50272 (TNS). — Pref. Yamanashi: Lake Yamanaka, 1938, Asahina 1017 (H, TNS). — Pref. Hiroshima: Sera-gun, Ueyama village (ASAHINA 1952).

Habitat ecology

ASAHINA (1951) merely stated it to be corticolous but later (ASAHINA 1952) mentioned two specimens growing on *Salix* and *Abies*. NAKANISHI (1962, Table 19) recorded *P. huei* sparsely on *Acer mono* in the cool temperate *Saseto-Fagetum crenatae* at 800 m on NE Honshu. This area is highly oceanic (e.g. annual precipitation ca. 3100 mm). OMURA (1953) studied a »*Parmelia olivacea* — *Lecanora subfusca* epiphyte-association» in *Fagus—Sasa* forests in the Iide Mtn. region (alt. 670—1050 m). The *P. olivacea*, which may be in fact *P. huei*, was found abundant on the twigs and boughs of the upper parts of the crowns of *Fagus crenata* and *Quercus crispula*. The association mentioned was regarded as favoured by a greater light supply than the other epiphytic communities found in this area. It has been also collected on *Morus bombycis*, *Alnus japonica* and (probably) *Abies holophylla*.

6. *Parmelia glabra* (Schaer.) Nyl.

Plate 3B.

P. glabra (Schaer.) NYLANDER 1872, p. 548. — *P. olivacea* α. [var.] *corticola* a. [f.] *glabra* SCHAERER 1840, p. 466. — Type: Switzerland (not seen; cf. SCHAERER, Lich. Helv. exs. 370).

P. olivacea β [var.] *imbricata* MASSALONGO 1853, p. 52. — *P. glabra* f. *imbricata* (Massal.) ZAHLBRUCKNER 1929, p. 91. — Type: Italy (not seen; cf. MASSALONGO, Lich. exs. Ital. 167).

P. olivacea var. *intermedia* HARMAND 1909, p. 533. — Type: France (not seen).

P. glabra var. *epilosa* STEINER in VORONOV 1916, p. 218 (nom. nud.); STEINER 1919, p. 23. — *P. epilosa* (Steiner) GYELNIK 1932, p. 221. — Type: U.S.S.R. Georgia: Adzhariya, the gorge Petzkir, on *Fagus*, October 1909, G. Woronow 78 (W, holotype).

P. glabra var. *remetehegyensis* GYELNIK 1931, p. 290/418. — Type: Hungary. Budapest, Remetehegy, *Quercus*, 7.V.1931, V. Gyelnik (S-Vr, isotype).

P. glabra var. *inactiva* HILLMANN in SERVÍT, HILLMANN, ERICHSEN & CRETZOIU 1934, p. 295. — Type: Rumania (not seen).

Concerning other infraspecific epithets, the types of which were not examined, and other nomenclatural combinations, see ZAHLBRUCKNER (1929, pp. 91, 97, 101) and GYELNIK (1930).

Foliose, adnate to somewhat ascending, often loosely attached to the substrate, forming rosettes up to 10 cm in diameter; shallowly incised, lobes 3—4 mm broad, convex, dull even at the periphery, minutely pubescent, coarsely wavy, not pseudocyphellate, uniformly dark olive-brown; lower surface black to dark brown, rhizinate to the ends of lobes, rhizinae simple, thin, 40—110 μ long, brown to black.

Lobes ca. (140)220—315 μ thick, upper cortex 18—27 μ, with many cell layers, algal layer ca. 15—30 μ, medulla proper 90—230 μ, lower cortex 8—12 μ.

Apothecia common, often numerous in central parts of old thalli, 5—7 (10) mm broad, essentially sessile, disc dark reddish-brown, margin thick, persistent, distinctly hairy, more or less crenulate and even reticulate, pseudocyphellate; subhymenium 60—90 μ, hymenium 50—75 μ, asci clavate, 15—20 × 45—50 μ, spores 7—8 × 12—14 μ, ovoid, 8 to ascus; pycnidia common, ca. 0.5—1 × 6—7 μ, straight, cylindrical.

Reactions: PD—, K—, C+ red, KC—; contains lecanoric acid.

Exsiccati examined: Agric. Res. Sta., Div. Pl. Pathol., Rehovot, Israel, Exs. 14 (M); ANZI, Lich. Exs. Ital. super. 113, as *Imbricaria olivacea* v. *glabra* (S, W); ARNOLD, Lich. exs. 986, as *Imbricaria glabra* (H, H-Nyl, M, W); Crypt. exs. Mus. Palat. Vindob. 875 (FH, H, M, S,W), 875 p.p. (H, M, S), 4224 (H, M); DESMAZIÈRES, Pl. Crypt. France 588, as *P. olivacea* var. *munda* (H, W); FLAGEY, Lich. Franche-Comté 19, as *P. olivacea* var. *glabra* (M); HASSE, Lich. S. Calif. 365 (O, US); HASSE, Lich. Exs. 16 p.p., as *P. olivacea* (O, S); KÖFARAGÓ-GYELNIK, Lichenoth. 128 (H, M); MASSALONGO, Lich. exs. Ital. 165, as *P. olivacea* (LE, W), 167, as *P. olivacea* var. *imbricata* (LE, M, W); PLITT, Lich. Exs. herb. Hasse rel. 222 (O); POELT, Lich. Alp. 95 (H, M, S); RABENHORST, Lich. Eur. exs. 447, as *P. olivacea* (H, M, W); ROUMEGUÈRE, Lich. Gall. exs. 432 (M); SAMPAIO, Lich. Portug. 245 (M); SCHAERER, Lich. Helv. exs. 370, as *P. olivacea* α *corticola* a. *glabra* (H, H-Nyl, M, W); SUZA, Lich. Bohemoslov. 144 (M, S-Vr, W); TOBOLEWSKI, Lichenoth. Polon. 119 (H, M, S), 221 (M, S); TREVISAN, Lichenoth. Veneta 44, as *P. olivacea* (H, M, W); VĚZDA, Lich. Bohemoslov. exs. 170 (M, MSC, Th); VĚZDA, Lich. Sel. Exs. 67 (H, M); ZWACKH-HOLZHAUSEN, Lich. exs. 1041 (H-Nyl, S, W).

Taxonomy

In Europe *P. glabra* has been recognized for a long time but in North America the status of the species has been in confusion (see the introduction to this paper and ANDERSON 1962, p. 254). However, a great number of specimens clearly belonging to *P. glabra* have been collected in California, although they have been usually referred to *P. olivacea*, even recently. HASSE (1898) may have first reported *P. glabra* for North America, apparently correctly, but some later reports are undoubtedly erroneous, e.g. that by HERRE

(1919) for Alaska (it is *P. glabratula* Lamy according to a duplicate in O) and those by FINK (1935) and HERRE (1946) for Nevada and New Mexico. The coarse thick thallus, the presence of fine hyaline hairs, which are best seen on the margins of young apothecia, and the positive C reaction make corticolous *P. glabra* generally an easy species to identify.

