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Alectoria and allied genera in North America

Irwin M. Brodo and
David L. Hawksworth

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Alectoria and allied genera in North America

Irwin M. Brodo and David L. Hawksworth

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Frontispiece. *Bryoria nadvornikiana* draping the branches of *Picea mariana* in Parc des Laurentides, north of Quebec City, Quebec.

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In the present monographic study of the North American taxa generally referred to the genus *Alectoria*, four genera and 38 species were recognized: *Alectoria* Ach. (8 species), *Bryoria* nom. nov. (27), *Pseudephebe* Choisy (2), and *Sulcaria* Bystr. (1). Nine new species are described: *Alectoria imshaugii*, *A. mexicana*, *Bryoria carlottae*, *B. friabilis*, *B. pikei*, *B. pseudocapillaris*, *B. salazinic*, *B. spiralis*, and *Sulcaria badia*. One species name is validated and transferred to *Bryoria*: *B. cervinula*. Combinations transferring 26 North American and 29 extra-North American taxa into the accepted genera are made. Some aspects of the cortical structure are useful in characterizing the genera and the sections within *Bryoria*. Secondary chemical products have been studied in all taxa. Olivetoric and gyrophoric acid were previously unknown for this group. Salazinic acid was definitely established as occurring in *Bryoria*. Atranorin and chloroatranorin are absent in *Alectoria* s. str. but present in *Bryoria*. Thamnic acid appears to be absent in *Bryoria*, but fairly common in *Alectoria* s. str. The group as a whole is northern in distribution in North America extending southward in the cordillera. Only *Sulcaria* appears to be essentially temperate. The corticolous species are mainly confined to trees with acid bark, and those on rock and soil seem to be more characteristic of acid, non-calcareous substrates.

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The production of a major taxonomic revision of a group of lichens by authors on different sides of the Atlantic presented us with a number of problems. The file of correspondence between the junior and senior authors stands some 5 cm high. The authors have been able to work together jointly on this project in May 1970 (in Kew), March and April 1973 (in Ottawa), and September 1973 (in Kew); most final points in the manuscript were discussed together at the XII International Botanical Congress in Leningrad in July 1975. We are indebted to the Commonwealth Agricultural Bureaux, the National Museums of Canada, and the Royal Society of London for making these meetings possible.

This study, made over a period of eight years, has profited from the help of many individuals and institutions. We would particularly like to thank the curators of all the herbaria from which we borrowed specimens, especially as we often had to keep the material longer than the allotted time, and frequently reborrowed certain specimens.

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with detailed comments on the chemistry of his material. Gary Schroeder also sent us many specimens of that species, including a large collection that we have designated as the type. E. D. Greenwood made special trips into the mountains of Oaxaca, Mexico, to search out and collect material of *A. mexicana*, *A. lata*, and *Oropogon* spp. Per Magnus Jørgensen gave us many valuable comments on species of the section *Divaricatae* of *Bryoria*. We also profited from discussions of certain taxonomic and nomenclatural problems with Peter James and Rolf Santesson.

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All the maps were prepared using the Goode Base Map Series, No. 102, copyrighted by the University of Chicago and used with their permission.

Introduction

The lichen genus *Alectoria* in North America, although containing some conspicuous and frequently collected species, has persistently proved to be a source of confusion and frustration among both amateur and professional lichenologists.

The first attempt to provide a monographic treatment of the North American species of this genus was that of Howe (1911), who accepted ten species. Howe's work was not sufficiently critical, however, and he misapplied several names. A number of new taxa were described from North America by Gyelnik in the 1930s (see Sjödin 1954), but most of these have been poorly understood by subsequent workers. More recently Motyka (1960) described three new species from North American material, and later (1964) published a revision of the thirty species he considered to occur in North America. Unfortunately, his paper was based on a study of very few North American specimens, and suffered from numerous errors and omissions. Attempts to follow Motyka's treatment have led to some confusions in the application of many names, and it became apparent that a thorough re-examination of the North American *Alectoriae*, in the broadest sense, was imperative.

The present paper provides a revision of the North American species (and those of Mexico) of *Alectoria* and its segregate genera *Bryoria*, *Sulcaria*, and *Pseudephebe*. *Oropogon* Th. Fr. is an essentially Asiatic genus (Sato 1967) also occurring in the Central and South American highlands. We have seen no North Ameri-

can specimens, and thus it has been excluded from the present study. It is much in need of a generic revision.

The introductory sections discuss the anatomical, morphological and chemical characters of these genera only so far as they affect the taxa treated here. This paper constitutes "Regional Studies in *Alectoria* (Lichenes) IV" of the junior author; part III appeared in *Annales Botanici Fennici* 11: 189–196 (1974).

Material

The information presented here is based on a study of nearly 9,000 specimens from North America. Besides studying the extensive material housed at the National Herbarium of Canada (CANL), we borrowed and revised material from the following herbaria (abbreviations follow Holmgren & Keuken 1974): ALA, AR, BM, COLO, DUKE, F, FH, H, LAM, MSC, NYBG, O, QFA, QUE, S, TRTC, UAC, UPS, US, WIS. In addition, the following private herbaria were consulted: DEGELIUS, ESSLINGER, PIKE, SCHROEDER, THOMSON. Type specimens and related materials were also examined from BP, FI, LBL, LE, M, MW, ORE, P, PC, and ZT. Some collections were made in Oaxaca, Mexico, by Mr E. D. Greenwood especially for this study.

A number of special field studies were made by the senior author to investigate the habitat ecology of some of the more puzzling or rare taxa, and one excursion was taken by the two authors together. Among the areas visited were the California and Oregon coasts; the Corvallis, Oregon, region; coastal British Columbia; some of the western mountains; and boreal forest segments near Moosonee, Ontario, and in Parc de la Verendrye, the Gaspé Peninsula, and Parc des Laurentides, all in Quebec.

Anatomy and morphology

Habit

The terms caespitose, subpendent, pendent, and decumbent are frequently used to describe the various growth forms of species of *Alectoria* s. lat. and they are used in the keys that follow. Our usage of these terms is as follows: *caespitose*: forming shrubby tufts, generally producing a thallus not more than twice as long as it is broad; a number of thick branches generally arise together at the base of the plant. *Subpendent*: producing many thick branches at the base of the thallus, but acquiring a more slender and pendulose appearance at the tip; generally several times as long as it is broad. *Pendent*: hanging vertically almost from the base; becoming very elongate. *Decumbent*: growing along the surface of the substrate and forming low cushions or rosettes. *Erect*: becoming more-or-less arborescent, usually with a main "stem" or branch with subordinate lateral branches arising from it.

Most species show only one type of growth form: caespitose: *Bryoria furcellata*, *B. abbreviata*, *Alectoria imshaugii*; subpendent: *Bryoria glabra*, *B. tenuis*, *B. nadvornikiana*; pendent: *B. fremontii*, *B. trichodes* subsp. *trichodes*, *B. capillaris*. Others can vary somewhat, such as *Alectoria sarmentosa* subsp. *sarmentosa* which can be subpendent when young, or *Bryoria simplicior* which can be caespitose or subpendent.

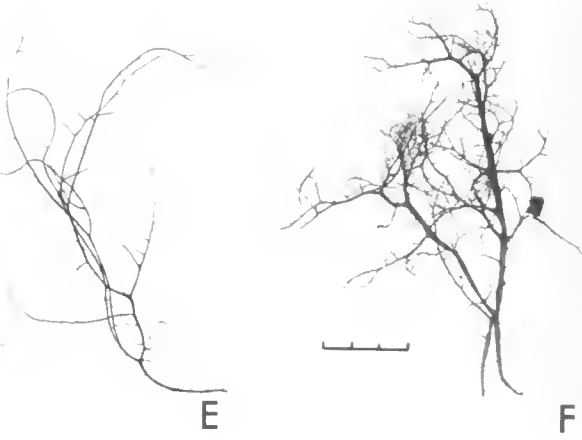
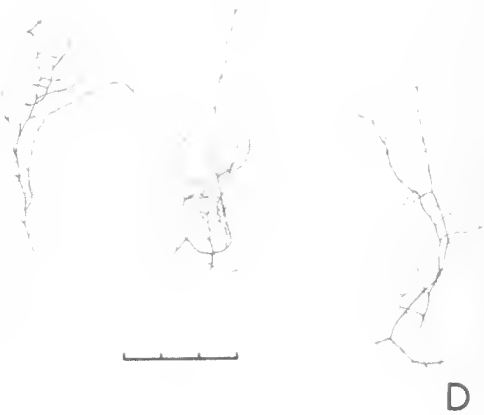
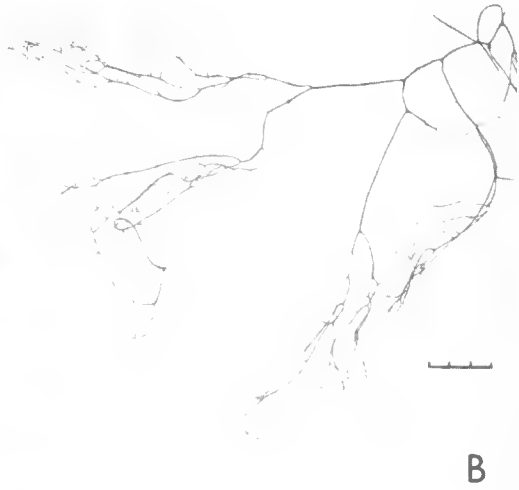
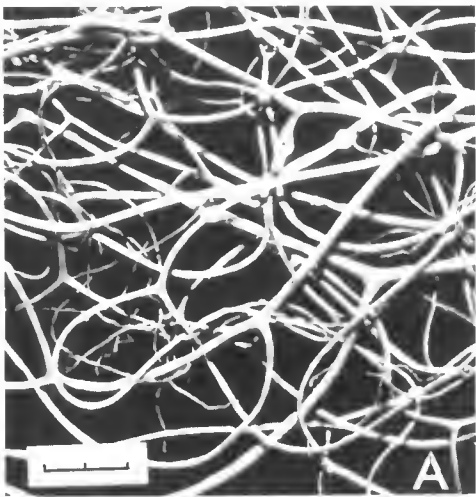
Branching

Terminology of branching basically follows Hawksworth (1972). Various types and some examples are illustrated in Fig. 1. Among the most clearly isotomic dichotomous types in North America is *Bryoria glabra* with even, regular, and broad dichotomies occurring over half the length of the thallus. *Bryoria lanestris* has clearly anisotomic dichotomies over almost its entire length; *B. trichodes* varies from isotomic in subsp. *americana* to anisotomic in subsp. *trichodes*. In *B. fuscescens* considerable variation in types of branching occurs even in the same thallus. The erect species are all clearly anisotomic.

Isidia

As pointed out by Hawksworth (1972), true isidia do not occur in the genus *Alectoria* s. lat. Isidioid branches and spinules do frequently appear, usually associated with soralia (as in *Bryoria furcellata*, Fig. 2 A) or pseudocyphellae (as in *Alectoria imshaugii* (Fig. 2 B) or, less frequently, in *A. sarmentosa* and *A. vancouverensis*). Spinulose branches characterize such species as *Bryoria nadvornikiana* (Fig. 3) and some forms of *B. nitidula*.

Fig. 1. Branching types in the Alectorioid genera. – A, B: Isotomic dichotomous: *Bryoria glabra*. Washington, Pike 843 (CANL). – C–F: Anisotomic dichotomous. – C: *Bryoria lanestris*. Yukon, Scotter 19753 (CANL). – D: *B. nadvornikiana*. Québec, Brodo 17012 (CANL). – E: *B. nadvornikiana*. Québec, Guimont 4442 (CANL). – F: *Alectoria nigricans*. N. W. T., Cody & Ferguson 10520B (CANL). – A: Scale 0.5 mm. – B–F: Scale 4 mm.



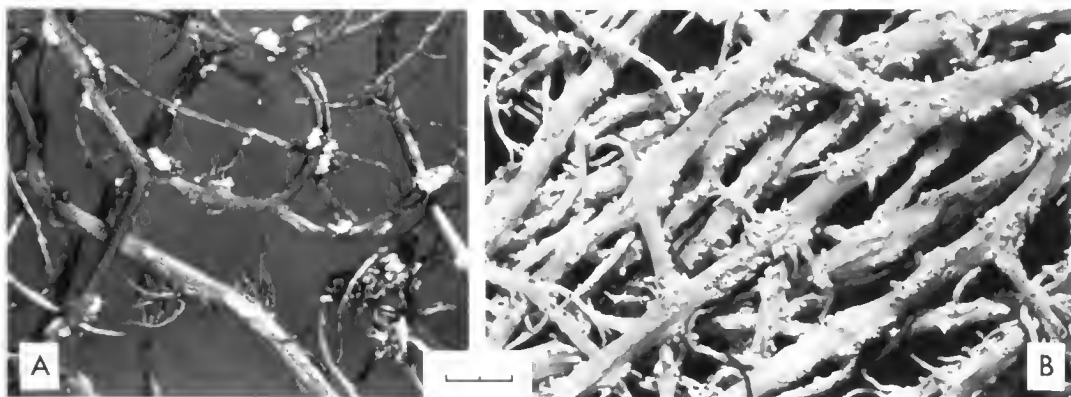


Fig. 2. Isidioid spinules. – A: *Bryoria furcellata*. Cummings, Decades No. 53 (CANL). – B: *Alectoria imshaugii* (holotype). – Scale 0.5 mm.

Soredia

Soredia always arise within discrete soralia of one of two types. *Fissural soralia* originate as a longitudinal split in the cortex and are generally elliptical and flat or concave (Fig. 4 A). *Tuberculate soralia* are round or irregular in outline, conspicuously project above the surface of the filament, and often display a narrow cortical rim (Fig. 4 B). *Bryoria glabra* and *B. simplicior* have only fissural soralia; *B. nadvornikiana* and *B. fuscescens* var. *positiva* have tuberculate soralia predominating.

The presence of soralia is constant in some species, but not in others. North American specimens of *B. capillaris* and *B. implexa* do not have soredia, although European specimens often do. Soralia range from abundant to

absent in *B. glabra*, although the latter situation is very rare. Both subspecies of *B. trichodes* have sorediate morphotypes. There is a rather rare, abundantly sorediate morphotype of *Alectoria sarmentosa* subsp. *sarmentosa* with tuberculate soralia, and rare specimens of *A. fallacina* and *A. mexicana* also show soralia.

The soralia in all four Alectorioid genera tend to be white, but in *Bryoria fremontii* (and in the rare sorediate morphotype of *B. tortuosa*), they are bright yellow due to the presence of concentrations of vulpinic acid. In *Bryoria lanestris* and especially *B. simplicior*, the soralia are black to greenish flecked, probably due to the remnants of cortical and algal tissues on their surface.

Pseudocyphellae

Pseudocyphellae are constant in *Alectoria* and *Sulcaria*, but are very variable in *Bryoria*. In the section *Divaricatae*, pseudocyphellae are generally dark and very inconspicuous. In taxa such as *B. trichodes* subsp. *trichodes*, they are white and are often somewhat raised (Fig. 5 A); in other taxa, they are plane (Fig. 5 B). Pseudocyphellae are yellow in *B. tortuosa* (Fig. 5 C), and are sunken into spiraled channels in members of the genus *Sulcaria* such as *S. badia* (Fig. 5 D). In *Bryoria pseudocapillaris* and *B. spiralifera*, the pseudocyphellae are linear, white, and very long (Fig. 5 E).



Fig. 3. Spinulose branches. *Bryoria nadvornikiana*. Quebec, Guimont 4442 (CANL). Scale 0.5 mm.

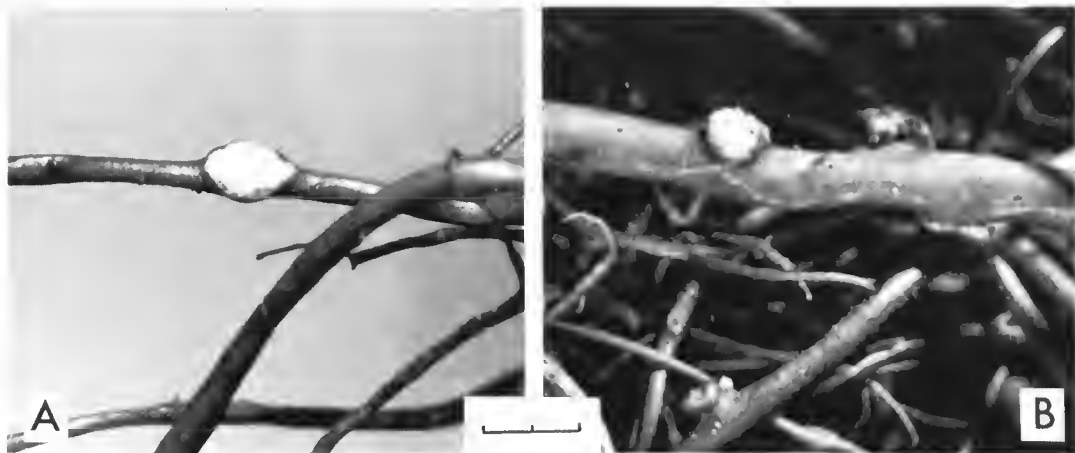


Fig. 4. Soralia. – A: Fissural soralium, *Bryoria glabra*, Washington, Pike 843 (CANL). – B: Tuberculate soralia, *Bryoria fuscescens* var. *positiva*, Newfoundland, Ahti 560 (CANL). Scale 0.5 mm.