However, there is a problematic saxicolous lichen in western North America referred to *P. glabra* by ANDERSON (1962) and others. ANDERSON even stated that in Europe *P. glabra* is only corticolous, whereas in America it is apparently more common on rocks. He also found that the saxicolous specimens are lacking the hair cover characteristic of *P. glabra* s.str. I have examined several specimens of this glabrous type, and in my opinion they are not *P. glabra*, but obviously an undescribed species, which shares the coarse habit and the positive C reaction with *P. glabra*.

Most of the varieties and forms of *P. glabra* recognised by GYELNIK (1930) and others either do not seem to merit taxonomic recognition or should be referred to other species, particularly *P. subargentifera* Nyl. However, the status of four varieties is discussed here.

VORONOV (1916), STEINER (1919) and TOMIN (1933) reported var. *epilosa* Steiner from Caucasia. It is said to be wholly glabrous. Without seeing the type, GYELNIK (1930, 1932) thought it might be a distinct species. However, the type is distinctly pubescent and in other ways it fully agrees with *P. glabra* s.str. as well.

A form consisting of numerous small lobuli instead of well-developed radiately lobed rosettes, f. *imbricata* (Massal.) Zahlbr., has been commonly recognised. However, in my opinion it is a modification without any taxonomic value.

Var. *inactiva* Hillm., reported from a few localities in Rumania (SERVÍT et al. 1934; CRETZOIU 1935, 1937), was described as being C— instead of C + red. I have seen neither the type nor other specimens fitting to the description. It is doubtful whether it really is lacking in lecanoric acid. SERVÍT (1935) pointed out that the C reaction in *P. glabra* is sometimes weak and difficult to observe in the vegetative thallus (the tests are preferably made on the margins of apothecia). The »*P. olivacea*» which SZATALA mentions as well as *P. glabra* in many of his papers dealing with Hungary and other areas in SE Europe, where *P. olivacea* should not occur, may in fact be the same as *P. glabra* var. *inactiva*.

P. olivacea var. *intermedia* Harm., reported from some localities in France (e.g. HARMAND 1909, p. 351), is regarded as reacting C + red only in the apothecia. As suspected by SERVÍT (1935), even this type is probably *P. glabra* s.str. weakly reacting to C.

Distribution

(Fig. 8)

In Europe and North America the range of *P. glabra* is well-defined, but the Asian distribution is poorly known.

The European area is centred on the Mediterranean and Balkan countries, extending to the arid districts of North Africa, southern Russia, and Middle East. The northernmost localities on the Volga in Russia, in southern Poland, Bohemia, Bavaria, and southern France are probably situated in the middle parts of the temperate (boreomeridional) zone. SUZA (1933) characterized *P. glabra* as a Mediterranean (meridional) epiphyte, which also grows in the colline oak belts of the European mountain ranges. He also stated that it is

FIG. 8. Distribution of *Parmelia glabra* (Schaer.) Nyl.

common in the forest steppe area called the Pannonian floristic province. On the other hand, in Switzerland (FREY 1959), it is reported to be confined to the montane and lower subalpine forest belts, ascending up to ca. 1.500—1.700 m. In the beech forests of the eastern Carpathian Mts. it may reach the altitude of 1.200—1.300 m (SUZA 1933). It is absent from the most humid oceanic areas of western Europe. However, a curious isolated station is in Scotland. Even in Portugal it is an indicator of continentality (TAVARES 1962, p. 7). MAKAREVICH (1963, p. 79) included it in her pannemoral element although it is not present in most of the true nemoral (= temperate tropophytic deciduous) lowland forests. However, it is best known in such forests in Europe. In Morocco (WERNER 1937b) *P. glabra* is characteristic of the Mediterranean subhumid mountain belts at elevations of 1.300 to 2.200 m. WERNER (1954) referred it to the subarctic-alpine element, which must be based on some misunderstanding.

The Asian localities in Caucasia, Iran, the Himalayas and central China are probably in climatically very similar areas, as is also the American range, which is concentrated at lower elevations (below 1.500 m) in central and southern California.

Great Britain

S. Aberdeenshire (v.c. 92): Braemar, banks of the »Cluny» (Clunie), *Alnus*, 1865, Crombie (BM).

France

Known at least from the following eastern and southern departments: Vosges, Doubs, Jura, Ain, Haute-Savoie, Savoie, Loire, Ardèche, Gard, Lozère, Aveyron, Haute-Garonne, Basses-Alpes, and Corsica (e.g. HARMAND 1909). It seems to be very common in some areas, as in Doubs, Jura and Haute-Savoie.

Portugal

Apparently rare. TAVARES (1945, p. 65) listed five localities in the provinces Trás-os-Montes — Alto Douro and Beira Baixa. Probably also on Madeira (STIZENBERGER 1890; TAVARES 1952).

Spain

Probably widespread and locally common, according to literature (e.g. NAVÁS 1910, as *P. olivacea*; WERNER 1937a) and some specimens examined. Also reported for the Canary Is. (see TAVARES 1952).

Germany

In southern Bavaria fairly common according to literature and numerous specimens (M) examined. Also known from the Black Forest and Saxony. GRUMMANN (1963, p. 186) reported it for the Rhine Highlands and Weser Hills, and even for the region Münster Bay, but these data are based on very uncertain sources and are omitted in the map therefore.

Switzerland

Common in Jura and in Mittelland — Jura, but otherwise the range is poorly known (FREY 1959, p. 216). In addition, I have seen specimens from Vaud, Valais, Graubunden, and Ticino.

Austria

In most part of the country probably common in lower elevations, especially in Tyrol, Steyermark, Carinthia and around Vienna according to literature (e.g. DALLA TORRE & SARNTHEIN 1902) and the numerous specimens (W, a.o.) seen.

Poland

Rare, only in the south, e.g. in the Pienin Mts. (TOBOLEWSKI 1958) and more common in the Beskides (GLANC & TOBOLEWSKI 1960).

Czechoslovakia

Rare in Bohemia, very common in southern Moravia but rare in the north, and in Slovakia probably fairly common (e.g. SUZA 1933, pp. 34—35).

Hungary

Common in most of the country according to numerous floristic papers (e.g. by SZATALA and GYELNIK).

Rumania

According to CRETZOIU (1941), KLEMENT (1941) and some other authors scattered to common up to the upper boundary of *Fagus sylvatica*.

Italy

According to JATTA (1909—11) present in most provinces. Probably rather common in most of the country except high mountains.

Yugoslavia

At lower elevations in Dalmatia common according to many authors (e.g. SERVIT, ZAHLBRUCKNER, SZATALA, KUŠAN). Also recorded from Slovenia, Bosnia, Vojvodina, Serbia, Montenegro, and Macedonia.

Albania

Bicaj, Galica Lums (GYELNIK 1930, p. 16).

Bulgaria

Several localities reported by various authors (e.g. GYELNIK 1930, NIKOLOV 1931, CRETZOIU 1936).

Greece

A few literature records (e.g. SZATALA 1940, 1959) and specimens seen, also from Crete and Rhodos.

Morocco

In the forests of Er Rif, Central and Greater Atlas (e.g. WERNER 1937b).

Algeria

Widespread, e.g. at Constantine (FLAGEY 1896).