Contrasting sharply with the flat or channelled pseudocyphellae described above, those of the genus *Alectoria* s. str. are conspicuously raised and striking (Fig. 5 F). Most are somewhat elongate, but in *A. fallacina* most pseudocyphellae are punctiform.

Colour

The use of colour causes particular difficulties which arise from differences in interpretation by individual observers. For this reason, we have endeavoured not to place too much emphasis on it. However, we found that after looking at many examples of various species, their characteristic colour tones began to become clear, and it seems evident that species do have characteristic colours, although these can be subtle and difficult to interpret.

It is most difficult to interpret colour changes due to the age of a specimen. For one thing, we have noticed that species which sometimes have a distinctly greenish appearance in the field or in fresh specimens gradually lose this tone in the herbarium with the death and bleaching of the algal layer. This is obviously most serious with the paler species such as *Bryoria capillaris*, *B. fuscescens*, *B. trichodes* subsp. *trichodes*, and *Alectoria sarmentosa*. Species with barbatolic acid or alectorialic

acid (e.g., *Bryoria capillaris* and *Alectoria nigricans*) gradually become pinkish or even reddish and may even stain their packets reddish in time. *Bryoria friabilis*, normally very pale olivaceous brown, turns to dark brown with age. Most other species retain their colour, however.

There are three basic hues in *Bryoria*: (1) the olivaceous or olive-black of species such as *B. glabra*, *B. carlottae*, *B. pikei*, *B. chalybeiformis*, and *B. vrangiana*; (2) the "cervine brown" (i.e., deer brown) of *B. trichodes*, *B. furcellata*, and *B. simplicior*; and (3) the white to grey-fuscos of *B. subcana*, *B. capillaris* and *B. nadvornikiana*. One might call the clear red-brown of *abbreviata* distinct as well as the unique chestnut brown of *Sulcaria badia* and *Bryoria spiralifera*, but it is difficult or impossible to distinguish them adequately from cervine brown using a verbal description.

Even the species with usnic acid show some constant variation in tone, although it is difficult to describe. *Alectoria sarmentosa* is extremely variable in colour, but is generally a very "yellow" yellow-green (i.e., straw-coloured) especially in the herbarium. *A. fallacina* has a much darker, greyer tone as does *A. vancouverensis*. There is a great deal of variation in the amount of green or green-black on *A. sarmentosa* and *A. ochroleuca*

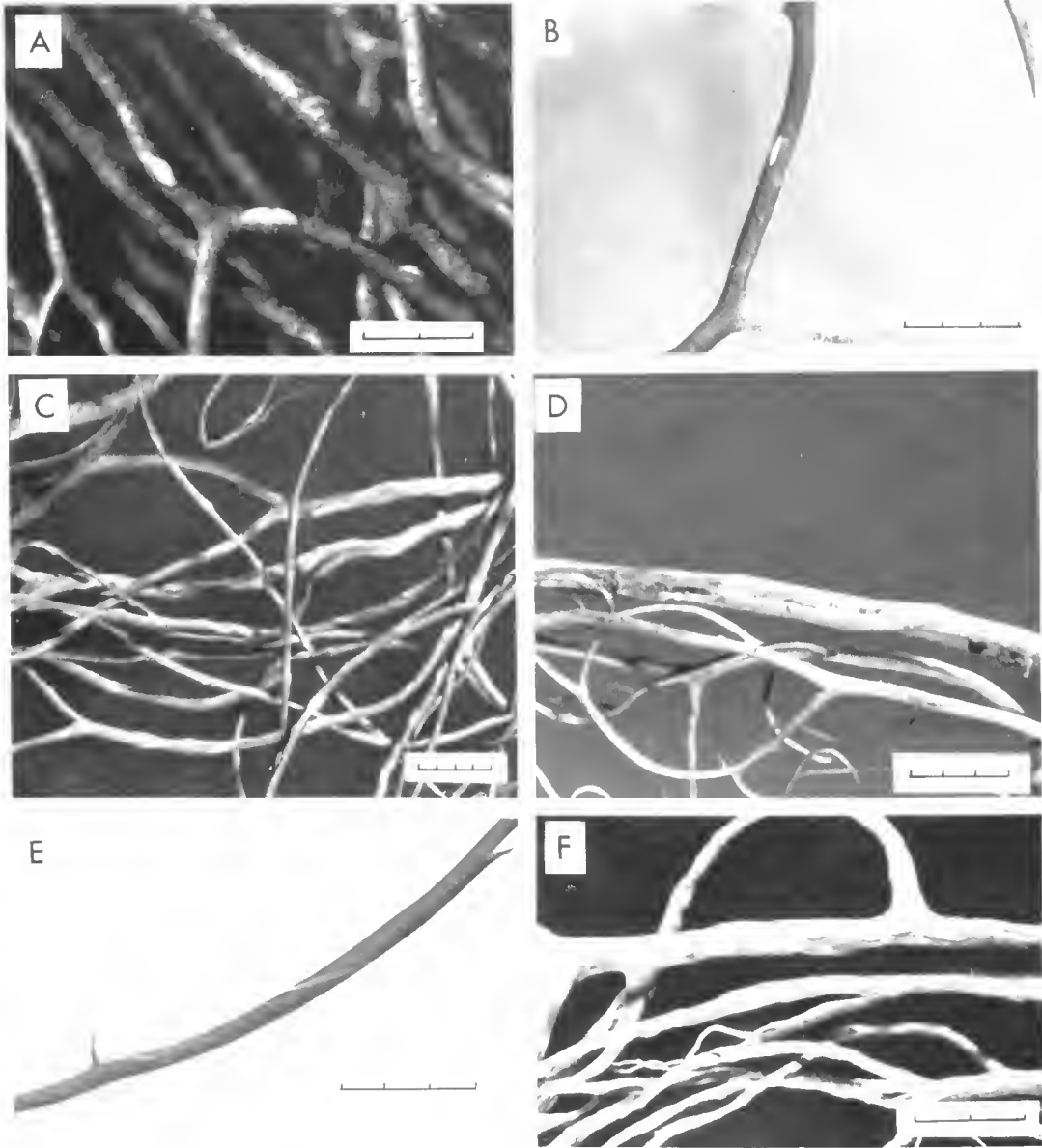


Fig. 5. Pseudocypellae. — A: Fissural, raised, *Bryoria trichodes* subsp. *trichodes*, Ontario, Brodo 13737 (CANL). Scale 0.25 mm. — B: Fissural, plane, *Bryoria carlottae*, Holotype. Scale 0.25 mm. — C: Twisted, yellow, *Bryoria tortuosa*, Rel. Tuck. No. 2 (CANL). Scale 0.5 mm. — D: Sulcate, *Sulcaria badia*, Oregon, Hall (F-H-Tuck. 504). Scale 0.4 mm. — E: In long spiral, *Bryoria spiralifera*, Holotype. Scale 0.5 mm. — F: Raised on ridges, *Alectoria vancoverensis*, B. C., Bird 28472 (CANL). Scale 1.0 mm.

apparently depending on the degree of exposure and moisture-availability.

Unhappily, there are a number of species which vary a great deal in colour. *Bryoria pseudofuscescens* can be pale brown, dark brown, or greenish-black with every possible intermediate. The possibility that the norstictic acid-producing species may actually consist of several taxa has been raised by Hawksworth (1972) (see Discussion under *B. pseudofuscescens*). *B. implexa* varies from pale brown to pale olivaceous, but so few fresh specimens have been seen, this difference may be due to ageing. The same is true of *B. salazinicola* which does seem to have a pale olivaceous caste when fresh. *Alectoria nigricans* varies from pale grey with black tips through yellowish grey with black tips, to entirely black with grey basal areas; rare specimens are a shiny brownish grey and blackened at the tips.

True black thalli are rarely found in any species, although some specimens of *Alectoria nigricans* and *Bryoria nitidula* are almost uniformly black. The bicolourous thalli of *B. bicolor* and *B. tenuis* have truly black main stems with only the secondary or tertiary branches remaining olivaceous brown. Some forms of *B. trichodes* subsp. *americana* have extensive blackened areas and in some cases appear somewhat like *B. tenuis*. These blackened areas are a type of fragmentation area referred to by Hawksworth (1972).

Only one colour is due to something other than the presence or absence of pigments in the cortex. In *B. tortuosa*, a thallus may acquire a bright emerald green colour by virtue of an accumulation of vulpinic acid on the surface of the cortex. Often thalli apparently collected on the same branch (being in the same packet) vary from red-brown to bright emerald green.

Shininess, or dullness, is tempting to use as a character, but it is usually too variable to be reliable. Certain species do, however, show clear tendencies. *B. glabra* is almost always very shiny; *B. abbreviata* is virtually always dull; *B. trichodes* can be very shiny or satiny; *B. lanestris* tends to be satiny; *B. capillaris* is almost always dull; *B. pseudofuscescens* can be shiny or dull.

Friability

Friability or brittleness was mentioned by Hawksworth (1972) as a reliable characteristic of *B. lanestris* in Great Britain, and this has proved to be the case in North America as well. *B. friabilis* is also extremely brittle and the same is true of many other species in the section *Implexae*. *B. abbreviata* and *B. oregana* in the section *Subdivergentes* are also very easily fragmented. The basis for this character seems to lie in the cortical structure (see below).

Ascocarps

Apothecia are very rare in the Alectorioid genera as a whole and many species are known only in a sterile condition, their classification within a certain genus being based on a combination of vegetative characteristics. In the case of the North American species, we have seen apothecia in North American collections of only 18 of the 38 accepted species. Even in those species able to produce apothecia, only a few regularly do so (e.g., *Bryoria abbreviata*, *Alectoria lata*, *Pseudephebe minuscula*, *P. pubescens*) and in some very widely distributed species, apothecia appear to be produced often in localized populations (e.g., *Bryoria trichodes* subsp. *americana*, *B. fremontii*, *Alectoria nigricans*, *A. sarmentosa*). The frequency of ascocarp production in some species is exceedingly low. In the present study, for example, out of 247 collections of *Bryoria capillaris* and 66 of *B. tenuis* examined, apothecia were seen in only one specimen of each (i.e., 0.40 % and 1.52 % of the collections examined, respectively). Even when an apothecium is produced, ascospores are often formed only sparingly and mature ascospores free from their asci are often difficult to observe.

Despite the wide distribution and size of these genera, there has been no detailed study published of ascocarp structure and ontogeny in any species. It seems probable that the asci in all these genera are of the "arrested bitunicate" type, that is, having inseparable exo- and endoascus walls, as is the case in almost all the lichenized ascohymenial fungi (Letrouit-Galinou 1974, Henssen & Jahns 1973).

Awasthi (1970) considered the presence of anastomosing paraphysoid tissue (which he called pseudoparaphyses), particularly at an early stage of development, to indicate a possible affinity between the genus *Alectoria* s. lat. and the family Roccellaceae Chev. This family was treated by Henssen & Jahns (1973) as belonging to the order Arthoniales, a "Zwischengruppe" between the ascohymenial and ascolocular groups. The presence of anastomosing paraphysoid tissue in ascocarps which seem to be ascohymenial in all other respects has long been a source of confusion to lichen systematists. Henssen & Jahns (1973) through an investigation of many types of ascocarps have done much to clear up this difficulty. They found that one must distinguish between *paraphysoid tissue* (originating from the generative tissue of many ascohymenial lichen fungi and often, but not always, gradually changing into true paraphyses with the maturation of the ascocarp), and *pseudoparaphyses* (which have an entirely different origin and development and are characteristic of the ascolocular fungi) (see Henssen & Jahns 1973 pp. 90, 116–117).

Our observations of the hymenial tissue of *Alectoria mexicana*, *A. lata*, *Bryoria pseudofuscescens*, *B. furcellata*, and *B. oregana* have shown that the cells of the paraphyses of all these species are short and tend to branch and even anastomose to some extent. This is particularly evident in *A. lata* and *A. mexicana* and is perhaps true of all members of the genus *Alectoria*. The short cells and branching are well illustrated by Galløe (1950) for *A. sarmentosa* and *A. ochroleuca*. In these species, one could well speak of *paraphysoid tissue* in the sense of Henssen & Jahns (1973) rather than paraphyses. These species would be represented by the type ascocarp illustrated in Figure 4.19 d of Henssen & Jahns (1973 p. 118).

In all species of *Alectoria*, *Bryoria* and *Pseudophebe* that we have examined, the excipulum proprium is well developed. Although Awasthi (1970) regards this as a character unique to *Alectoria* s. lat. and *Oropogon*, we have seen a distinct excipulum proprium in the closely related *Cornicularia californica* (Tuck.) DR. Galløe (1947) has illustrated the same condition in other species of the Parme-

liaceae (e.g., *Cetraria nivalis* (L.) Ach. and *Evernia prunastri* (L.) Ach.).

Thus, there seems to be no reason to regard any of the Alectorioid genera as a possible member of the Arthoniales, and indeed, little reason to isolate these genera from other closely related genera such as *Cornicularia* and *Parmelia*, as was suggested by Awasthi (1970).

The numbers of spores per ascus (i.e., 2–4 vs. 8), their pigmentation when mature (i.e., brownish vs. hyaline), and their septation and size, are of importance in the recognition of the four genera accepted here (see Table 2).

Within the genera, however, ascospore size appears to be of very limited taxonomic value for the characterisation of species to judge from the information so far available. In view of this and the practical difficulty of finding mature apothecia in many species, only scant attention has been paid to these characters in the present survey.

Anatomy of the vegetative tissues

The anatomy of the vegetative tissues was studied in some detail because of its potential value in the delimitation of species. Our intention was merely to survey the anatomical features of a majority of the species to see if trends could be noted and useful characters discovered. No attempt was made to examine large numbers of specimens within each species although this would obviously be desirable, as pointed out below. Wherever possible, type specimens were examined.

Our methods for preparing the microtome sections were almost precisely those employed by Wetmore (1960 p. 375). Sections were made at 12 μ m using a freezing microtome after the material had been soaked overnight in an alcohol-detergent solution. The material was then mounted in lactophenol and cotton blue. This stain colours the cytoplasm within the cell lumina making the lumina easy to see and measure. It also stains the chloroplasts of the algal cells dark blue. The lactophenol served as a semi-permanent mounting medium when the coverslips were sealed with two coats of clear nail polish. To see finer characters of the conglutinated cortical hyphae and the extent of the matrix material, all the sections were also examined in phase-contrast illumination.

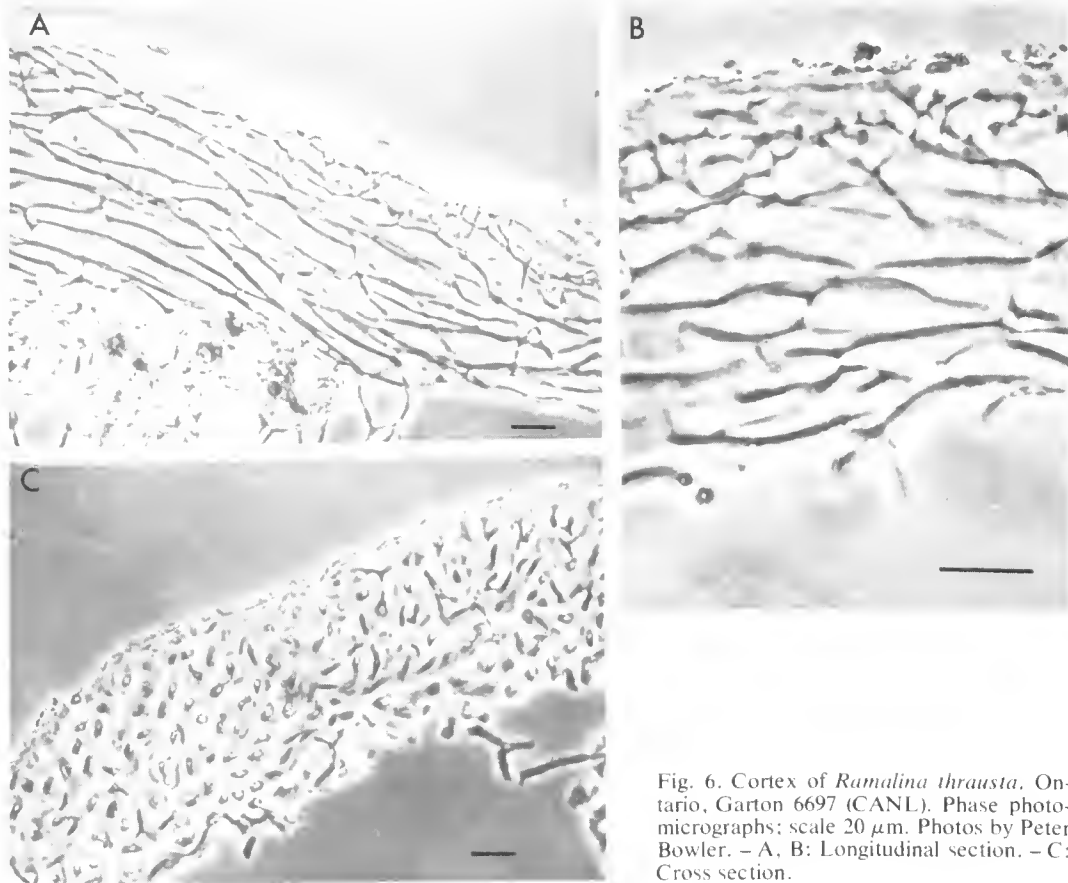


Fig. 6. Cortex of *Ramalina thrausta*, Ontario, Garton 6697 (CANL). Phase photomicrographs; scale 20 μ m. Photos by Peter Bowler. – A, B: Longitudinal section. – C: Cross section.

Cortex

Characters of the cortex have been used by many authors to distinguish *Alectoria* s. lat. from related (or at least superficially similar) genera, especially *Cornicularia*, *Parmelia*, and *Ramalina*. For example, Hawksworth (1969 a) showed that characteristics of the surface of the filaments as revealed by scanning electron microscopy (SEM) for the most part do correlate well with classical generic concepts.

Studies carried out in connection with the North American species have shown that there is much more variation in cortical tissue than previously suspected. This is especially true in the extent of septation and emergence of the superficial layer of cortical hyphae. However, we must hasten to add that we have

found even the most "*Alectoria*"-like species of *Cornicularia* (e.g., *C. pseudosatoana* Asah. and *C. californica*) and *Ramalina* (i.e., *R. thrausta*) to be quite distinct from any species in any genus studied here. The cortex of *Cornicularia pseudosatoana* has clearly distinguishable periclinal and netlike layers of prosoplectenchyma. *C. californica* almost develops a paraplectenchymatous outer layer. *Ramalina thrausta* has a fibrous, periclinal cortex similar in some respects to that of species of *Alectoria* but with a noticeable increase in the branching of the superficial hyphae (Fig. 6). This, however, is not the two-layered cortex considered by many authors to be typical of *Ramalina* and illustrated by Jahns (1974) in his figures 30 and 31. The surface features of *R. thrausta* (Hawksworth

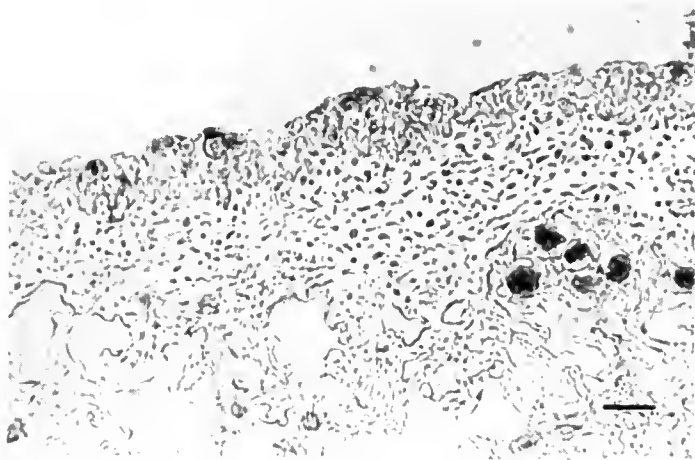


Fig. 7. Decomposed cortex of *Alectoria vancouverensis*. California, Tavares 371 (CANL), cross section. Scale 20 μ m.

1969 a pl. IV c) obviously would not reveal this.

Basically, the Alectorioid cortex is made up of periclinal hyphae fused into a chondroid mass to varying degrees. In some species, it is composed of fairly distinct interwoven hyphae and in others, it is clearly prosoplectenchymatous with only the lumina distinguishable (a "skleroplektenchym" in the terminology of Frey 1936). This structure is particularly well seen in scanning electron micrographs of cut ends and longitudinal slices of branches (Hawksworth 1972, Hale 1976, Jørgensen 1975). The cortex in *Alectoria* s. lat. has been called a stereome by a number of recent authors (Ozenda 1963, Hawksworth 1969 a, 1972) in the context of its being a supporting tissue. This term has been used by lichenologists more frequently to refer to chondroid medullary tissue (as in *Cladonia* and *Usnea*) (e.g., Galløe 1947, 1954) and so we will simply refer to this tissue in the Alectorioid genera as the cortex. (It should be noted that all these tissues are remarkably analogous in anatomy as well as function.)

Internally, the cortex is generally very distinct from the medulla. The surface of the cortex is relatively rough and sometimes ridged (see Hawksworth 1969 a), but sometimes this roughness is due to a heavy deposition of pigmented material, and in other cases, the superficial hyphae themselves protrude to varying degrees. A non-cellular epicortex, as

seen in *Parmelia* and some allied genera (Hale 1973, 1976), is not found in any of the *Alectoria*-like genera. In many species of *Alectoria* s. str., especially *A. vancouverensis*, the surface of the cortex seems to decompose to some extent giving rise to a highly irregular surface (Fig. 7) (Hawksworth 1969 a pls. I f, III a).

As mentioned above a number of species are noticeably more brittle than others. The basis for this friability apparently lies in the quantity of matrix material in which the cortical hyphae are embedded, i.e., the ratio of lumen area to wall-matrix area in the cortex. Brittle species such as *Bryoria friabilis* and *B. implexa* have little matrix material apparent (Fig. 8) whereas strong, resilient species such as *Alectoria fallacina* and *Bryoria glabra* have a great deal (Fig. 9). Species such as *B. trichodes* and *B. fuscescens* are more or less intermediate (Fig. 10).

We have implied above that there are certain cortical characters which are correlated with certain genera, and with sections within *Bryoria*, and this indeed appears to be true in certain cases.

In *Alectoria* s. str., the cortex is generally thick, averaging about 50–80 μ m and commonly going as high as 120 μ m; in the other genera, the cortex is generally between 30 and 40 μ m rarely exceeding 50 μ m. In addition, the cortex in *Alectoria* is highly cartilaginous with a great deal of matrix material. As mentioned

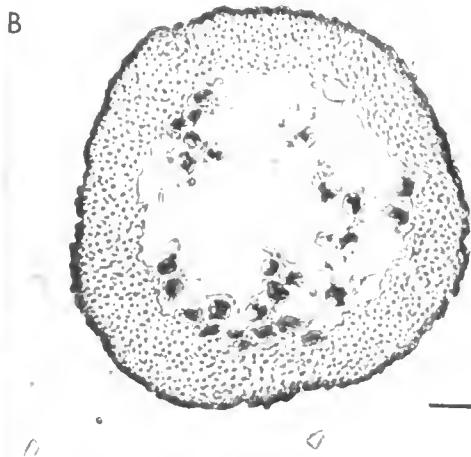
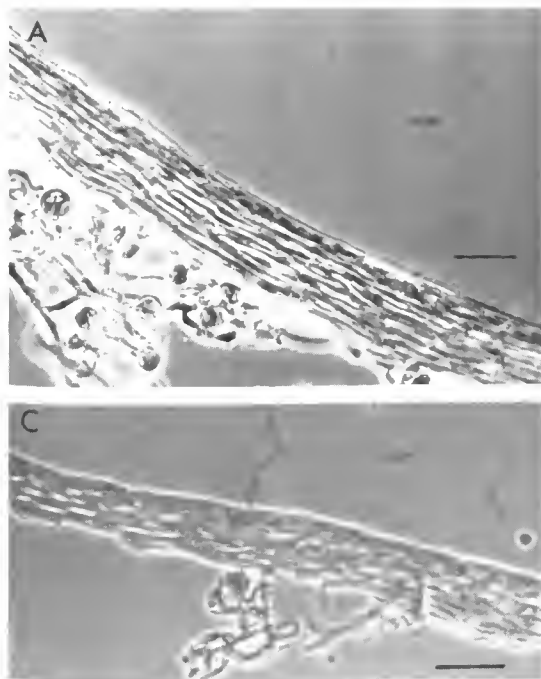


Fig. 8. Cortex with little matrix. Scale 20 μ m. - A, B: *Bryoria friabilis*. Oregon, Hawkins (WIS). - A: Longitudinal section, phase contrast. - B: Cross section, light microscopy. - C: *Bryoria implexa*. Quebec, Macoun? (CANL 16294), longitudinal section, phase contrast.

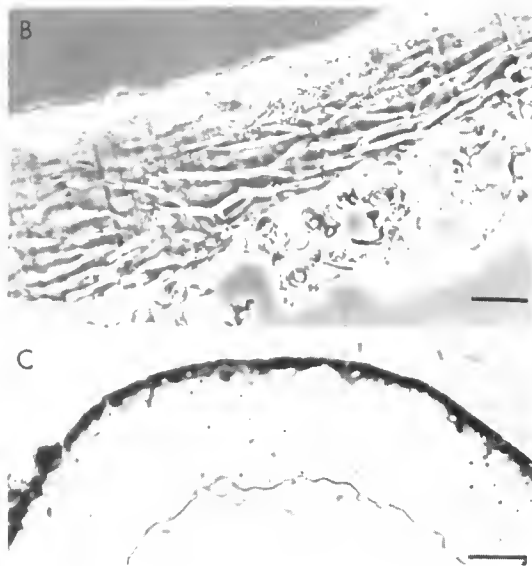
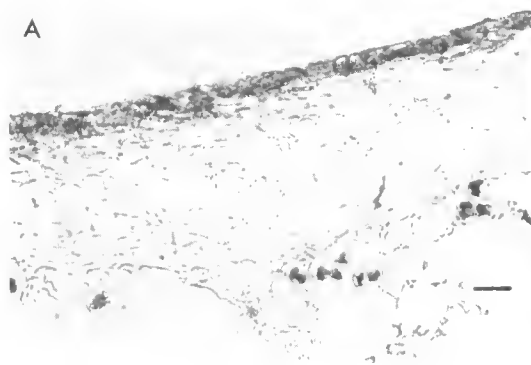


Fig. 9. Cortex, much matrix. Scale 20 μ m. - A, B: *Alectoria fallacina*. Isotype (US). - A: Longitudinal section, light microscopy. - B: Longitudinal section, phase contrast. - C: *Bryoria glabra*. Isotype (CANL), cross section, light microscopy.

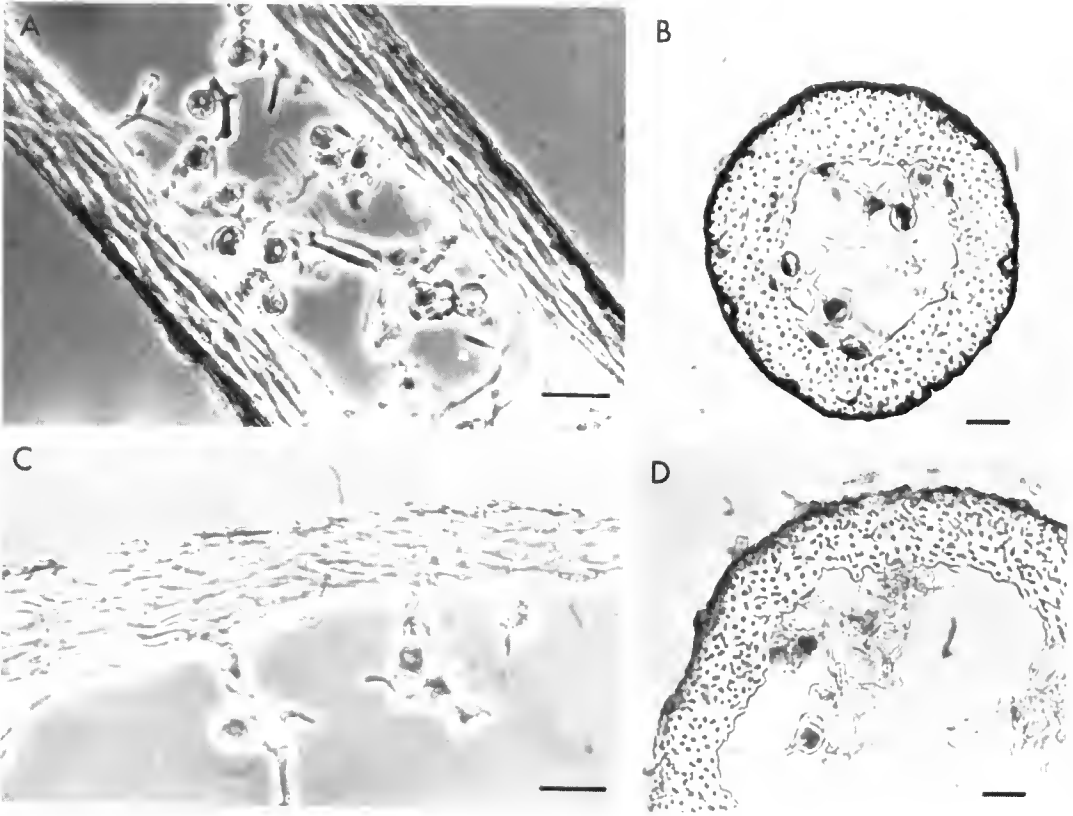


Fig. 10. Cortex, intermediate matrix. Scale 20 μm . – A, B: *Bryoria trichodes* subsp. *americana*. B. C., Brodo 11668 (CANL.). – A: Longitudinal section, phase contrast. – B: Cross section, light microscopy. – C, D: *Bryoria fuscescens*. Isotype (CANL.). – C: Longitudinal section, phase contrast. – D: Cross section, light microscopy.



Fig. 11. Cortex with hyphae arranged in fascicles. Scale 20 μm . – A: *Bryoria furcellata*. Quebec, Masson s.n. (QUE), cross section. – B: *Bryoria cervinula*. B. C., Brodo 17769 (CANL.), cross section.

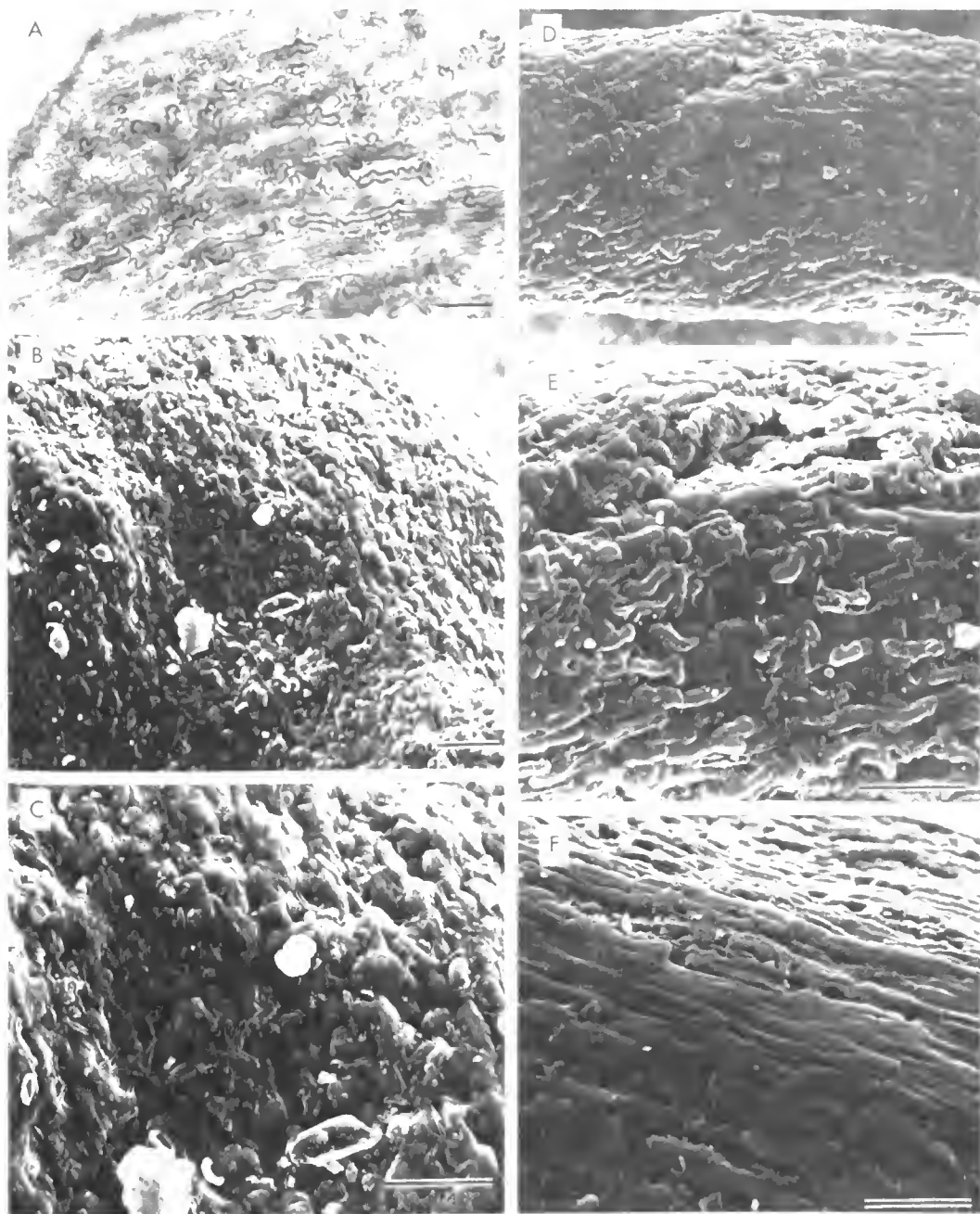


Fig. 12. A–F: Surface cortical features of *Bryoria* sect. *Subdivergentes*. Scale 20 μ m. – A: *Bryoria oregana*, B. C., Brodo 8178 (CANL), surface view of cortex showing jigsaw pattern of superficial cortical cells. Light, transmission microscopy. – B–F: Scanning electron micrographs (SEM). – B, C: *Bryoria abbreviata*, Alberta, Bird & Takusta 16703 (CANL). – B: Negative frame 290 \times . – C: Negative frame 580 \times . – D, E: *Bryoria oregana*, Washington, Imshaug 6237 (CANL). – D: Negative frame 290 \times . – E: Negative frame 580 \times . – F: *Bryoria fremontii*, Alberta, Bird & Glenn 14214 (CANL), negative frame 580 \times . There are no projecting superficial cells of the cortex in this species which is in the section *Lortuosae*.