Tunisia

WERNER (1954) reported »*P. olivacea*» at l'Oued Zem, N. Tunisia.

Israel

Upper Galilee, Rameh, *Olea*, 1957, Galun, Agr. Res. Sta. Rehovot, Div. Pl. Path. Exs. 14 (M).

Iran

Two localities were recorded by SZATALA (1957) from Elburz and Prov. Gorgan.

India

»Himalaya»: sine loco, leg. Watt (BM, GLAM). Sad Village, 9.500 ft, 1878, Watt (BM). Pengi, 8.000 ft, 1878, Watt (BM). Lolab Valley, 1.600 m, *Cedrus*, 1962, Schubert (Klem). New to India since not mentioned by AWASTHI (1965).

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Ukraine

Common in the Zakarpatskaya Dist. according to some Czech authors and MAKAREVICH (also 1965, in litt.). It is also found in parts of Crimea (e.g. MEREZHKOVSKIY 1920b). Elsewhere Dr. MAKAREVICH (in litt.) has reported only two localities:

L'vov Dist. Drogobychk area, near Slonskoe, *Qu.* (MAKAREVICH 1947).

Nikolaev Dist. Vladimirskaya lesnaya dacha, leg. Postrygan' (KW).

Russia

A few localities have been reported from Voronezh, Saratov and Ul'yanovsk Districts, Bashkir A.S.S.R. and on the Caucasus (VAINIO 1899, ELENKIN 1906, MEREZHKOVSKIY 1920a, TOMIN 1926b). Certainly rare even in southern Russia (e.g. MEREZHKOVSKIY 1919).

Georgia

A number of localities have been reported by several authors (e.g. VAINIO 1899, VORONOV 1916, PAKHUNOVA 1933, 1956). Common at least locally.

Azerbaidzhan

Several localities were mentioned on Mt. Talysh by BARKHALOV (1957). His *P. »olivacea»* may also belong here.

China

Shensi. Mt. Si-kutzui-san, 1894, Giraldi (W). — N part: Mt. Kuan-tou-pin, 1896), Giraldi 201 (W). Mt. Tui-kio-san, 1896, Giraldi 210 (BM), 213 (BM, M). JATTA (1902) reported these specimens and several others as *Imbricaria glabra* or *I. olivacea*. Also *P. »olivacea* var. *corrugata»* of MOREAU & MOREAU (1951) is apparently *P. glabra*.

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California

Butte Co. 5 mi. E of Chico, *Qu. douglasii*, 1914, Heller (FH, MIN, NY, US). — Canyon of Big Chico Creek, *Qu. douglasii*, 1914, Heller (FH).

Colusa Co. Bear Creek, 1946, Macbride (UC). — 2 mi. S of Ladoga, *Qu. douglasii*, 1950, Gardner 93 (H, US, WIS).

Contra Costa Co. Mt. Diablo, 1896, Howe (NY).

Glenn Co. 7 mi. W of Elk Creek, *Qu. dumosa* (?), 1963, Tavares & Gashwiler 1432 (UC).

Kern Co. Caliente, 1893, Wilson 60 (NY). — Tehachapi Mts., rocks, 1907, Hasse (FH); 1.700 m, rocks, 1907, Hasse 1286 (W).

Lake Co. 1 mi. S of Bottle Rock Road along Hwy 29, S of Kelseyville, 1940, Koch 965b (FH, H, OULU, UC, UPS).

Los Angeles Co. San Gabriel Mts.: 1.800 m (when altitude indicated), *Qu.* (when substrate indicated), 1894—1909, Hasse, numerous specimens (HSI, NY, O, S, US);

3.500 ft, 1911, Kingman 1322 (FH). San Antonio Canyon, 1909, Hasse, PLITT: Lich. Exs. herb. Hasse rel. 222 (O). Rubis Canyon, 1911, Kingman 1220 (FH). — San Antonio Mts.: Camp Baldy, 4.700 ft, rocks, 1909, Hasse (FH). Evey Canyon, 2.000 ft, *Qu. agrifolia*, 1916, Johnston 3031 (FH). Cucamonga Canyon, shaded cliff, 4.500 ft, 1918, Johnston 3152 (FH).

Mariposa Co. Yosemite, 1885, leg. ? (FH). — Yosemite Valley, 1896, Hasse, HASSE: Lich. Exs. 16 p.p. (O, S).

Monterey Co. Hastings Natural History Reservation, E of Jamesburg, *Qu. douglasii*, 1956, Tavares 68f (UC).

Placer Co. Auburn Sierras, *Qu.*, 1865, Bolander 4623 (UC, US).

Riverside Co. San Jacinto Mts.: 1.600 m, *Qu.*, 1903, Hasse (MIN). »Strawberry Valley», *Qu.*, 1903, Hasse (FH).

San Bernardino Co. San Bernardino Mts.: *Qu.*, 1894, Hasse (NY), HASSE: Lich. S. Calif. 365 (O, US); 4.600 ft, 1894, Hasse (H-Nyl). Mill Creek, 1899, Hasse (FH).

San Joaquin Co. Corral Hollow Road, near Alameda Co. line, *Qu. douglasii*, 1956, Tavares 38b (UC).

Shasta Co. Stillwater, leg. Baker (UC).

Co. unknown. Sine loco, 1864—70, Bolander (MIN, NY), 1893, Hasse (FH).

Habitat ecology

P. glabra, as delimited in this paper, is so strictly corticolous that I have seen few specimens collected from rocks (in California). In Europe it is especially found on the bark of *Fraxinus* spp., *Acer pseudoplatanus*, *Castanea vesca*, *Quercus* spp., *Aesculus hippocastanum*, *Fagus sylvatica*, and other temperate deciduous trees (e.g. SUZA 1925, pp. 82—94). More rarely it grows on conifers, e.g. in Switzerland (FREY 1959), Provence (DUGHI & DUCOS 1938, on *Pinus halepensis*), and Albania (GYELNIK 1930, on *Pinus heldreichii*). Most of the American specimens for which statements about the substrate are available come from oaks (*Quercus agrifolia*, *Q. dumosa*, *Q. douglasii*, *Q. wislizenii*).

P. glabra is clearly nitrophilous (BARKMAN 1958, p.174) and photophilous (TAVARES 1945, p. 64) and therefore it is often common on trees growing along roads or in villages and towns. Barkman even designated it as a faithful species of the alliance *Xanthorion parietinae*, in which it would be present particularly in the variant *parmelietosum glabrae* of the association *Physcietum ascendentis* and in the eucontinental subvariant of the var. *glabrosum* of the association *Parmelietum acetabulae*. KLEMENT's (1941) analyses on the epiphytic vegetation in oak forests in Valachia, Rumania, give a good idea of the composition of communities with *P. glabra*.

7. *P. multispora* Schneid.

Plate 4A.

P. multispora SCHNEIDER 1898, p. 154 (as *P. multisporum*). — *P. olivacea* var. *multispora* (Schneid.) MERRILL 1909, p. 73. — Type: U.S.A. Idaho. Bonner Co.: Lake Pend Oreille, 1870, J. B. Leiberg (NY, preliminary lectotype, as »*P. multisporium* n.sp.»).