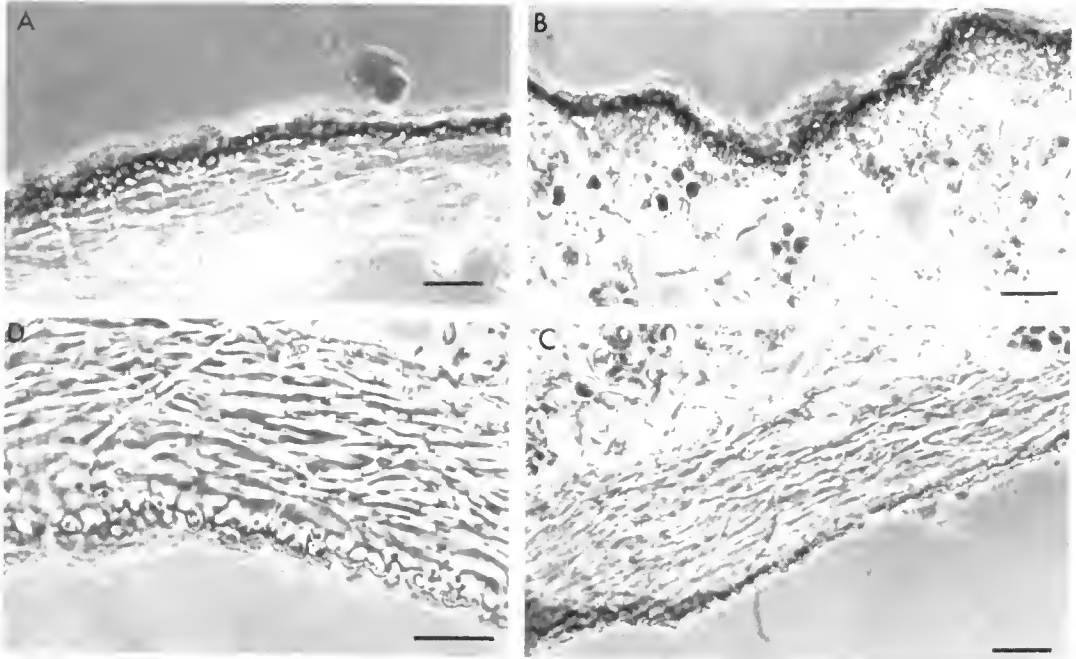


Fig. 13. Anatomy of *Pseudephebe*. – A: *Pseudephebe pubescens*. – B, C., Brodo 14209 (CANL), longitudinal section of the cortex showing superficial cellular layer. Scale 20 μm . – B–D: *Pseudephebe minuscula*. Colorado, Shushan 8323 (CANL), longitudinal sections of the cortex, phase contrast. Scale = 20 μm . – B: "Lower" cortex of a flattened branch. – C: "Upper" cortex of a flattened branch. – D: Cortex of a terete branch.

above, the surface is also somewhat decomposed.

In a number of species of the section *Divaricatae* of *Bryoria* (e.g., *B. furcellata*, *B. nitidula*, *B. cervinula*), the cortical hyphae



Fig. 14. Lax, arachnoid medulla in *Bryoria implexa*, Quebec, (Macoun?) s.n. (CANL 16294). Longitudinal section. Scale 60 μm .

are, at least in part, distinct with conglutinate thick-walled filaments often in fascicle-like groups (Fig. 11). Most have superficial cells protruding above the surface giving it a somewhat knobby or ridged appearance, and most are also encrusted with pigmented material.

Bryoria oregana, *B. abbreviata*, and *B. subdivergens* have a great many similarities in habit, colour, spores, etc. and are obviously closely related. They are treated here as comprising the section *Subdivergentes*. It was very interesting to discover, therefore, that the cortices of all three are very similar and very unusual. In these species (and only these species) the outermost cells of cortical hyphae become short, irregular, and knobby forming a jigsaw-like pattern on the thallus surface (Fig. 12 A). They also extend above the surface giving the cortex a very rough, bumpy appearance with SEM or under the light microscope (Fig. 12 B–E) and a dull or matt texture to the eye. (Compare this cortical

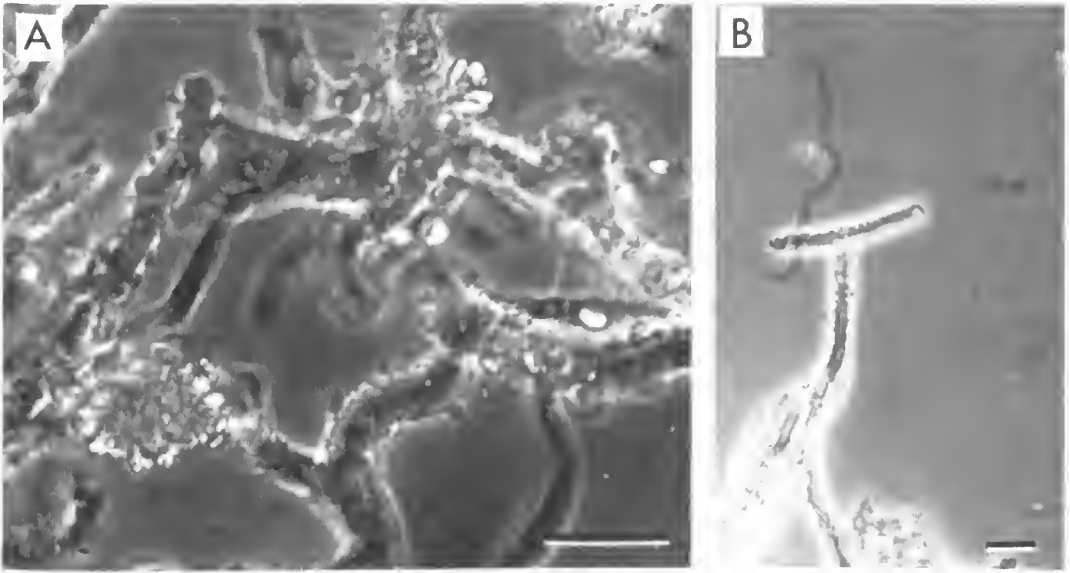


Fig. 15. Ornamented medullary hyphae in *Alectoria sarmentosa*, phase contrast. Scale 20 μ m. – A: Subsp. *sarmentosa* B. C., Brodo 12792 (CANL). – B: Subsp. *vexillifera*, Quebec, Guimont 4446 (CANL).

surface with the relatively smooth, encrusted surface of *B. fremontii*, Fig. 12 F.) The SEM photograph of the surface features of *Bryoria divergescens* (syn. *Alectoria divergescens*) in Hawksworth (1969 a pl. II d) as well as the comments of Dahl (1950) and Awasthi (1970) lead us to believe that this mainly Himalayan species may belong in this section as well.

It is not surprising that *Pseudephebe minuscula* and *P. pubescens* have similar cortices. The cortical anatomy reflects the general habit of the plant closely, especially in *P. minuscula*. In the more "foliose" parts of the thallus, there is a net-like prosoplectenchyma (as in Jahns 1974 fig. 12) forming the "upper" cortex, and a fibrous, periclinal prosoplectenchyma forming the "lower" cortex (Fig. 13 A–C). In the terete branches, the cortex is more uniformly periclinal, but one can still make out a distinct shortening of the superficial cells which results in a kind of false pseudoparenchyma at the surface (Fig. 13 D). We noted no encrusting pigmented material on the surface; all the pigment (and there is a great deal) is within the cell walls of the superficial cells.

Algal layer

As stated by Hawksworth (1972) and illustrated by Galloë (1950), the algal layer of almost all species of the Alectorioid genera is located just inside the cortex. If the medulla fills the filament cavity (as in *Alectoria vancouverensis* and extreme morphotypes of *A. sarmentosa* subsp. *vexillifera*), one may find algal cells even in the centre of the filament, but in a much reduced number. In addition, the distribution of algal cells along the length of the filament is often very discontinuous and clumped (Galloë 1950 figs. 573, 570, 575). For example, there are no algae in the blackened "fragmentation areas" of e.g. *B. trichodes* subsp. *americana* (see Hawksworth 1972).

No studies on the taxonomy of the algal components have been carried out in connection with this revision. This would have necessitated investigations of the algae from pure cultures. Further studies on the systematics of lichen phycobionts at the species level are desirable in view of their possible role in influencing thallus form and chemistry (see the section Taxonomic concepts: species).

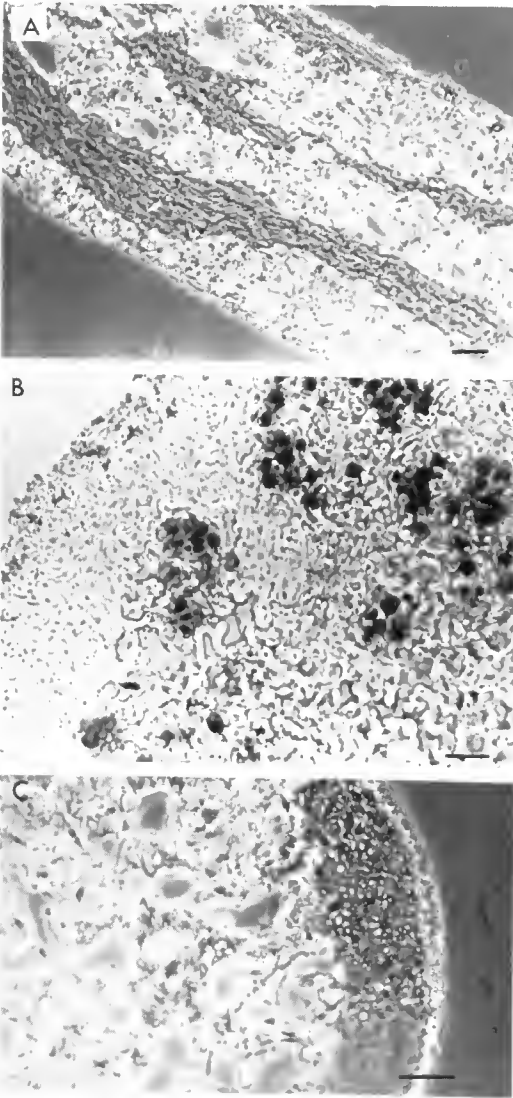


Fig. 16. Cortical material invading the medulla. — A, B: *Alectoria vancoverensis*. B. C., Bird 28472 (CANL). — A: Longitudinal section, phase contrast. Scale 60 μm . — B: Cross section, light microscopy. Scale 20 μm . — C: *Bryoria pseudocapillaris*. Holotype, cross section, phase contrast. Scale 20 μm .

Medulla

The medulla in most Alectorioid species is very lax and "arachnoid" (Hawksworth 1972 pl. I c; Fig. 14). Most species have medullary hyphae between 3.5 and 5.0 μm in diameter. The hyphae are generally smooth, but in most species of *Alectoria* s. str. the medullary hyphae are "ornamented" with knobs and projections (Fig. 15). The only exceptions were *A. ochroleuca* and *A. uigricans*. A similar ornamentation occurs rarely in *Bryoria fuscescens* (M. Skytte Christiansen, *in litt.*).

Among those species with a consistently dense medulla (*Alectoria vancoverensis*, *A. mexicana*, *A. fallaciua*, *Bryoria pseudocapillaris*), a few have bundles of cortical-like hyphae running through the medulla, joining and then leaving the cortex proper. Most noteworthy in this regard is *A. vancoverensis* where the fibrous medulla apparently can be used as a species character (Fig. 16 A, B). According to the drawings of Galloë (1950 figs. 603, 604, 607), the same is true of *A. sarmentosa* subsp. *vexillifera*. An anastomosing network of conglutinate fibres was also seen in the medulla of *Bryoria pseudocapillaris* (Fig. 16 C).

Chemistry

Methods

Spot tests

A great many misidentifications exist in herbaria and even in the literature due to errors in interpreting gross colour tests with the standard PD, KOH, and C reagents. With few exceptions (mentioned below) we believe it is possible to use these reagents with reliability if certain procedures are followed.

For our tests, "K" is a 10% aqueous solution of KOH, "C" is fresh, undiluted household bleaching solution (such as Clorox or Javex in North America and Parazone in the United Kingdom) which is a concentrated sodium hypochlorite solution, and "PD" is either a solution made from a few crystals of dry *p*-phenylenediamine in one or two drops of 70% ethanol, or Steiner's solution, a saturated aqueous solution of PD in 10% sodium sulphite to which a few drops of a strong wetting agent (detergent) has been added. For a "KC" test, a small quantity of C is added to a spot still moist from the application of K. A "CK" test is made by reversing the order of application of these two reagents.

"IKI" solution (Melzer's reagent, undiluted or diluted 1:1) was tested on all species of *Bryoria*, section *Divaricatae*, and on a number of other species from other sections and genera. No cortical or medullary reaction such as that reported by Bystrek (1969) for "*Alectoria perspinosa*" Bystr. was seen in our material.

The reagents are applied in various ways depending on the tissues being tested or the substances expected. In most cases, tests of medullary reactions are most satisfactorily made with melting point capillary pipettes of about 1.6–1.8 mm outside diameter drawn to a fine tip. The reactions are observed under a dis-

secting microscope. As is the case with most lichen spot tests, the smaller the quantity of reagent, the more sensitive the test. The most sensitive PD tests of soralium reactions are made with a capillary tube and fresh alcoholic PD.

Almost all other PD tests and most K tests are made in the following manner. About 5 to 15 filaments of the specimen, including some of the finest tips and growing portions, are put on a small piece of white filter paper (about one cm²). The paper squares are placed on a microscope slide which, in turn, is on a piece of cardboard to prevent the table surface from becoming stained (Fig. 17). The filaments are then *flooded* with two or three drops of reagent (K or Steiner's solution). There must be sufficient liquid reagent remaining around the filaments to permit the diffusion of any coloured material out of the thallus and onto the paper. On the other hand, if too much reagent is used, the chemical reaction will be obscured by excess dilution.

A positive reaction might be indicated in one of two ways. The more obvious one is the oozing out of colour onto the filter paper. This will occur with all species having PD + yellow reactions and with thalli containing fumarprotocetraric acid in the outermost portion of the cortex (Fig. 18 A). Equally dependable is the PD + red reaction of the inner portion of the cortex together with the medulla which produces no colour at all on the filter paper (Fig. 18 B, C). The tissues turn deep red and the reaction is visible *through* the pigmented outer cortex which is rendered semi-transparent by Steiner's PD solution itself. If the fumarprotocetraric acid is abundant, permeating almost the entire cortex as well as the medulla, the entire filament will seem to develop a red

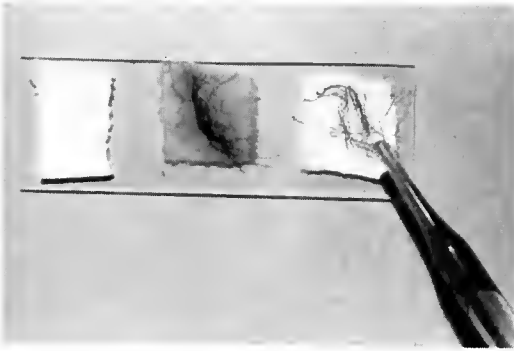


Fig. 17. Filter paper method for colour reactions. Three squares of white filter paper have been placed on a microscope slide. The piece in the center with some filaments of *Bryoria* sp. has been flooded with Steiner's solution; the piece on the right is about to be treated.

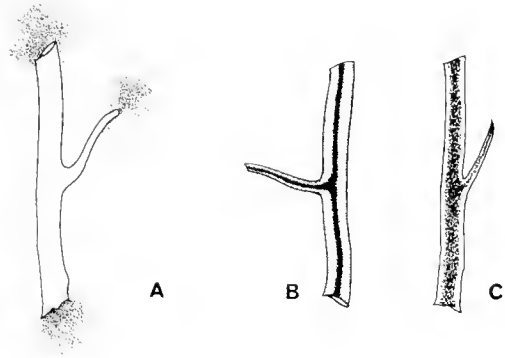


Fig. 18. Types of reactions on filter paper with Steiner's solution. – A: If there is a positive cortical reaction, the resulting colour diffuses out onto the filter paper. A positive KOH reaction will have the same effect. – B: The Steiner's solution "clears" the filament and a positive reaction of the inner cortex or medulla is visible *through* the cortex as a red, centrally located line. – C: If the inner tissues react strongly, the entire filament will turn red, but the colour will not diffuse out.

colour (Fig. 18 C). However, unless the surface of the cortex contains the substance, no pigment will ooze out (except at breaks in the cortex, e.g., at soralia or pseudocyphellae). More frequently, the red reaction is indicated by a thin red "line" within the filaments (Fig. 18 B). The test is extremely sensitive, sometimes detecting the presence of fumarprotocetraric acid in small portions of a filament even when TLC techniques fail.