Parmelia olivacea var. *polyspora* HERRE 1910, p. 199. — Type: U.S.A. California. Santa Clara Co.: Santa Cruz Mts., Black Mtn., on *Quercus wislizenii*, 1.600 ft, 1904 A. C. Herre 426 (380) (FH, MIN, W, isolectotypes).

Foliose, adnate, forming rosettes ca. 5 cm in diameter; lobes 1—2 mm broad, flat but slightly involute, commonly with narrow lateral or laminal lobules and teeth, sometimes imitating erect isidia, upper surface uniformly dark to light brown, rarely blue pruinose, dull and rugose in the centre, shiny and slightly rugulose at the periphery, pseudocyphellae absent; lower surface black to dark brown, densely rhizinate from the centre right up to the margins, sometimes slightly veined and trabeculate; rhizinae dark brown, fairly thin, simple or sparsely branched, 35—50 μ long.

Lobes ca. 80—105 μ thick, upper cortex 10—15 μ, usually one-layered, algal layer 20—40 μ, medulla proper 45—75 μ, lower cortex 10—15 μ.

Apothecia common, fairly numerous and present even at the periphery, 2—2.5 mm in diameter, essentially sessile, plane to convex when old, disc dark red-brown, margin verrucose to smooth, sparsely pseudocyphellate; subhymenium 45—70 μ, hyaline, hymenium 60—80 μ, pale brown, asci clavate, 15—20 × 45—65 μ, spores subspherical to short-ovoid, 6—8 × 6—10(13) μ, usually 16 (sometimes more) in the ascus; pycnidia scattered, pycnoconidia 0.5—1 × 4—5 μ, straight, cylindrical.

Reactions: PD—, K—, C—, KC—. No substances could be identified by crystal tests, aithough a residue is obtained by acetone extraction and crystals may sometimes appear n GE and other solutions.

Taxonomy

Although *P. multispora* is recognized in several handbooks (see particularly HASSE 1913, FINK 1935, BERRY 1941, HERRE 1946, HOWARD 1950), it is relatively poorly represented in herbaria under this name. The taxonomic importance of the number of spores — usually 16, which was at one time thought to be unique in the genus — has been doubted by some authors; e.g. HERRE (1946) regarded it as a variety of *P. olivacea*. Otherwise *P. multispora* resembles *P. subolivacea* very much, but apart from the number and minor differences in the size of the spores, it may be distinguished by the thinner thallus (with a one-layered upper cortex), the tightly appressed habit and the tendency to produce small marginal lobules. Sometimes *P. multispora* resembles *P. trabeculata*, another species with 16 spores per ascus, indicating that they may be closely related. However, the distinctly veined lower surface and different chemical constituents of *P. trabeculata* are good distinguishing characters.

In his original description of *P. multispora* SCHNEIDER (1898) wrote: »thecae bearing from 50 to 100 colorless elliptical spores, 5×4 μ». Neither the number nor the size of the spores conforms with the data given by most later authors, including myself. Nevertheless, the specimens that are apparently authentic (the lectotype and Piper no. 55 p.p.; NY) proved to be this species rather than an *Anzia* (cf. also MERRILL 1909), although SCHNEIDER compared it with *A. taeniata* (= *Parmelia taeniata*), a widely different lichen with numerous small spores per ascus. In addition, no *Anzia* spp. are known from Washington, Idaho or Utah (cf. CULBERSON 1961), where SCHNEIDER reported *P. multispora*. However, HERRE (1946, pp. 322, 323) claimed that the taxon

described by SCHNEIDER (i.e. with 50—100 spores per ascus) was not the same as the widespread Californian taxon, which the referred to as *P. olivacea* var. *polyspora* Herre and which usually has 12—20 spores. Only one Californian specimen (Sisson, July 1894, M. A. Howe) was identified by HERRE as belonging to what he regarded as the genuine »var.» *multispora,* which he evidently supposed to be more northern in range. In my examination of the three duplicates of this particular gathering that were available to me, none of them proved to contain 50 to 100 spores. In my opinion, SCHNEIDER's report of this high number of spores is based on an error. Also, the dimensions given by BERRY (1941, p. 65) to the spores of *P. multispora,* 1—4 μ in diam., must have been based on inadequate material.

FIG. 9. Distribution of *Parmelia multispora* Schneid.

Distribution

(Fig. 9)

The map of *P. multispora* clearly indicates that it is confined to oceanic western North America. It is most frequent near the coast and on the coastal mountains, and is probably common in some areas (e.g. HERRE 1946); it also occurs where rainfall is high in the Rocky Mountains and its foothills in Idaho, Montana, Washington and British Columbia. SCHNEIDER's (1898) record for Utah is very uncertain. Near the sea it extends as far as the south coast of Alaska.

The specimens examined:

C a n a d a

British Columbia

Victoria: 1893, Macoun 24 (CAN, US), 63 (FH), Can. Lich. 24 (BM, TUR), Can. Crypt. 48 (CAN, K, NY); Sea's Farm, *Populus*, 1893, Macoun 716 (= 88; CAN). — Sidney, 1912, Macoun 21 (FH); 1913, Macoun 66 (CAN), 243 (FH); *Alnus*, 1915, Macoun 7-16 (= 4; CAN). — Revelstoke, *Alnus*, 1890, Macoun 19 (UPS), 712 (CAN). — Wells Gray Park road, Hemp Creek, *Alnus tenuifolia*, *Sx scouleriana*, *Prunus*, 1961, L. & T. Ahti 13049, 13079, 15503 (H). — Wells Gray Park, Murtle L., *Populus tremuloides*, 1961, L. & T. Ahti 13599 (H).

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Alaska

C e n t r a l P a c i f i c C o a s t D i s t. Kenai Pen., Ninilchik, 1957, Krog 2602 (O). — N. Cook Inlet area, Knik R., 1953, Krog 131 (O).

E a s t e r n P a c i f i c C o a s t D i s t. Juneau, Mendenhall L., 1957, Krog 5604 (O).

Washington

C h e l a n C o. Rainbow Trail, 3.600 ft, 1931, Howard 1269 (FH).

F e r r y C o. Republic: *Alnus sinuata*, 1912, Foster (FH); Curlew L., *Sx scouleriana*, 1912, Foster 2291 (Th).

K l i c k i t a t C o. Goldendale, *Qu. garryana*, *Prunus demissa*, 1909, Foster 1163 (NY), 1163 p.p. (FH).

P i e r c e C o. (?) Mt. Rainier Natl. Park, White R., *Populus*, 2.750—3.000 ft, 1948, Imshaug 7627 (FH, WIS).

S p o k a n e C o. Spokane, Fort Wright Grounds, *Crataegus douglasii*, 1907, Bonser (FH). — Deadman Creek, *Alnus*, 1906, Bonser 7 (FH).

W a h k i a k u m C o. Cathlamet, *Acer circinatum*, 1907, Foster (FH).

W h i t m a n C o. Pullman: 1893, Piper 55 p.p. (NY); *Crataegus douglasii*, 1900, Beattie 32 (FH), 1913, Weaver (FH); 2550 ft, *Amelanchier*, 1931, Howard 1576 (S). — Tekoa Mts., *Pinus*, 1931, Howard 1593 (WIS).

C o. u n k n o w n. »Near the 49th parallel», 1858, Lyall, Oregon Boundary Commission (FH, K).

HOWARD's (1950) records have also been mapped.

Oregon

U n i o n C o. Mill Creek, 4.000 ft, *Alnus*, 1897, Sheldon 9018 (FH, NY, US).

W a s h i n g t o n C o. Forest Grove, 1893 Lloyd (NY), 1899 Lloyd 136 (NY).

C o. u n k n o w n. Sine loco: *Acer*, 1895, Lloyd 58 (NY); *Hamamelis*, 1897, Lloyd (NY); 1922, Plitt (WIS); leg. Calkins, N. Am. Lich. 3 (FH, Th).

Idaho

B o n n e r C o. Lake Pend Oreille, 1870, Leiberg (NY).

Montana

Flathead Co. Columbia Falls, 1897, Williams 25a (NY).
Glacier Co. (?) Glacier Natl. Park, L. McDonald, 3.200 ft, *Acer*, 1950, Imshaug 7627 (MSC).
Granite Co. Lolo Natl. Forest, Rock Creek, Kitchen Gulch, *Crataegus*, 1959, Stickney 531 (WIS).
Lake Co. St. Ignatius, 2.800 ft, 1901, Harris 61 (NY). — Swan Valley, Swan L., *Populus tremuloides*, 1950, Cotter 1630 (MIN).
Co. unknown. Rainbow Falls, 1888, Williams 25 p.p. (NY).

California

Humboldt Co. Trinidad, Spruce Cove, *Sx*, 1933, Parks 4413 (FH).
Los Angeles Co. San Gabriel Mts., 1906, Hasse 2153 p.p. (FH).
Modoc Co. 20 mi. NW of Davis Creek, W side of Goose L., 4.700 ft, 1953, Weber & Rose S1843 (US, WIS).
Monterey Co. Hastings Natural History Reservation: E of Jamesburg, *Cercocarpus*, 1941, Linsdale (UC); Old County Road, gate to the reservation, *Qu. agrifolia*, 1961, Tavares et al. 959 (UC); Schoolhouse Hill, *Qu. agrifolia*, 1962, Tavares et al. 789 (UC); 1962, Tavares et al. 837, 856 p.p. (UC). — Paloma Canyon, road to Greenfield, *Qu. agrifolia*, 1956, Davis et al. 96 p.p. (UC).
Plumas Co. Rich Gulch, 3.750 ft, *Alnus rhombifolia*, 1944, Follett 49 (UC), s.no. (FH, NY, UPS).
San Luis Obispo Co. Between Simmler and Santa Margarita, 2.300 ft, 1956, Stuart (UC).
San Mateo Co. Santa Cruz Mts., Gazos Creek, 75 ft, *Alnus*, 1906, Herre 968 p.p. (NY). — Pilarcitos Creek Canyon, *Sx*, 1957, Thomson 4733 (Th).
Santa Clara Co. Santa Cruz Mts., Black Mtn., 1.600 ft, *Qu. wislizenii*, 1904, Herre 426 (= 380; FH, MIN, W), s.n. (NY).
Shasta Co. Goose Valley, leg. Baker (UC).
Siskiyou Co. Sisson, *Bet.*, 1894, Howe 60c (FH, NY, UC, US).
Co. unknown. Leg. Bolander 277 (NY, US).

Habitat ecology

P. multispora has been collected from several species of deciduous trees and shrubs belonging to the genera *Alnus, Populus, Quercus, Salix, Cercocarpus, Betula, Prunus, Hamamelis, Acer,* and *Amelanchier.* No records from conifers are known to me. Alders (e.g. *Alnus rhombifolia, A. rubra*) and oaks (at least *Quercus agrifolia* and *Q. wislizenii*) seem to be especially common habitats for this species. In British Columbia I found it most abundant on *Alnus tenuifolia*, in a thicket by a brook.

8. ***Parmelia trabeculata*** Ahti n. sp.

Plate 4B.

Type: Canada. Ontario: Cochrane Dist., west end of Martison Lake (50° 23′ N, 83° 11′ W), on trunk of big willow tree (probably *Salix bebbiana*) on lake shore, 1958 T. Ahti 4667 (H, holotype; CAN, O, isotypes).

Thallus foliaceus, fuscobrunneus, orbicularis, adnatus, vulgo 2—5 cm in diametro, lobatus; lobis 1—2 mm latis, convexis, vulgo nitidis (raro pruinosis); centro laevis vel rugulosus vel panniformis (lobulis secundariis dense obtectus), isidiis genuinis sorediis

pseudocyphellisque destitutus; subtus brunneus, rhiziniis brunneis, densiter usque ad marginem distincte reticulatus et trabeculatus; apotheciis sat copiosis vulgo 2—3 mm latis, curte stipitatis, margine verrucoso vel etiam lobulato, parce pseudocyphellato, subhymenio 70—105 μ, hymenio 65—80 μ crasso, ascis vulgo 16-sporis, clavatis, circa 10—24 μ latis, 40—48 μ longis; sporis globosis vel subglobosis, 5—7 × 5—8 μ, membrana sat crassa; pycnidiis sat numerosis, pycnoconidiis rectis, 0.5 × 6 μ.

Reactiones: PD + rubens, K + rubens, C—, KC—, acidum norsticticum et atranorinum continens.

Foliose, rather closely appressed, forming rosettes 2—5 cm in diameter; major lobes 1—2 mm broad, deeply divided, often growing in several layers in the centre and more finely lobed, the lobules resembling isidia when small; upper surface pale to dark brown, sometimes white pruinose, dull or shiny, almost smooth to wrinkled, without pseudocyphellae; lower surface dark or pale brown to almost white, with veins, trabeculae and rhizinae right up to the margins, rhizinae brown, slender, 30—45 μ long, simple or irregularly branched, frequently anastomosing.

Lobes ca. 110—130 μ thick, upper cortex 10—25 μ, with several cell layers, algal layer 40—60 μ, medulla proper 30—50 μ, lower cortex 10—15 μ.

Apothecia common, scattered over the lobes, 2—3(6) mm broad, very shortly stalked, disc shining, dark to pale brown, margin crenate or even lobulate, pseudocyphellate; subhymenium 70—105 μ, pale, hymenium 65—80 μ, light brown, fulvous, asci clavate, ca. 10—24 × 40—48 μ, spores subglobose, simple, ca. 5—7 × 5—8 μ, with fairly thick membrane, usually 16 in the ascus; pycnidia abundant, pycnoconidia straight, cylindrical, 0.5 × 6 μ.

Reactions: PD + red, K + yellow to red, C—, KC—. Contains atranorin (det. in GAo-T) and norstictic acid (GAo-T). One chemical test was made by Dr. CHICITA F. CULBERSON.

Taxonomy

This new species is very distinct from *P. olivacea* because of the number, size and shape of the spores, the veined lower side, and the chemical constituents. It is easy to distinguish from *P. olivacea* by habit characters alone and in the field it superficially resembles *Physcia ciliata* or *Cetraria fendleri* (AHTI 1964, p. 21, as *Parmelia* sp.).