The position of a positive PD reaction appears to be relatively species-specific. As seen in Fig. 19, one can classify the reactions into five categories: (A) occurring in the outer cortex alone; (B) occurring in the inner cortex alone (sometimes expanding to include the entire cortex, as in B'); (C) including all tissues except the outermost part of the cortex; (D) occurring both in the outer and inner portions of the cortex (and usually the medulla as well); (E) occurring in the medulla alone.

Type E reactions are encountered most frequently in the genus *Alectoria*, as in the thamnolic acid test with *A. imshaugii* (see comments below). It never has been seen as a fumarprotocetraric acid reaction. Type A reactions are due to the presence of the acid on or just below the thallus surface. As a PD+ red reaction, it is seen only in *Bryoria subcana* and rarely in *B. fuscescens*. On the other hand, it is the characteristic reaction

for alectorialic, barbatolic, norstictic and salazinic acids. Specimens producing a strong PD+ red oozing reaction are most frequently of type D.

The most commonly seen reactions, however, are those of type B and C. American *Bryoriae* of the section *Divaricatae* which contain fumarprotocetraric acid (e.g., *B. furcellata*, *B. nitidula*) are always type C. *Bryoria trichodes* (both subspecies) usually give a type B reaction (occasionally developing into B'), but thalli with type C reactions have also been seen. After the addition of PD solution, *Bryoria cervinula* starts as either type B or C, but generally finally oozes some red coloration (thus resembling a type D reaction) apparently due to the sheer quantity of acid in the cortex.

In some species fumarprotocetraric acid appears to be largely restricted to the soralia (e.g. *Bryoria chalybeiformis*, *B. glabra*, *B. laevis*) so that an intense PD+ reaction is obtained from these structures which is very strictly localized (a phenomenon apparently first recorded and figured by Frey 1952, for "*A. jubata* var. *prolixa*"). When testing specimens for cortical and medullary reactions

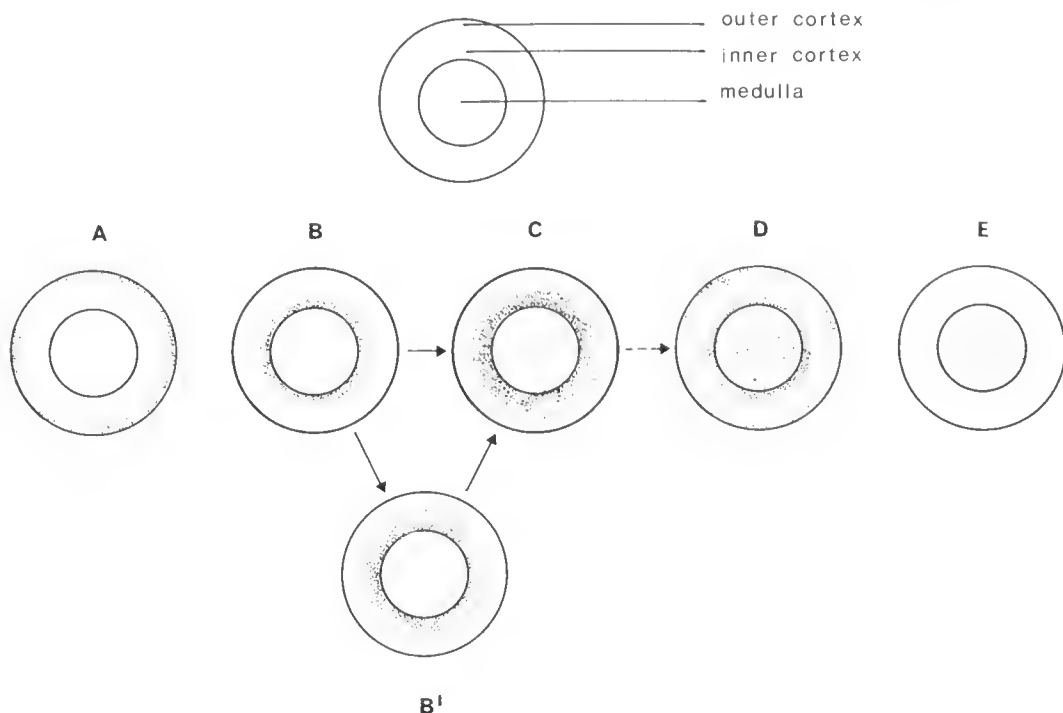


Fig. 19. A classification of possible colour reactions on filament cross sections. See text for explanation.

with this reagent, it is consequently important to test portions of the thallus which lack not only mature but also developing soralia (these appear as somewhat swollen areas or breaks on the branches). In a few species PD reactions are characteristically rather "patchy" and it may be necessary to test several branches before concluding a specimen is really PD- (this is especially true for *B. tenuis*; see Discussion under this species). Blackened basal stems of some species are often apparently devoid of algal cells and habitually fail to provide PD+ reactions even when these are obtainable in other parts of the thalli (e.g., *B. bicolor*, *B. cervinula*, *B. nadvornikiana*, *B. tenuis*).

The K test conspicuously fails with species containing the K+ red substances, norstictic and salazinic acids. With those species, a positive K test is typically indicated on the filter paper by a flash of yellow followed by the formation of a brownish red, orange-brown, or "dirty" brown ring at the edge of the reagent front. The yellow reaction is easily missed, and unless

the substance is very abundant, the brownish colour may be very diffuse. The PD+ yellow (to yellow-orange) reaction of norstictic and salazinic acids is constant, however. With a K reaction which appears to be negative, one might assume the presence of psoromic acid and thus be in error. Fortunately all of these substances are very easily demonstrated by microchemical crystal tests (see below).

The KC medullary reactions in the genus *Alectoria* are generally without problems, although it is well to test a portion of the filament having well-developed medullary hyphae rather than a portion which is virtually hollow. It is interesting to note, in this connection, that except for usnic acid, alectorialic acid, and one K+ red unknown, all the secondary metabolic substances found in the genus *Alectoria* s. str. are apparently restricted to the medulla (e.g., alectoronic, olivetoric, thamnolic, diffractaic, and presumably barbatic and squamatic acids). (An exception worth noting is the thamnolic acid-containing chemotypes

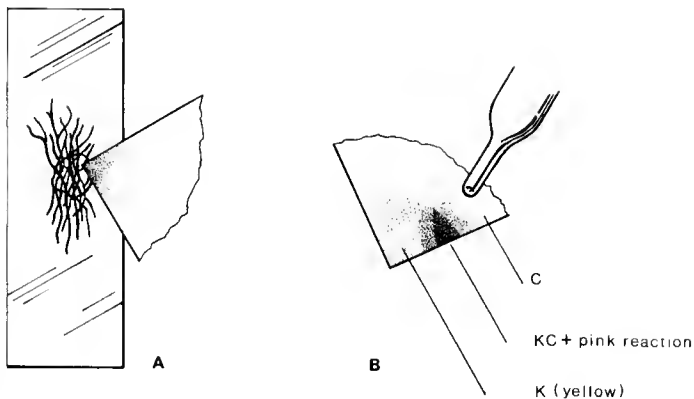


Fig. 20. The KC test using a square of filter paper. See test for description.

of *A. sarmentosa* and *A. vancouverensis* from California, some of which produce this acid in the outer cortex and not in the medulla at all.)

The KC test (K followed by C) for barbatolic acid is often most easily demonstrated by adding a small drop of K to a concentration of filaments and absorbing this onto a piece of filter paper as the drop turns deep yellow (Fig. 20). If a spot of C is placed next to the yellow spot formed by reaction with K and allowed to run into it, a pinkish red colouration is produced where the spots overlap which is easily seen against the white of the filter paper. Care should be taken not to employ too much C since excess C will itself rapidly bleach the pinkish red colour.

A positive CK test (C followed by KOH) was often useful in establishing the presence of diffractaic acid in *Alectoria ochroleuca*. If the acid is present in fairly high quantities, one gets a strong yellow-orange or gold reaction in the medulla. If the acid is in low concentration, the reaction is correspondingly weaker. The same test for diffractaic acid was discovered independently on *Parmelia diffractaica* Essl. and was reported by Dey (1974).

The general rule that the best reactions can be obtained from rapidly growing tissues such as soralia, pseudocyphellae, filament tips and apothecial margins applies to *Alectoria* and its related genera as it does to other lichens.

Microchemical tests (MCT)

Crystal tests were made most frequently in the identification of norstictic, salazinic and psoromic acids. The former two were determined from acetone extracts using "double-K" (KK, K²; 5% potassium hydroxide and 5% potassium carbonate, 1:1). Psoromic acid was demonstrated using GE solution (glycerine and acetic acid, 1:3; Fig. 21 D). Gyrophoric and olivetoric acids were also verified using microchemical tests, but thin layer chromatography proved more reliable. GE, or GAQ (glycerine, ethanol, quinoline, 2:2:1) was used for gyrophoric acid tests, and GAW solution (glycerine, ethanol, water, 1:1:1) was used to detect olivetoric acid. Crystal tests are necessary to distinguish diffractaic acid from barbatic acid since the two substances run together in TLC, but, as Kurokawa (1967) points out, diffractaic acid is often very difficult to demonstrate. With adequate concentrations of the substances, however, they can readily be crystalized from GE solution. Diffractaic acid produces colourless to very slightly yellowish lamellae, with pointed blade-shaped crystals. They are usually abundantly overlapping and become fanned out producing fasciculate clusters (Fig. 21 A, B). In concentrated preparations, the clusters become arborescent and curved (see Asahina 1936 p. 871, Kurokawa 1967), and some crystals curve strongly to one side or produce a longitudinal split and side branches, but this curving and "curly" form is relatively rare. On the other hand, the characteristic "splitting" can often be found.

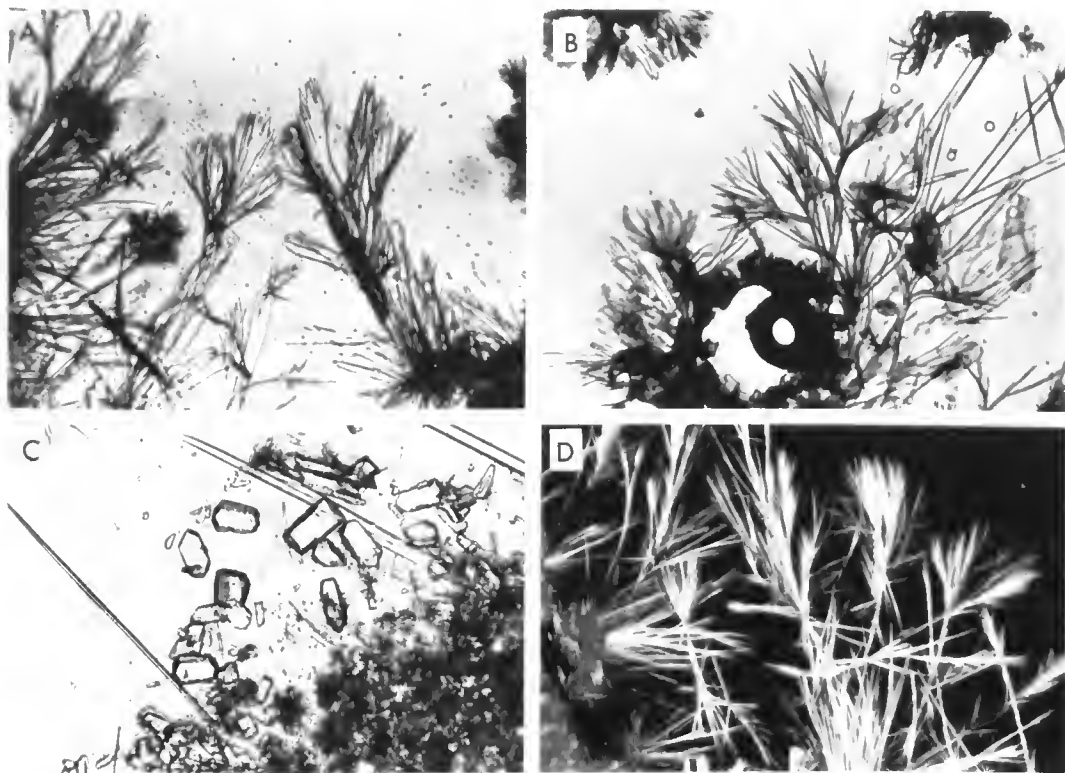


Fig. 21. Crystals produced by lichen substances in GE solution. – A, B: Diffractaic acid from *Alectoria ochroleuca*. – C: Barbatic acid from *A. vancouverensis*. – D: Psoromic acid from *Bryoria implexa*.

Usnic acid crystals are easily distinguished by the fact that they are always truncate at the ends and, of course, they are generally yellow. Barbatic acid in GE produces short, prismatic or rhomboid colourless crystals (Fig. 21 C). Alectoronic acid crystals are colourless lamellae, always straight and truncate, and occurring in radiating clusters. Alectorialic acid could often be demonstrated with GAoT solution (glycerine, ethanol, *o*-toluidine, 2:2:1) (see Krog 1968 pp. 103–104) or GAQ solution (Hawksworth 1972 pl. 3 A) but again, TLC proved to be more sensitive.

Thin layer chromatography (TLC)

The techniques used in our thin layer chromatographic analyses were largely those recommended by Culberson & Kristinsson (1970) and later expanded by C. Culberson (1972).

Acetone extractions made in small culture tubes were spotted on 10×20 cm Merck pre-coated aluminum sheets with silica gel F-254, or 60F-254. The latter sheets were equilibrated in an acidic atmosphere as recommended by C. Culberson (1974). Runs were made to a height of approximately 60–65 mm. Spots were examined in long and short wave ultraviolet light, outlined in pencil, and then sprayed with either 10% sulphuric acid, Steiner's solution or *bis*-diazotized benzidine depending on the substances being identified. The resulting spots were then related to the norstictic and atranorin standards as recommended in Culberson & Kristinsson (1970) and C. Culberson (1972) or compared to standards run alongside the unknowns. The results were recorded both within the specimen packets and in a log book. The chromatogram sheets, being thin and light, were retained for future reference.

We had some difficulty with resolution in solvents "B" and "C" until it was discovered that the spot crowding was due to our use of an Eastman Chromagram "Sandwich" Chamber Plate set. From that point on, standard chromatogram tanks (c. 25 cm high, 10 cm deep, 22 cm wide) were used for those solvents. The tanks did not require filter paper liners. Solvent "A" runs were no different in the tank, and so the Sandwich Chamber was used for those.

There was no difficulty in identifying the majority of compounds, although a number of spots of uncertain identity which appeared in some specimens of a species and not others were ignored. It is possible that some of these compounds are of importance and should be studied further. Of course, there were some unknowns of obvious significance, and these were always recorded (see Table 1).

Other compounds, particularly some of the β -orcinol depsides, run at similar Rf's in all commonly used solvents. It was therefore necessary to perform microhydrolyses on them as described by C. Culberson (1972) to verify their identity. The technique worked extremely well as long as Culberson's instructions were followed carefully.

Since chloroatranorin and atranorin are virtually indistinguishable with solvents A, B, and C (C. Culberson 1972), a separation of these two compounds was made by using chloroform-acetone, 1:1 as a solvent. In this system, most other PD compounds found in our species run close to the source. Chloroatranorin and atranorin are then revealed, using a spray of Steiner's solution, at Rf's of 31-57, and 75-95, respectively. It is apparent that the ranges are very broad. In this solvent, it seems the more concentrated the substance, the higher it migrates.

Results

An unexpected development in this study was the discovery of a number of lichen substances new for *Alectoria* s. lat. in the North American species: two orcinol depsides, gyrophoric acid and olivetoric acid; and one β -orcinol depsidone, salazinic acid. Thamnic acid was reported for *A. nigricans* by Solberg

(1967) and by Huneck & Follmann (1970) for a number of other species (see Table 1) but this substance could not be confirmed in our work on North American material of those species. (In a more recent study of *A. nigricans*, Solberg (1975) found only alectorialic acid, a mixture of tetrahydroxy fatty acids, and 5,7-dihydroxy-6-methyl phthalide; no mention was made of the presence of thamnic acid.) On the other hand, several other species do indeed contain thamnic acid, as will be pointed out below. There are a number of unknown substances which apparently are of some taxonomic importance as well.

As might be expected from a reading of the recent literature (especially W. Culberson 1969, and W. Culberson & C. Culberson 1970), the substances which we found seem to fit taxonomic groups distinguishable by traditional morphologic criteria. We should add that this is particularly true when we disregard the sometimes conflicting literature reports and rely only on our own investigations.

For example, orcinol derivatives are abundantly represented in *Alectoria* s. str., the only genus to produce olivetoric and alectronic acids. (A specimen of *Sulcaria sulcata* from Japan (Yoshimura 1680, Shikoku [BM]) apparently contains some alectronic acid, besides psoromic acid and atranorin, as evidenced by repeated TLC tests). In the olivetoric acid containing specimens, in all but a few rare cases, the olivetoric acid entirely replaces the alectronic acid and characterizes a morphologically distinguishable species. The only other orcinol derivative, the tridepside gyrophoric acid, is found in two species of *Bryoria*. All the β -orcinol depsides with the exceptions of atranorin, chloroatranorin and barbatolic acid are restricted to *Alectoria* s. str.; atranorin and chloroatranorin appear to be entirely absent from that genus. We have examined the North American specimens of *A. sarmentosa* reported by Hawksworth (1972) as containing atranorin, and no trace of atranorin could be found in them by TLC. The identity of the high Rf compound which he detected by paper chromatography remains unknown. The reports of Huneck & Follmann (1970) should be regarded with some scepticism until they are confirmed. Usnic acid is restricted to this genus. On the other hand, β -orcinol depsidones, so common

in *Bryoria*, are entirely absent from *Alectoria* s. str.

Fumarprotocetraric acid is by far the most common chemical in the species under study, having been found in 14 out of 38 species. It is apparently a constant constituent of *Bryoria nadvornikiana* occurring along with alectoralic and barbatolic acids and atranorin and is quite possibly the basis for the report of thamnolic acid in that species by Huneck & Follmann (1970) (see comments by Jørgensen 1972 p. 196).

Although Huneck & Follmann (1970) reported atranorin in a number of "*Alectoria*" species, it appears that this compound and the related chloroatranorin have relatively restricted occurrences. *Sulcaria badia* and some other non-American *Sulcaria* species contain atranorin alone; *Bryoria trichodes* and *B. fuscescens* have chloroatranorin alone; *B. nadvornikiana* in almost all cases has both atranorin (in traces) and chloroatranorin. In the specimens tested so far (several dozen) chloroatranorin has been restricted to the sorediate morphotypes and the subsp. *trichodes* of *B. trichodes* although not all specimens of this taxon contain the substance. It also appears that only specimens of *B. fuscescens* east of the Rocky Mountains contain chloroatranorin, but again, the presence of this substance is not constant. Solberg (1975) reported the presence of atranorin in one specimen (out of 4) of *Bryoria fremontii*, and in a 19.6 gm sample of *Bryoria bicolor*. These reports should be verified.

Barbatolic acid, a β -orcinol depside best classified as a benzyl ester (C. Culberson 1969, Persson & Santesson 1970), is found in *B. capillaris*, *B. pseudocapillaris*, and *B. nadvornikiana* as characteristic components, and occasionally in *Alectoria nigricans*.

Alectoralic acid is a very similar benzyl ester (Persson & Santesson 1970). It is the main constituent of *Alectoria nigricans* and *Bryoria pikei*. It is always present at least in trace amounts along with barbatolic acid in *B. capillaris* and *B. nadvornikiana*, a fact not surprising in view of the similarity of the two compounds in chemical structure. Specimens in the *B. capillaris*-aggregate with large amounts of alectoralic and trace amounts of barbatolic acid seem to be morphologically

distinguishable and have generally been referred to *B. pikei* (see Discussion under that species). The depsidone salazinic acid occurs in a species closely related to *B. implexa* and *B. capillaris* (named *B. salazunica* here). Norstictic acid has so far been found only in the very variable species, *B. pseudofuscescens*, and in the new species *B. spiralifera*. In a puzzling specimen from Dungeness, Washington (Foster 2552 a [FH]), both norstictic and barbatolic acids were found, pointing out how closely related *B. pseudofuscescens* and *B. capillaris* are. If lichen-forming fungi hybridize, this specimen could be thought of as a hybrid.

The presence of barbatic acid in many specimens could neither be confirmed nor denied due to the possible confusion of that substance with diffractaic acid in TLC. The substance turned out to be diffractaic acid in *Alectoria ochroleuca* in all cases in which it was checked using the microhydrolysis methods of C. Culberson (1972), or crystal tests in GE solution. Spots corresponding to these substances were seen with several specimens of *A. vancouverensis* and with *A. sarmentosa*. Since microchemical crystal tests conclusively established the presence of barbatic acid in an aberrant specimen of *A. vancouverensis* it is likely that barbatic acid also occurs in some other specimens of *vancouverensis* and *sarmentosa*. Krog (1968) reported having demonstrated good barbatic acid crystals in GE solution for *A. "vexillifera"* as well as *A. ochroleuca*, and she reported barbatic acid from several "varieties" of *sarmentosa*.

Squamatic acid has been reported as frequent in *A. sarmentosa* (Hawksworth 1972), but although this is true for Europe, we could not detect this substance in the North American material. It is interesting that the corresponding metadepside, thamnolic acid, was seen in several west coast specimens. This may be another case of vicarious chemical races within the well-documented west coast - west European disjunct distribution pattern. *Alectoria imshaugii* demonstrates the interchangeability of squamatic and thamnolic acids within a taxon or closely related taxa, as in *Cladonia*, sect. *Cladonia* (e.g., *C. squamosa* (Scop.) Hoffm. and *C. subsquamosa* (Nyl. ex Leight.) Vain.). Thamnolic acid occurs as a main constituent only in *A. imshaugii*.

One of the more interesting unknown substances, again occurring only in *Alectoria* s. str., produces K+ red (persistent) and C+ green-black (ephemeral) reactions on the thallus cortex. It is generally restricted to the older parts of the plants, especially at the bases of terricolous species, but occasionally can be demonstrated throughout the plant, as in a remarkable specimen of *Alectoria nigricans* from Southampton Island (Parker SP-70-14 [CANL]). Chromatographic results confirm that the substance is often present above the base in many species, but in very small amounts. The substance has relative Rf position values of 3 or 3-4, 3, 2 in solutions A, B & C of Culberson & Kristinsson (1970), is strong UV+ blue-white under both long and short wave illumination, and is PD-. In sulphuric acid charring, it is yellowish to pale brown. This is almost surely the substance responsible for the K test referred to by Räsänen (1939) for his "f. *rubropunctata* Räs." of *A. sarmen-tosa*, and by Krog (1968) for *A. "vexillifera"*. Solberg (1975) recently reported a PD- substance with low Rf values in the same solvents from Norwegian material of *A. nigricans*. This substance, named "AN-X", was identified by Solberg as 5,7-dihydroxy-6-methyl phthalide. It is conceivable that our unknown K+ red, C+ green-black substance may be Solberg's AN-X, but we have not had an opportunity to test this possibility.

Other unknown substances and chemical problems specific to certain taxa will be discussed later in the treatments of those taxa.

Certain substances presented particular problems in either TLC or microchemistry. These problems may be the cause of some of the

unconfirmed reports of substances in the genus. For example a spot which appeared to correspond to α -collatolic acid often, but not always, occurs as an accessory substance with alectorononic acid. This joint occurrence is well documented (see Culberson & Culberson 1968) but we feel that the presence of α -collatolic acid requires verification in *Alectoria*. However, alectorononic acid apparently degrades in solvents B & C resulting in several spots, one highly fluorescent and the other not.

Alectorialic and barbatolic acids often occur as mixtures, but not always. If barbatolic acid is absent, the cortex of the specimen is often K- or K+ very light yellow; if it is present, the specimen has a distinct K+ yellow reaction. Both alectorialic and barbatolic acids are C+ and KC+ pink. The taxonomic significance in the variation of this chemical pair is still not clear (see Discussion under *Bryoria capillaris*).

The appearance of olivetoric acid in a group already known to contain alectorononic acid was not extraordinary, since these substances occur in closely related taxa in *Cetrelia* and are biogenetically related (Culberson & Culberson 1968 p. 472). Gyrophoric acid is biogenetically isolated from the other orcinol compounds, and it is therefore perhaps not surprising that it occurs in a different genus.

Besides the compounds discovered and reported here, it is conceivable that through the use of specialized techniques such as mass-spectrophotometry, other compounds may be found in these genera, or that certain compounds will be found in trace amounts in species other than those for which they were reported here.

Taxonomic concepts

Genera

Hawksworth (1972 p. 199) emphasized that a case could be made for recognizing the four subgenera of *Alectoria* as distinct genera. Subsequent investigations reported here have revealed additional chemical and anatomical characters supporting this separation. In view of the now overwhelming evidence (Table 2) it is clear that the maintenance of *Alectoria* as a single genus cannot be justified and the four subgenera of Hawksworth (1972) are thus treated as genera here. The characters distinguishing the genera are mostly independent of one another and clearly are of considerable taxonomic importance (i.e., ascospore colour, size and septation; the major groups of lichen products present; cortical structure).

The suggestion that *Alectoria* be subdivided is by no means new. Fries (1860) was the first author to clearly distinguish units at the rank of genus, although he later modified his views (Fries 1871). Fries' earlier views were, however, followed by a few authors (e.g., Stein 1879) but have not been generally accepted by most specialists concerned with the genus (e.g., Du Rietz 1926, Motyka 1962, 1964, Stizenberger 1892). Bystrek (1971) proposed that *Alectoria* should be divided into three genera but presented no new information supporting his treatment. Data which have come to light in the course of the present study, however, support Bystrek's conclusions, and his generic concepts are basically those adopted here (with the addition of *Psendephebe*).

Unfortunately this taxonomic decision means that a new generic name is required for the bulk of the species formerly placed in *Alectoria*. *Bryopogon* Link cannot be taken up in the manner proposed by Bystrek (1971) on nomen-

clatural grounds (see Discussion under *Bryoria*). We were first reluctant to take this step in the interests of nomenclatural stability but following discussions with various colleagues, especially during the XII International Botanical Congress in Leningrad, we came to the conclusion that this should be done.

In the last decade there has been an increasing tendency to recognize subdivisions of well-established genera at the rank of genus in the lichen-forming fungi (e.g., Poelt 1965, Hale & Culberson 1970, Hale 1974). In most instances these changes in taxonomic opinion reflect a better understanding of the species concerned leading to more natural groupings. This is also true for *Alectoria* s. lat. We might add that there is now probably more justification for subdividing *Alectoria* into several genera than there is for the recognition of some segregates now becoming widely accepted from *Cetraria*, *Cladonia*, *Parmelia* and *Physcia*.

The characters distinguishing the genera *Alectoria*, *Bryoria*, *Oropogon*, *Psendephebe* and *Sulcaria* are indicated in Table 2 and will be readily apparent from both this and the Key to the genera; they will not be discussed in further detail here.

Species pairs

The concept of species pairs ("Artenpaare") has come to assume an increasingly important role in lichen systematics below the generic level following the important papers of Poelt (1970, 1972). The essential thesis of the concept is that existing lichen species which only very rarely or never form ascocarps and reproduce by vegetative methods (secondary species) have been derived from extant or extinct species reproducing by means of ascospores with

Table 2. Diagnostic characters separating the five Alectorioid genera. Included are characters of non-North American species.

| Character | <i>Alectoria</i> | <i>Bryoria</i> | <i>Pseudephebe</i> | <i>Sulcaria</i> | <i>Oropogon</i> |
|---|--|--|------------------------------------|--------------------------------------|--|
| Ascospores | | | | | |
| No. per ascus | 2-4 | 8 | 8 | (6-)8 | 1 |
| Colour when mature | Brown | Colourless | Colourless | Yellow to brownish | Brown |
| Septation | Simple | Simple | Simple | 1(-3)-septate | Muriform |
| Length (μm) | 20-45 | 4-15 | 7-12 | 22-44 | 75-100 |
| Width (μm) | 12-25 | 3-7 | 6-8 | 8-15 | 25-38 |
| Excipulum thallinum | Persistent and incurved | Becoming excluded; not incurved | Becoming excluded; not incurved | Persistent and incurved | Persistent; incurved at least when young |
| Pycnidia | Usually rare | Rare | Common, opening by a broad ostiole | Unknown | Unknown |
| Vegetative structure | | | | | |
| Cortex | | | | | |
| Surface texture | Decomposing | Usually smooth | Smooth | Uneven | Uneven to knobby |
| Differentiation of superficial cells | Absent | Present in a few species | Present in all species | Absent | Usually present |
| Thickness (μm) | 50-110 | 25-45 | 25-75 | 15-40 | 25-60 |
| Matrix, relative to hyphae | Abundant | Little to abundant | Moderate | Moderate | Little to moderate |
| Medullary hyphae | Usually ornamented | Not ornamented | Not ornamented | Not ornamented | Ornamented |
| Cyphellae-like perforations | Absent | Absent | Absent | Absent | Always present |
| Pseudocyphellae | Always present, scattered, conspicuous, raised | Variable, when present adpressed or rarely slightly raised | Absent | Present in long longitudinal furrows | Depressed, developing into perforations |
| Pigmentation | Usnic acid crystals in outer cortical layers | Mostly in a superficial crust | In cortical cells | Granular on surface | Mostly in superficial cortical cells |
| Colour of thallus | Usually yellow | Brown to olivaceous, rarely grey | Dark brown to almost black | Grey to badious, or bright yellow | Fuscos to grey; rarely red-brown |
| Habit | Pendent to erect | Pendent to erect | \pm Appressed, rosette-forming | Pendent to caespitose | Pendent to caespitose |
| Chemical components | | | | | |
| Usnic acids | Present in all but one species | Absent | Absent | Absent | Absent |
| Atranorin and (or) chloroatranorin | Absent | Frequent | Absent | Frequent | Absent |
| Orcinol depsides | Frequent | Rare (tridepside) | Absent | Absent | Absent |
| Orcinol depsidones | Frequent | Absent | Absent | Rare | Absent |
| β -orcinol depsides (excl. atranorin s. lat.) | Frequent | Absent | Absent | Absent | Rare |
| β -orcinol benzyl esters | Rare | Frequent | Absent | Absent | Absent |
| β -orcinol depsidones | Absent | Very frequent | Absent | Present | Frequent |
| Pulvinic acid derivatives | Absent | Rare | Absent | Present | Absent |
| Hydroxyanthraquinones | Absent | Absent | Absent | Absent | Present |
| Unknown: K+ red, C+ green | Very frequent | Absent | Absent | Absent | Absent |
| Centre of diversity | Temperate | Boreal | Arctic-alpine | Temperate | Temperate-subtropical |
| Number of species known | 8 | 48 | 2 | 3+? | 4+? |

little or no alternative method of reproduction (primary species). Primary and secondary species normally have identical (or sometimes closely related) chemical components (Poelt 1972, Culberson & Culberson 1973, C. Culberson & Hale 1973, Hawksworth 1976) and secondary species have a tendency to have wider distributions and ecological amplitudes than the primary species if the latter is extant.

As emphasized above, ascocarps are very rare in most Alectorioid genera and it is clear that, for most species, vegetative methods of propagation are of paramount importance. This suggests that the bulk of the species, whether reproducing by thallus fragmentation, spinule abscission, soredia, or combinations of these, are to be viewed as secondary. A few species, however, are clearly primary (e.g., *Pseudephebe minuscula*, *P. pubescens*, *Bryoria abbreviata*, *B. divergens*, *B. subdivergens*, *Sulcaria sulcata*) but, except in the case of *Bryoria abbreviata* of which *B. oregana* may perhaps be the secondary counterpart, secondary species derived from these are unknown. A further group of species may be primary but currently in the process of speciation to form secondary species since some populations are commonly fertile, others lack ascocarps and soredia, and yet others lack ascocarps and form soredia (e.g., *Bryoria trichodes*, *B. fremontii*, *Alectoria sarmentosa*). *A. sarmentosa* is of particular interest in this respect as *A. imshangii* might have been secondarily derived from some chemotypes of *A. sarmentosa* (see Discussion under *A. sarmentosa* subsp. *sarmentosa*).

Many of these secondary species are very widely distributed on a global scale indicating that the group is of considerable antiquity. (The only Alectorioid fossil specimen known to us is *Alectoria succini* Mägd. represented by a single plant embedded in amber discovered in Tertiary (?) deposits in the Baltic region (Mägdefrau 1957). This material (examined by D.L.H.) has an Alectorioid cortex, a single ascocarp, and a structure that might be a sorolium; superficially it is strongly reminiscent of *Bryoria subcana*.)

Species

The production of what is termed a lichen "species" now appears to result from the interplay of a fungal partner with a particular algal one which together form a single biological unit with a characteristic anatomy, morphology, and chemistry, and with certain distributional and ecological requirements. The extent to which the algal partner can be important in this connection is only just becoming to be appreciated (James & Henssen 1976); the importance of its role in genera such as those treated here, presumably with a single algal genus as phycobiont, remains unknown. Some, but not all, chemical components used in lichen taxonomy may be affected in a complex manner by the alga present (James & Henssen 1976, Hawksworth 1976). As a result of these fundamental questions which must necessarily remain largely unanswered for most lichens for many decades to come, it is evident that for practical purposes when we use the term "species" in the lichen-forming fungi we are applying it to the dual organism and not only to the fungal partner. (That for nomenclatural purposes the names of lichens refer to the fungal partner alone is immaterial in this connection.) In the case of the species studied here, it is of interest to note that with regard to the ascocarps and ascospores, the mycobionts involved seem to have undergone very little divergent evolution (a phenomenon rather unusual in the non-lichen-forming Ascomycotina where in the larger species, differences in vegetative tissues tend to be correlated with differences in ascocarps and ascospores).

The lichen taxonomist has to delimit his taxa on the basis of examinations of large numbers of herbarium specimens and studies of populations in the field. If too few herbarium collections are studied and sufficient field work is not carried out, there will be a tendency to recognize too many taxa. This is due to an incomplete sampling of populations which precludes any reliable assessment of the extent of environmental impact on the genotype. (See the discussion of Hawksworth 1973 on this topic.) In the case of *Alectoria*, environmental factors exert profound effects on thallus colour, contortion, and the production of secondary branchlets and spinules. On the basis of our

field and herbarium studies we have, in most instances, been able to arrive at what we consider to be clearly delimited taxa. Most prove to be readily recognizable in the field (indeed some appear more distinctive there than when pressed in the herbarium) but a few difficult groups nevertheless remain. In an attempt to introduce some degree of consistency in the application of taxonomic ranks in the lichen-forming and non-lichenized fungi, Hawksworth (1974) proposed that individual species should be based on well-marked discontinuities in several apparently unrelated characters and we have endeavoured to adhere to this tenet in the present revision.