P. trabeculata is apparently most closely related to *P. multispora* (see under this species), but there is no doubt that it deserves specific rank. It is surprising that it has not been described before, since it has been collected in several places in Minnesota and Michigan, e.g. by FINK.

Distribution

(Fig. 10)

In Ontario *P. trabeculata* is scattered in the boreal regions, even reaching to the coast of Hudson's Bay. In Michigan and Minnesota it is found in the hemiboreal »mixed forests», but is not known from the true temperate zone.

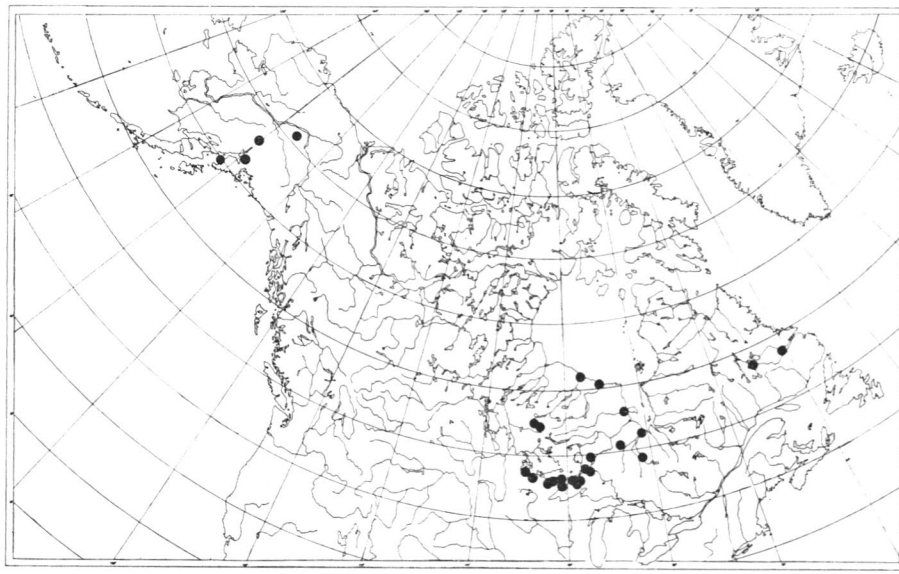

FIG. 10. Distribution of *Parmelia trabeculata* Ahti.

Elsewhere its range is poorly known, but it is apparently a strictly North American species with a transcontinental boreal range. However, the few records from the east and west coasts indicate that it may be somewhat continental.

The specimens examined:

Canada

Ontario

Cochrane Dist. Martison L., *Sx bebbiana*, 1958, Ahti 4667 (CAN, H, O). — Gardiner, *Populus balsamifera*, 1959, Wetmore 5762 (MSC). — NW of Cochrane, Greenwater Prov. Park, *Populus balsamifera*, 1959, Wetmore 5803 (MSC). — Moose R., opposite to Moosonee, 1959, Wetmore 5932 (MSC).

Kenora Dist. Attawapiskat, *Picea glauca*, 1958, Ahti 4668 (H). — Winisk, *Populus balsamifera*, 1958, Ahti 4669 (CAN, H). — Fort Severn, *Picea glauca*, 1958, Ahti 4785 (H). — E of McInnes L., »Sayers L.», *Populus tremuloides*, 1958, Ahti 3744 (H). — Deer Lake, *Populus tremuloides*, 1958, Ahti 4671 (H).

Thunder Bay Dist. Geraldton, Kenogamisis L., *Sx*, 1958, Ahti 4670 (H). — Slate Is., Patterson I., McCreevy Har., *Bet. papyrifera*, 1958, Ahti 4672 (H). — 20 mi. W of Rossport, *Bet.*, 1959, Erbisch 812 p.p. (MSC).

Newfoundland

Labrador North Dist. Grand Falls area, Unknown R., Twin Falls, *Populus balsamifera*, 1963, Kallio (TUR).

Labrador West Dist. Northwest River, Grand L., Cape Caribou, 1963, Kallio (TUR; a very small scrap among *Parmelia exasperatula* on *Lobaria pulmonaria*).

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Alaska

Alaska Range Dist. Mt. McKinley Natl. Park, on McKinley R., S of Wonder L., 1.800 ft, *Populus*, 1956, Weber & Viereck S7217 (WIS).

Central Pacific Coast Dist. Kenai Pen., Ninilchik, 1958, Krog (O). — N. Cook Inlet area: Rabbit Creek road, 1957, Krog 1463 (O). Knik R., 1953, Krog 128 (O).

Central Yukon River Dist. White Mts., Lower Fossil Creek, 1953, Krog 641 (O).

Minnesota

Cook Co. Grand Portage, 1897, Fink 100 (MIN, S, UC, US). — Gunflint, 1897, Fink 260 (MIN). — Tofte, 1897, Fink 585 p.p. (MIN).

Koochiching Co. »Koochiching», 1901, Fink 889 p.p. (MIN).

Lake Co. Snowbank Lake area, 1897, Fink 848 (MIN).

Lake of the Woods Co. »L. of the Woods», *Abies balsamea*, 1896, MacMillan 6 (MIN).

St. Louis Co. Ely, *Abies balsamea*, 1897, Fink 1004 (MIN).

Michigan

Keweenaw Co. Isle Royale: between Conglomerate and Tonkin Bays, *Populus balsamifera*, 1959, Wetmore 4238a (MSC). Amygdaloid I., 1959, Wetmore 4613 (MSC). Island Mine, *Populus balsamifera*, 1959, Wetmore 4965 (MSC).

Habitat ecology

The ecology of *P. trabeculata* is also different from that of *P. olivacea*. The former seems to prefer tree species with eutrophic bark (*Populus balsamifera, P. tremuloides, Salix* spp.), but it grows on oligotrophic bark (*Betula papyrifera, Picea glauca, Abies balsamea*) as well. This may be due to secondary enrichment of the bark, in some cases at least, as is indicated by its occurrence in mixed stands with *Physcia aipolia* on conifers in northern Ontario. All the stations in Ontario in which I saw this species were situated on the shores of lakes or rivers in mesic to moist forests.

9. ***Parmelia laciniatula*** (Flag.) Zahlbr.

This inconspicuous finely lobed species which rarely produces apothecia is only briefly mentioned here, since its taxonomy, ecology and distribution have been discussed rather thoroughly by, for example, Maas Geesteranus (1947, pp. 109—111) and Almborn (1948, pp. 149—156), who gives a dot map of its range in Scandinavia. In several handbooks and keys *P. laciniatula* is included amongst the isidiate species, but it may be more correct to regard its isidioid structures as fine lobes comparable to those of *P. panniformis* (Nyl.) Vain., as was done, for instance, by Poelt (1962, p. 457).