The taxonomy of *Alectoria* has been regarded as exceptionally difficult by many contemporary lichenologists. While many of the difficulties prove to be man-made and due to inadequate study and errors in descriptions which appear in the literature, our present investigations have demonstrated that a great deal of work is still required in some groups of species. Certainly, we are only likely to arrive at an entirely satisfactory understanding of the taxa when more information on the group in Europe and Asia is available. These problems are discussed in some detail under the taxa concerned but it is pertinent to refer to two particular areas of difficulty here.

Firstly, the *Bryoria chalybeiformis*-*B. fuscescens*-(*B. glabra*)-*B. lanestrís*-*B. vrangiana* group. (The non-North American *B. intricans* also belongs here.) While, in our view, these species are distinct, in a significant number of cases we have had some difficulty in deciding to which of two (or sometimes three) species a particular specimen belongs. This problem is discussed in detail under *B. fuscescens*. In view of the characteristic habitats, distributions and distinctness of the bulk of collections, we are inclined to the opinion that phenotypic parallelism arising from environmental stress is of paramount importance here, particularly as some other species are able to produce morphotypes not dissimilar from these (these being readily separable, however, by virtue of distinctive chemistries or other characters, e.g., *Bryoria trichodes* subsp. *trichodes*, *B. pseudofuscescens*).

Secondly, during the course of the present survey, a number of chemotypes came to light

which had been previously entirely unknown. In most cases, species delimited here on the basis of morphological criteria have both distinctive distributions and constant (or \pm constant) chemistries. The difficulties for the taxonomist arise from the association of two or more chemotypes with a single morphotype. The employment of chemical criteria in lichen taxonomy has been a source of controversy for over a century. In a recent review of this subject Hawksworth (1976) proposed some guidelines for their taxonomic treatment which have been adhered to here except that infraspecific taxa have not generally been employed (see below). Attention is also drawn here to the problems in the *Bryoria capillaris*, *B. fuscescens*, *B. pseudofuscescens* and *Alectoria sarmentosa* groups. In addition, a few apparently very rare chemotypes have come to light which might conceivably be hybrids (pp. 71, 116, 119). The phenomenon of hybridization has only recently been suggested as an important consideration in lichen evolution (C. Culberson & Hale 1973). If it occurred in the evolutionary past in one group, it presumably may well be occurring in others at the present time. A discussion of the possible mechanisms involved can be found in connection with the chemical variation in *Alectoria sarmentosa* (see Discussion under this species).

Infraspecific taxa

In the early stages of the present work we were inclined to recognize a number of infraspecific taxa within certain species but in the final analysis decided to refrain from doing this except in two cases where subspecific rank seemed particularly appropriate (*Alectoria sarmentosa* subsp. *vexillifera*, *Bryoria trichodes* subsp. *americana*). This decision is not to be taken as indicating that no further taxa meriting infraspecific ranks occur among the North American species studied here. It was simply done because we felt that our primary task in undertaking the present survey was to endeavour to provide a satisfactory delimitation of the species. In the future more detailed studies of the species accepted here should be carried out with a view to analyzing some of the variations in chemical components and morphology noted in the discussions of the

various species. In this way, one may be able to arrive at soundly based conclusions as to the taxonomic importance of these variations. In many instances such studies will also have to consider non-North American material. Within the discussions of individual species

(and occasionally in the descriptions of them) we have, however, noted the names of some of the more distinctive infraspecific taxa accepted by European authors which also occur in North America.

Ecology

Although it is admittedly hazardous to generalize about the ecology of a series of four genera of lichens, in the case of *Alectoria*, *Bryoria*, *Pseudephebe*, and *Sulcaria*, certain general statements can be made which will indeed characterize the majority of the species. With regard to the corticolous species, coniferous trees and trees with similar bark characteristics such as birch are by far the most frequently encountered substrates. However, it is not at all clear whether the species actually *prefer* acidic bark (in a statistical sense) due to some physiological requirements, thus explaining their abundance in coniferous forests, or whether the species require the climate and general environment of coniferous forests and simply happen to be found on the most available substrate there, namely coniferous trees. It seems the latter is more likely, to judge by the wide variety of dominant tree species used as substrates by the lichens in each forest type.

Rock-dwelling species include those enduring highly exposed and well-illuminated surfaces (e.g., *Pseudephebe pubescens*) and those frequenting more shaded rock walls (e.g., *Bryoria nadvornikiana*). The rock substrates, however, are almost invariably non-calcareous. Soil-dwelling species generally can tolerate a wide variety of soil types and pH levels.

It would probably be instructive to examine various habitat types with the aim of determining which species share the same habitats and are likely to be found together. It is one of the burdens of would-be "Alectoriologists" that these species very frequently grow mixed together and are collected that way. Knowing which species are likely to be found together may be a help in their determination.

Since the western mountains of North

America show a great diversity of species, we will begin the discussion by trying to dissect out the various montane forest types and describe the species most characteristic of each. At the outset, it should be pointed out that other species may be present in these communities; we are merely listing the most characteristic ones.

The mountains we are mainly concerned with here are centered in the Canadian Rockies (basically along the British Columbia-Alberta border) and Columbia Mountains, extending southward to include most of the Idaho and Montana mountains north of the Columbia plateau. Most of the ecological information in the discussions pertaining to western North America is based on Krajina (1965).

An examination of the altitudinal distribution of the 12 most common montane taxa (comprising 11 species) (Fig. 22) is interesting but not very helpful. As one might expect, a forest type at one altitude on a south-facing slope may be several thousand feet higher than the same forest type a few hundred miles north and on a north-facing slope. On the other hand, certain species are closely associated with certain forest types.

The Interior Douglas Fir zone, a rather dry zone with only about 16–19 inches (410–480 mm) of precipitation per year, is the preferred habitat of *Alectoria inshaugii*, *Bryoria abbreviata*, and *B. fremontii*. The most common trees in this zone, *Pseudotsuga menziesii*, *Pinus ponderosa*, *P. contorta* var. *latifolia* and *Larix occidentalis* are also the most frequent substrates.

The Interior Western Hemlock zone, having many of the same tree species as the Coastal Western Hemlock forest (e.g., *Tsuga heterophylla*, *Thuja plicata*, *Pseudotsuga menziesii*),

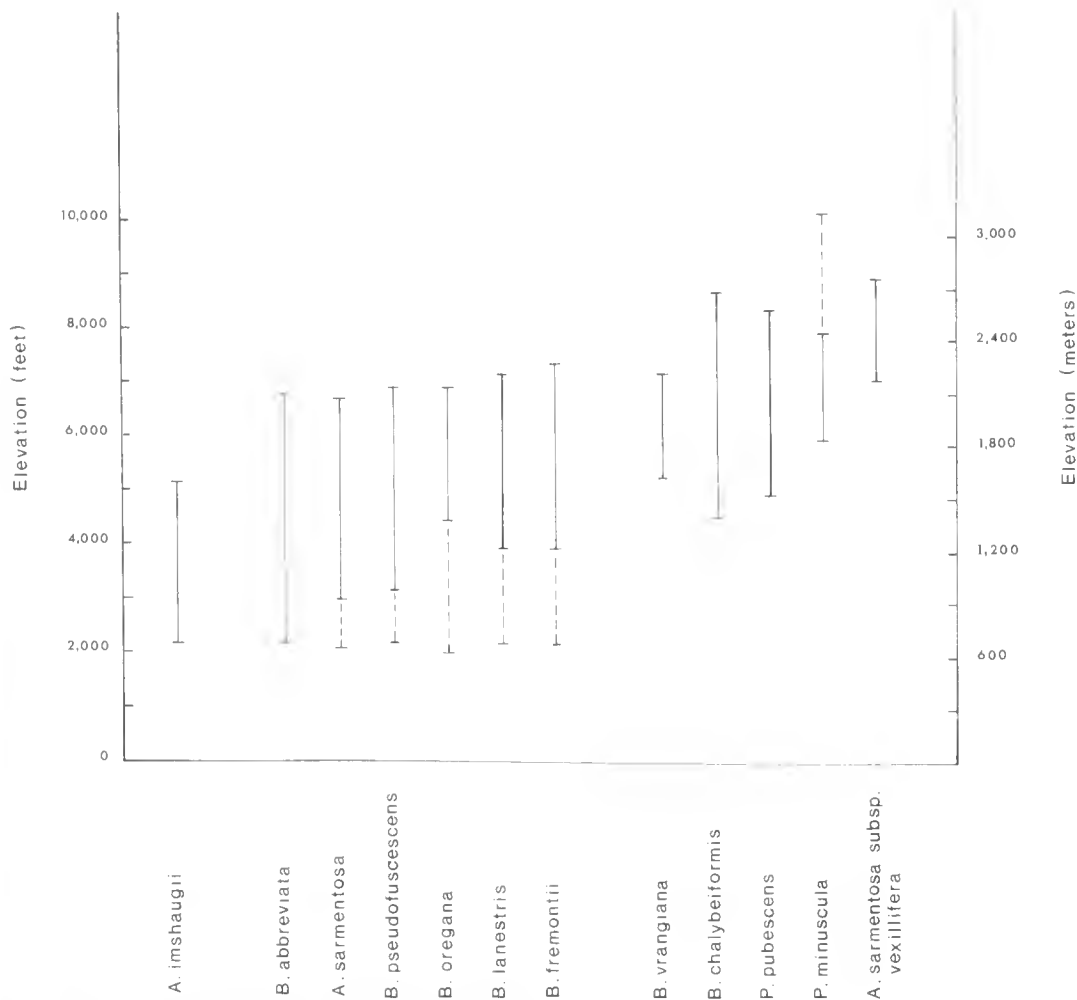


Fig. 22. Altitudinal distributions of several species found in the western mountains. Solid line = principal range; broken line = aberrant extension of the range.

also resembles that forest in being relatively moist. Montane populations of *Alectoria sarmentosa* are most frequently found here.

The Sub-boreal Spruce zone is basically an extension of the northern boreal forest, or at least, its ecological affinities are with that forest region. The dominant trees are *Picea glauca*, *P. engelmannii*, and *Pinus contorta* var. *latifolia*. *Bryoria lanestris*, a very conspicuous boreal forest species, is, not unexpectedly, also found in this zone.

The Subalpine *Abies lasiocarpa*–*Picea engelmannii*–*Larix lyallii* zone found on the higher mountains, is the characteristic habitat of *B. oregana*, *B. pseudofuscescens*, and *B. vrangiana*.

On the alpine heath and rocky ground, one can find mixtures of *Alectoria sarmentosa* subsp. *vexillifera*, *B. chalybeiformis*, *Pseudophebe pubescens*, *P. minuscula*, and, especially in the northern mountains, *Alectoria ochroleuca*.

The Pacific Coast Mesothermal Forest is

composed of two parts: a relatively dry segment (26–65 inches (660–1650 mm) precipitation per year) called the Coastal Douglas Fir zone by Krajina (1965), and a wetter zone with an annual precipitation ranging from about 70 to over 260 inches (1780–6600 mm). The wetter zone, the Coastal Western Hemlock Zone, is a veritable rain forest in places. It is dominated by *Tsuga heterophylla*, *Thuja plicata*, *Picea sitchensis*, and *Acer macrophyllum*. Inhabiting this zone are: *Bryoria trichodes* (both subspecies), *B. bicolor*, *B. tenuis*, *B. capillaris*, *B. glabra* (which is also montane), and *Alectoria sarmentosa*.

The Coastal Douglas Fir zone, with *Pseudotsuga*, *Arbutus menziesii*, and *Quercus garryana*, often contains the following species: *Alectoria vancouverensis*, *Bryoria fuscescens*, *B. fremontii*, *B. friabilis*, and *B. tortuosa*.

The Boreal Forest of North America stretches from Alaska southeastward to Ontario, Quebec and the maritime provinces with very little basic change in tree dominance: *Picea mariana* and *Larix laricina* in the wetter sites, and *Pinus banksiana*, *Picea glauca* and *Populus tremuloides* in the drier sites. In the southern and eastern boreal forest, *Abies balsamea* is very important. Throughout this entire region (with the few exceptions noted below) the following *Bryoriae* are found: *B. simplicior*, *B. laeustris*, *B. furcellata*, *B. fuscescens*, *B. nadvornikiana*, *B. trichodes* subsp. *trichodes*, and *B. capillaris* (especially in the humid southern boreal section; see Ahti 1964).

In the *Abies fraseri* forests of the southern Appalachian Mountains, one can find *Alectoria fallacina*, *Bryoria tenuis*, and *B. bicolor*. *Bryoria furcellata* is more characteristically found in the pine forests of the Appalachian chain.

The coniferous associations of the Acadian forest on the east coast are indicated by the presence of *Picea rubens*. In other respects they are very similar to parts of the southern boreal forest but with many more deciduous species. Often found in mixed collections, especially from exposed, humid, coastal localities, are: *Bryoria fuscescens*, *B. trichodes* (especially subsp. *americana* and its sorediate morphotypes), and *B. capillaris*.

In the arctic tundra, *Alectoria ochroleuca*, *A. uigricans*, *A. sarmentosa* subsp. *vexillifera* and *Bryoria chalybeiformis* are found over

calcareous or non-calcareous soil and rock. On non-calcareous rock and soil, one also may find *B. nitidula* in great abundance.

In the British Isles, the concept of lichen species which are "old forest indicators" (i.e., species which are restricted to very old, undisturbed sites) has recently been extended to consider taxa of coniferous woodlands (Rose 1976): *Bryoria capillaris* and *Alectoria sarmentosa* subsp. *sarmentosa* both fall into this category in that country (Rose 1976). This phenomenon may be an important aspect of the local distribution of some species in North America (e.g., *Bryoria abbreviata*, *B. fremontii*, *Alectoria inshaugii*) and requires further study.

In Europe *Bryoria fuscescens* has a tendency to be abundant in localities affected by man (Hawksworth 1972) and this also appears to be true for North America, at least in Newfoundland (Ahti & Hawksworth 1974). *B. furcellata* is also an "opportunist" in the east becoming not uncommon on fence-rails. This species, together with *B. trichodes* subsp. *trichodes*, is apparently a rapid colonizer of young coniferous trees and can be found recolonizing clear-felled areas in Quebec.

Air pollution is considered to be an important factor in the extant distribution of several species of the genus in Europe (e.g., Barkman 1958, Hawksworth 1972) and this, together with other effects of urbanization, certainly limits the occurrence of Alectorioid species in major conurbations (e.g., Brodo 1968) and in the vicinity of industrial plants (e.g., Rao & LeBlanc 1967, LeBlanc et al. 1972, 1974). The information currently available indicates that species of these genera differ in their sensitivity to air pollutants but is insufficient to clearly indicate relative sensitivities in north America at the present time; indeed these might be expected to vary according to climate and other factors in such a diverse area for a variety of reasons (Hawksworth & Rose 1976).

As noted above, Alectorioid species may prefer relatively acidic barks in North America as they do in Europe (Barkman 1958, Hawksworth 1972). Sulphur dioxide in the air leads to bark acidification and thus can enable species to occur on phorophytes from which they are normally absent as long as conditions are not too severe. In a site in Sweden, Skye &

Hallberg (1969) noted an increase of "*A. jubata*" following a prolonged pollution episode, apparently due to bark acidification. This phenomenon would also be expected to occur in North America, enabling species to colonize deciduous trees under moderate pollution stress.

Distribution

Although there are exceptions, *Alectoria*, *Bryoria* and *Pseudephebe* as a whole can be thought of as cold climate genera, with most species either decidedly northern or associated with mountains. This is well documented in North America, where two-thirds of the species have the major portion of their range within Canada, and only 4 are found entirely south of the Canadian border. *Sulcaria* appears to be more temperate both in North America and in Asia. The four genera are apparently unrepresented in Florida (Moore 1968), or for that matter, in any of the southeastern states (South Carolina, Georgia, Mississippi, Alabama, Louisiana, and Arkansas). They are apparently also absent from the central plains, probably due to the hot, dry summers and lack of coniferous forest. There are no records of Alectorioid species from Texas, Oklahoma, Kansas, Nebraska, or North Dakota. The only species of this group from South Dakota are from the Black Hills (Wetmore 1968).

With the exception of *Bryoria furcellata*, extensions into the southeastern mountains are restricted to occurrences in the "southeastern spruce-fir forest" (Küchler 1964). The map of *Bryoria trichodes* subsp. *trichodes* shows this well. The absence of these genera in the Ozark region (northern Arkansas and southern Missouri) correlates well with the lack of any northern forest remnants there.

Other dry, warm areas such as southern California and the Ponderosa Pine forests of Montana and Arizona largely lack species from this group.

Porsild's (1958) treatment of some geographic elements in the Canadian flora is one of the most useful in a discussion of the distribution of species covered here. Since lichens, like mosses, have relatively few North American

endemics (see Crum 1966), the same degree of representation in his "North American Species" group will not be seen here. In fact, "wide-ranging" species endemic to North America, while comprising the bulk of the Canadian vascular plant flora (Porsild 1958), are virtually nonexistent in lichens.

Indeed, circumboreal taxa are well-represented among the North American species of *Alectoria*, *Bryoria* and *Pseudephebe*. They are found in Europe in climatologically and vegetationally equivalent areas, especially in Scandinavia and the U.S.S.R. but also in the central and eastern European mountains, and sometimes in mountainous areas of Asia, Australasia, and Africa as well.