P. laciniatula is probably endemic to Europe, and in any case is not known from North America.

Summary

In the northern hemisphere there are nine corticolous species in the *Parmelia olivacea* complex, which resemble one another in habit and lack both isidia and soredia. Among them, *P. olivacea* (L.) Ach. em. Nyl. is essentially boreal, although incompletely circumpolar, since it is absent from the interior of North America. In east Asia and Alaska a distinct variety, var. *albopunctata* (Asah.) Ahti n. comb. is provisionally recognised. *P. septentrionalis* (Lynge) Ahti n. comb. is also boreal, but completely circumpolar. *P. subolivacea* Nyl. in Hasse is centred on the temperate to subtropical arid regions of western North America. *P. halei* Ahti n. sp. is a temperate species which is essentially Appalachian. *P. huei* Asah. is confined to the oceanic parts of Japan and the adjacent mainland. *P. glabra* (Schaer.) Nyl. has a discontinuous subtropical to middle temperate range in Eurasia and western North America. The two species with 16 spores per ascus are also exclusively North American: *P. multispora* Schneid. belongs to the oceanic Pacific element, while *P. trabeculata* Ahti n. sp. probably has a range over the boreal parts of the continent from Alaska to Newfoundland.

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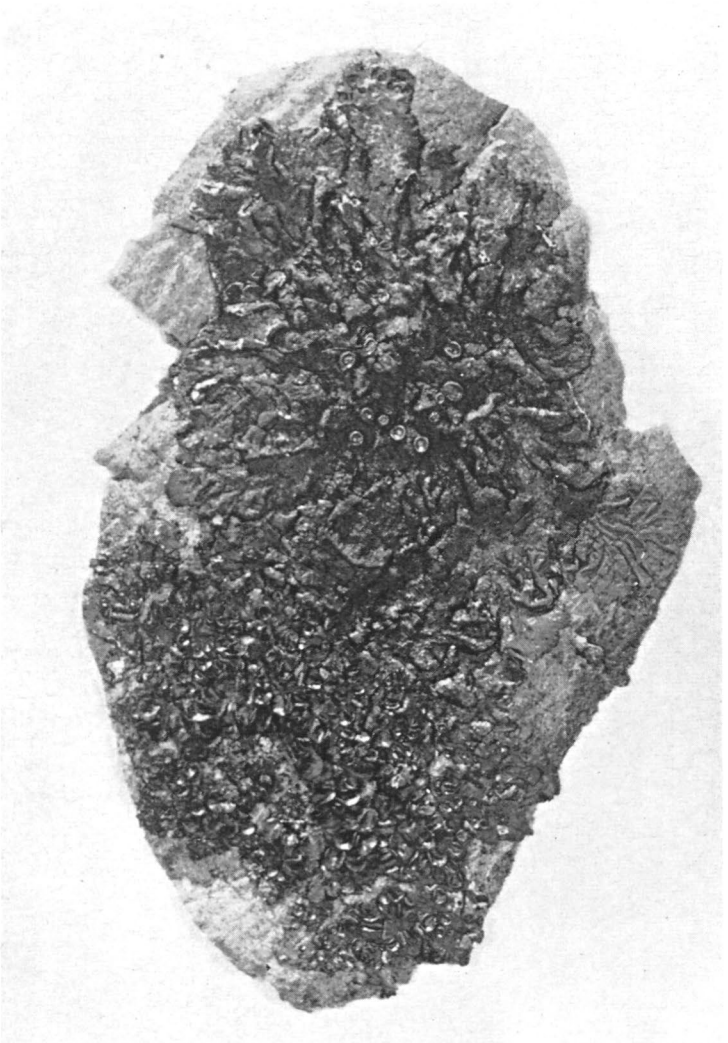
Explanations to the lists of localities, the figures and the plates

In addition to the herbarium symbols listed in the Introduction, the locality lists include the following abbreviations: *Bet.* = *Betula*, *Sx* = *Salix*, *Qu.* = *Quercus*.

The lists of exsiccati do not usually include sets kept separately in the herbaria.

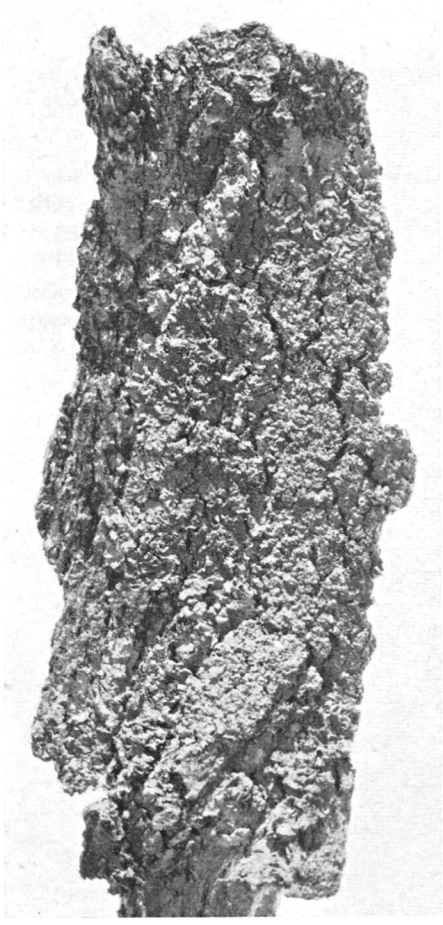
On the maps solid black circles indicate specimens verified by me. The small open circles represent literature records considered to be reliable. Stations which can only be approximately located are indicated by large open circles (when literature records) or by a black dot within a circle (when specimens seen).

PLATE 1

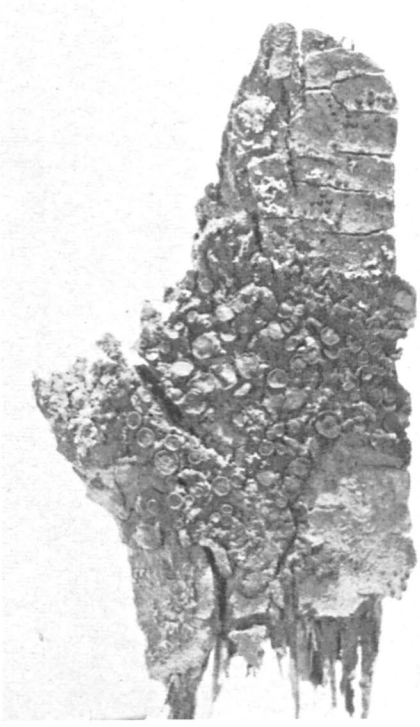


Parmelia olivacea (L.) Ach. (upper) and *P. septentrionalis* (Lynge) Ahti (lower) on the same piece of willow bark. Note the broad wrinkled lobes and few apothecia of the former species, while in the latter the smaller and smoother lobes are crowded with numerous mature apothecia. — Sweden: Härjedalen, Tännäs, Ljusnedal, 11.V.1912, Östman (S).

PLATE 2



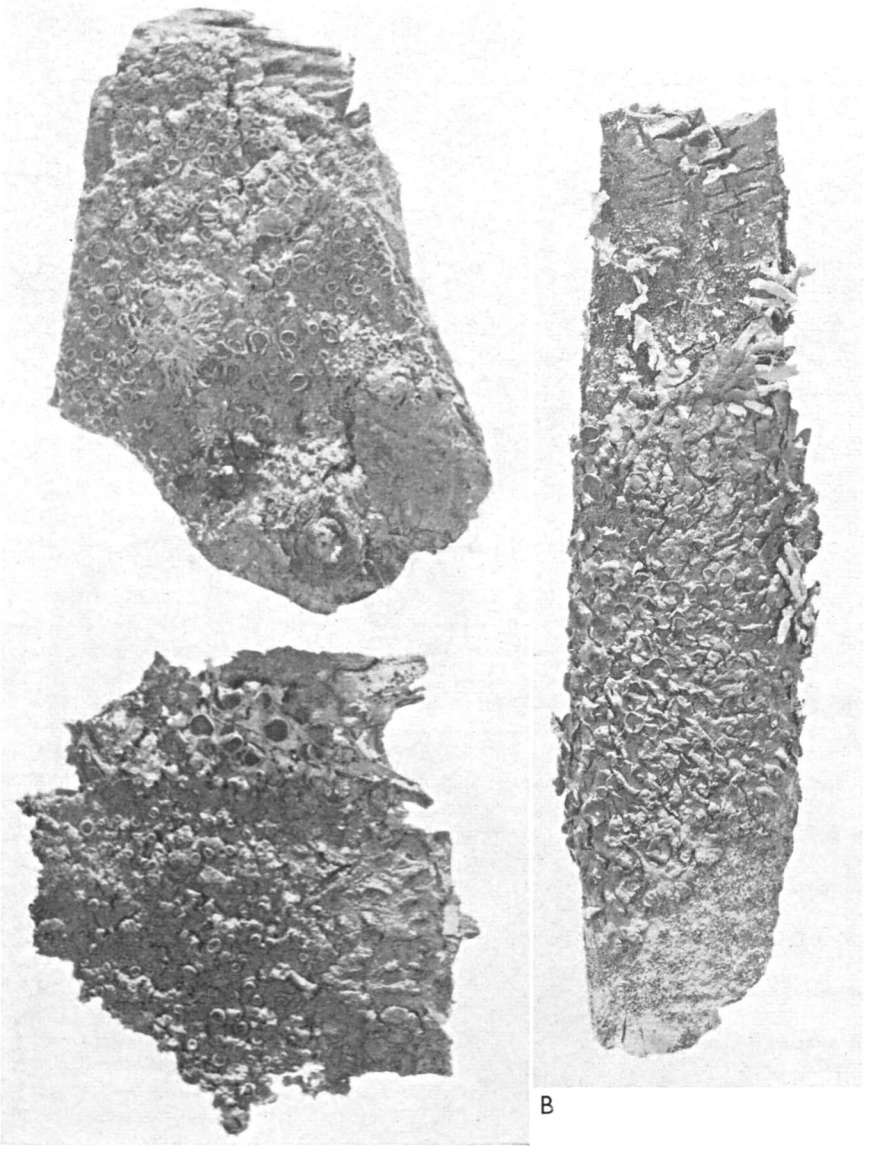
A



B

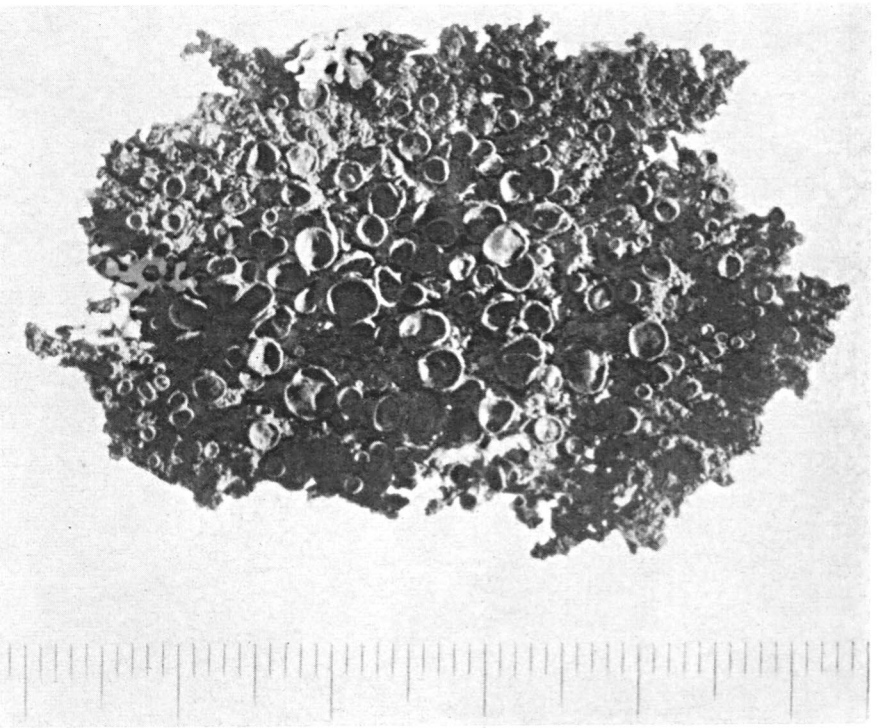
A. *Parmelia halei* Ahti — Massachusetts: Berkshire Co., Imshaug 24105 (MSC).
B. *Parmelia subolivacea* Nyl. — California: Santa Monica Mts., 1902, Hasse (HSI).

PLATE 3

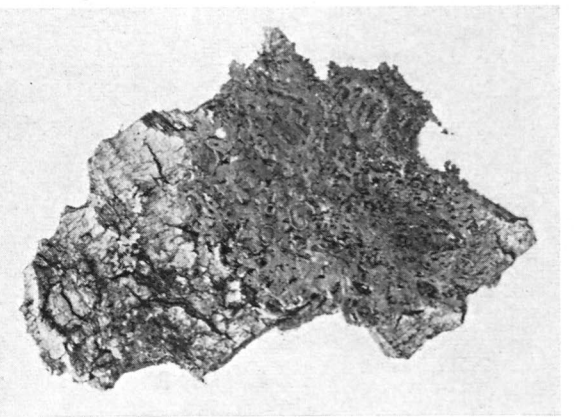


A. *Parmelia huei* Asah. — Japan, 1853—56, Wright (US).
B. *Parmelia glabra* (Schaer.) Nyl. — California: San Gabriel Mts., 1902, Hasse (HSI).

PLATE 4



A



B

A. *Parmelia multispora* Schneid. — British Columbia: Wells Gray Park, Ahti 15503 (H).
B. *Parmelia trabeculata* Ahti — Ontario: Slate Islands, Ahti 4672 (H).

47. **E. J. Valovirta:** Über die Strandhöhenzonen als Hilfsmittel bei der Erforschung der Schärenflora im Landhebungsgebiet. 24 S. (1950).
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60. **Harald Lindberg:** Växter, kända från Norden, i Linnés herbarium. Plantae e septentrione cognitae in herbario Linnaei. 133 pp. (1958).
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67. **Carl Eric Sonck:** Die Gefässpflanzenflora von Pielisjärvi und Lieksa, Nordkarelien. 311 S. (1964).
68. **F. W. Klingstedt:** Über Farbenreaktionen von Flechten der Gattung *Usnea*. 23 S. (1965).
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