Circumboreal-circumpolar species

All the arctic Alectorioid species appear to be wide-ranging in the tundra region. The zonations with regard to northern distributional limits of vascular plants which are so well demonstrated and discussed by Young (1971) apparently do not apply to lichens. Young showed that these limits correspond closely with the amount of available warmth during the growing season. Since lichens have a "growing season" quite different from that of flowering plants, and their microenvironment is even more restricted and critical than that of cushion plants, it is easy to see why the same factors would not apply. Young (1971) also points out that this warmth is most critical for the flowering and fruiting process in the vascular plants, something which would have no bearing on the presence or absence of asexually reproducing lichens, although the positive effect of warmth on ascocarp production in some lichens has been documented (Sernander-Du Rietz 1957).

To a limited extent, probably due as much to historical as to climatic factors, one can recognize some of Porsild's (1958) floristic elements among the North American species.

(1) Arctic-alpine element: *Pseudephlebe minuscula*, *P. pubescens*, *Bryoria chalybeiformis*, *Alectoria nigricans*, *A. ochroleuca*.

Different species have southward extensions into the western Cordillera to various degrees. The alpine range of *A. ochroleuca* stops close to the Canadian border (although *A. ochroleuca* is seen again in the Mexican highlands and in South America). *Pseudephlebe minuscula* is more abundant in the Rocky Mountain system, with *P. pubescens* being most common in the Cascade ranges.

(2) Low-arctic element: *Bryoria nitidula*.

Although *B. nitidula* ranges well into the Queen Elizabeth Islands, its main area of distribution is clearly the low arctic. Other species extending into the low arctic and even the northern boreal zones (e.g., *Alectoria nigricans* and *A. ochroleuca*) seem to be better characterized by their northern limits rather than their southern limits. Like the arctic knotweed *Polygonum viviparum* (see Porsild 1958), they are best classified with the wide-ranging arctic-alpine species.

(3) Amphi-atlantic, southern element: *Alectoria sarmentosa* subsp. *vexillifera*.

Although this taxon has disjunct populations in the western mountains and in the Aleutians, it is placed here due to its apparent amphi-atlantic character. Its interesting distribution is discussed more fully in the taxonomic part.

(4) Boreal forest element: *Bryoria capillaris*, *B. fuscescens*, *B. implexa*, *B. lanestris*, *B. nadvornikiana*, *B. simplicior*, (*Alectoria sarmentosa* subsp. *sarmentosa*).

This element is difficult to interpret on a North American scale since it has obviously been dissected during glaciation and reassembled depending upon rates of dispersal, edaphic factors, and historic factors which differed from one species to the next. However, one can conveniently apply the zonations suggested by Sjörs (1963) and modified by

Ahti (1964) to eastern North America. The coniferous forests of the western mountains are not entirely equivalent to those of the Boreal Forest Region, although, by virtue of the general similarities of these forests, many boreal species, especially those of the middle and northern boreal forest zones, have been able to survive there.

Bryoria simplicior is a narrowly restricted Hemicarctic to northern boreal zone plant (see Ahti 1964). *B. lanestris* is also found in these zones, but is more common in the western mountains. *B. fuscescens* and *B. implexa* appear to be middle boreal zone species, although the former is much more common and widely distributed than the latter both in Europe and North America.

The southern boreal zone is represented by two species: *B. nadvornikiana* and *B. capillaris*. Both show preferences for strongly humid locations, as was mentioned by Ahti (1964) for *B. nadvornikiana*.

Alectoria sarmentosa seems to have a severely dissected middle boreal forest distribution, and might better be described simply as having a bicoastal distribution, although it is not at all "coastal" in the strict sense.

(5) Appalachian-Great Lakes, temperate: *Bryoria furcellata*.

Bryoria furcellata is surely the most temperate of the North American *Bryoriae* or *Alectoriae*. Having originated as a circumboreal species, it may well have been displaced southwards onto the Appalachian chain during glaciation, and only gradually attained the more northern boreal localities. In Canada, its northern limit roughly coincides with the 13°C July isotherm according to Ahti & Hawksworth (1974), in agreement with Ahlner's (1948) observations for Scandinavia.

(6) Oceanic-suboceanic species: *Bryoria bicolor*, *B. tenuis*.

Bryoria bicolor and *B. tenuis* have almost identical distribution patterns in North America, i.e., they are largely restricted to the humid and mild coastlines and foggy Appalachian mountain tops.

The marked disjunction between the highest "peaks" of the southern Appalachians (especially in Great Smoky Mountain National Park)

and the high mountains of the northeast (e.g., the Adirondacks, the White Mountains and Mt. Katahdin in Maine) is repeated in the distribution of many lichen taxa including *Nephroma parile* (Ach.) Ach. (Wetmore 1960), *Pseudovernia cladonia* (Tuck.) Hale & Culb. (Hale 1955), and *Parmelia halei* Ahti (1966) in addition to *Bryoria bicolor*, *B. tenuis* and *Alectoria fallacina*. It is likely that this disjunction resulted from the gradual reinvasion of populations towards the north with the retreat of the last major ice sheets. Presumably, the intervening areas became too dry or warm to support these species, some of which, like those listed above, are clearly suboceanic. Thus, a careful search of suitable microclimatic habitats in other parts of the Appalachians may well turn up some of these species which require cool temperatures and high humidities.

Widely distributed circumboreal oceanic distributions of this type are generally thought of as representing remnants of the ancient Arcto-Tertiary flora (Schofield 1969).

(7) Western American-European disjuncts: *Bryoria fremontii*, *B. pseudofuscescens*, *B. subcana*, (*B. tortuosa*).

It is widely accepted that this disjunct pattern results from a circumboreal distribution (Schofield 1969), probably eliminated from eastern North America by continental glaciation. Eastward migration in post-Pleistocene times was prevented by the expanse of the Great Basin.

Although *B. subcana* is the only one of this group which might possibly be called "oceanic" (see Hawksworth 1972), moisture requirements might have limited several species in this element to the west coast (see Schofield 1969). *Alectoria sarmentosa* might well have had an identical history in North America, but with the survival of an additional remnant on the east coast as suggested for *Platismatia norvegica* (Lynge) Culb. & C. Culb. (W. Culberson 1972) which has a similar distribution. *Bryoria tortuosa* is tentatively included here pending a reexamination of the single European plant reported (see under *B. tortuosa*, Distribution).

This element is very well known among flowering plants and bryophytes (Schofield 1969, Schofield & Crum 1972).

Asian affinities

(8) Bicoastal, Appalachian-West Coast disjuncts: *Bryoria trichodes*.

Asian-Appalachian disjuncts are generally thought of as relicts of an ancient Arcto-Tertiary flora which at one time extended across Eurasia and later became reduced through extinctions (W. Culberson 1972). The presence of the species on the west coast could have come about from a pre- or post-Pleistocene establishment from Asia via the Aleutian route, or the species may have persisted south of the ice along the west coast (Schofield 1969). The subspeciation of *Bryoria trichodes* is even more difficult to deal with, but morphological evidence points to subspecies *trichodes* as being the older of the two, having more similarities with the Asian populations. This would be supported by its presence in the southern Appalachians. Subspecies *americana* presumably became distributed across North America, possibly in a boreal forest environment that existed along the ice front, becoming disjunct and restricted to available humid zones after glacial retreat. (See the discussion under category 11 below. See also category 15 for a discussion of *Alectoria lata*, another Asian-North American disjunct.)

North American endemics

(9) North Pacific: *Bryoria cervinula*, *B. carlottae*.

The close relationship between these species and some Asian species in the "*Alectoria asiatica* group" (see also Motyka 1964) suggests that they may have been pre-Pleistocene, amphiberingian or North Pacific arrivals which became isolated in certain nonglaciated headlands and slopes along the north Pacific coast during glaciation (see Calder & Taylor 1968). Schofield (1969) elaborates on this element, giving many examples of species found on both sides of the Pacific. Other lichens, such as *Cocotrema maritimum* Brodo, have similar distributions and probably had comparable histories (Brodo 1973).

(10) Coastal lowland: *Sulcaria badia*, *Alectoria vancouverensis*, *Bryoria spiralifera*, *B. pseudocapillaris*.

All of the species in this category are found basically between southern Vancouver Island and northern California either corresponding to the "cool, moist (conifer) forest" (Daubenmire 1969), or, as in the case of *Sulcaria badia*, to the drier *Pseudotsuga* forest. The evolutionary relationships are varied: *Alectoria vancouverensis* is clearly closely related to *A. sarmentosa* (a boreal species); *Sulcaria badia* has Asian affinities; *Bryoria spiralifera* and *B. pseudocapillaris* are members of the section *Implexae* which seems to have more boreal-montane, if not oceanic tendencies. All these species would be included in the "Californian" element of Schofield (1969). Species of this element such as *A. vancouverensis* may have spread northward into British Columbia during the Hypsithermal Interval (Schofield 1969).

Most California endemics occupy, and apparently developed, in a region with a Mediterranean climate (moderate to heavy winter precipitation and extreme summer drought (Stebbins & Major 1965). Since California has never been connected with another area of Mediterranean climate, the plants there had to adapt *in situ* from a flora adapted to other kinds of climatic regimes. This would have occurred towards the latter part of the Tertiary when California developed its present climate. Stebbins & Major point out that this is why California has endemic elements from the northern flora whereas the Mediterranean region itself, by and large, does not. *Alectoria*, and *Bryoria* of course, would be a good example of this.

If *Bryoria pseudocapillaris* and *B. spiralifera* are ever proved to be members of the genus *Sulcaria* (which is possible, to judge from their chemistry and morphology) this Californian element (together with *S. badia*) would be represented by three endemic species with Asian affinities. The presence of many such "relict endemics" in the coastal northern California-Oregon area is well documented, corresponding, for example, to the distributions of *Sequoia*, *Sequoiadendron*, and *Torreya* (Stebbins & Major 1965). These trees apparently represent remnants of the Arcto-Tertiary flora of the mesic coniferous and deciduous forests.

Alectoria lata is a more montane species which shows a present-day relict disjunction

with eastern Asia. *Alectoria vancouverensis* perhaps evolved somewhere along the coast and succeeded more than the other species in invading more northern as well as southern coastal localities. At the southern edge of its range, where the climate is marginally acceptable and the forests and topography are very mixed, the development of chemical races and perhaps hybridization would be more likely. This would be in close accordance with the thoughts of Stebbins & Major (1965) on the origin of the California vascular plant endemics. According to such a hypothesis one would have to assume that physiological adaptations in the lichens, rendering them better suited to survive in these less climatologically stable, marginal regions, accompanied the changes in external form and secondary metabolic products.

(11) Lowland to western montane (humid forests): *Bryoria glabra*, *B. friabilis*, *B. pikei*.

These species occur from open lowland to humid montane localities mainly on the Coast and Cascade Ranges, but often (as with *B. glabra*) extending to the humid Interior Western Hemlock zones in southeastern British Columbia (see Daubenmire 1969 pp. 120-123). Interestingly, all three species have disjunctions with humid localities on the east coast. Packer (1971) lists a number of Canadian endemic flowering plants with similar bicoastal distributions.

The question of the origin of such striking east-west disjunctions has been discussed by many authors and reviewed by Morisset (1971). Morisset begins with the assumption that such disjunctions represent relict populations of distributions which were at one time continuous. (Thus he quickly dispenses with long-distance dispersal.) The possibility of migrations from the western cordillera eastward along the receding ice front (the so-called "sidewalk" hypothesis of Stebbins & Major 1965) presents some problems for arctic-alpine species. The presumed tundra belt was apparently extremely narrow in the west, which would interfere with any eastward migration, and fossil evidence is lacking. Boreal forest species, however, may well have been able to use this route. On the other hand, Morisset points out that the exposed coastal plain would have been not

only available but ideal as a refugium south of the ice front, and would have permitted an easy reinvasion of coastal and even montane localities as the ice retreated. In the absence of localities of these bicoastal disjuncts in suitable microhabitats within the intervening area, one would have to say that at least for these lichens, the coastal plain refugium hypothesis seems the most plausible.

(12) Western montane and intermontane (dry forests): *Alectoria imshangii*, *Bryoria abbreviata*, *B. oregana*.

The main ranges of these species occur in the relatively dry, montane *Pinus ponderosa*–*Pseudotsuga* forests which extend from the Idaho–Washington border (and parts of Montana) through central Oregon south to the northern California highlands (Daubenmire 1969).

Alectoria imshangii may have evolved as an isolated population in or bordering the dry interior plains as have numerous other endemic flowering plants and bryophytes (Schofield 1969). It apparently extended its range to the California and Oregon coasts in open stands of *Pinus contorta* or *Pseudotsuga*. *Bryoria oregana* and *B. abbreviata* probably had their origin as more montane endemics.

(13) Appalachians: *Alectoria fallacina*.

The Appalachian mountains, due to their age and long isolation, have been the site of speciation in many groups of plants. Even with the relatively slow rate of evolution in lichenized fungi, endemism can be seen in the Appalachian lichen flora, for example, in *Cladonia caroliniana* Schwein. ex Tuck. (Ahti 1973) and *Lecanora caesiornbella* Ach. subsp. *caesiornbella* (Imshaug & Brodo 1966) in addition to *Alectoria fallacina*. However, many species regarded as endemics at one time are now

known from other areas of the world, especially from eastern Asia and the Alps (Schauer & Brodo 1966), and others have closely related vicariad species elsewhere (Yoshimura 1968).

(14) Northeastern coastal plain: *Bryoria salazinicola*.

Many coastal plain endemics are known in the lichen flora of eastern United States and adjacent Canada (Brodo 1968). Those with restricted distributions in New England and the maritime provinces such as *B. salazinicola*, and perhaps *Cladonia boryi* Tuck. (also known in Japan; see Ahti 1973), probably occupied the expanded coastal plain as the Pleistocene ice sheet receded to the north, adapting to, and then becoming restricted to coastal localities (see Morisset 1971). Whether the endemic species evolved here or simply represent fragments of a once world-wide population is usually impossible to determine in lichens, which have virtually no fossil record.

(15) Central American highlands: *Alectoria mexicana*, *A. lata*.

Alectoria mexicana is a rare plant, and its origins and relationships are still very unclear. *A. lata*, on the other hand, is a species of cool, high montane pine forests in subtropical and tropical latitudes and occurs in similar forests in the Pacific Northwest from California to Washington, as well as in Asia (Hawksworth 1972).

Asian affinities with plants of Mexico have been the subject of numerous papers (see especially Sharp 1966). Some Asian-Mexican disjuncts are known to occur in western American mountains as well. These most probably represent ancient Arcto-Tertiary distributions, disrupted by "the rigors of the late Tertiary and Pleistocene" (Sharp 1966 p. 231).

Importance to man and nature

Few groups of lichens are considered to be of major importance to man. *Cladina*, comprising the reindeer lichens, is certainly the most outstanding example of an "economically" important lichen genus. *Alectoria* s. lat., as a "genus", has probably been used by man directly and indirectly more than any other genus except *Cladina*. Since one of these uses, that of caribou forage, partly led us to undertake this study, it seems appropriate to review the subject briefly, as regards the species in North America.

Forage

Although the terricolous reindeer lichens are the most abundant and important winter food for caribou, arboreal lichens are generally plentiful enough in the winter range of the barren-ground and woodland caribou (*Rangifer tarandus groenlandicus*, and *R. t. caribou*, respectively; Banfield 1974) to be of major importance. In some regions such as Wells Gray Park in eastern British Columbia, arboreal lichens, especially species of *Alectoria* s. lat., provide caribou with most of their winter food (Edwards et al. 1960). Edwards and his coworkers go so far as to say that the survival of caribou in the region depends on the availability of *Alectoria* s. lat. In other areas such as northern Saskatchewan (Scotter 1962) and northern Ontario (Cringan 1957, Ahti & Hepburn 1967), *Alectoria* s. lat. forms a significant, although not dominant, role in winter food requirements, especially when the snow is exceptionally deep or encrusted.

The quantities of arboreal lichens produced in these forests are impressive. In northern Saskatchewan, one can find 359–572 kg/acre in a black spruce forest, and 217–1167 kg/acre

in mature jack pine stands (Scotter 1962). Maxima of 114 kg/acre and 1332 kg/acre of dried *Alectoria* s. lat. can be produced in lodgepole pine forests and timberline spruce-fir forests, respectively, of Wells Gray Park (Edwards et al. 1960).

In Saskatchewan, caribou can sometimes reach branches 3.3 m from the ground giving them access to an average of 154–275 kg/acre (Scotter 1960). In Wells Gray Park, where the snow is often much deeper and the caribou can reach up to 5 m above ground level, the animals can find 52–329 (with an average of 116) kg/acre (Edwards et al. 1960 Table 1; the figures given in their summary for a reach of 2.6–5 m are 5–128 kg/acre).

One cannot compare these productivity data with too much confidence since the samples in both studies were relatively small, but it seems safe to say that the heavier the snow cover, the more difficult it is for caribou to find and utilize ground lichens (e.g., *Cladina* spp.), and the easier it is for them to reach and utilize arboreal lichens (e.g., species of *Alectoria* and *Bryoria*).

Caribou in northern Saskatchewan prefer *Bryoria* species ("Alectoria jubata") to leaves, according to Scotter (1962). In Ontario fallen trees laden with *Alectoria* s. lat. are quickly eaten bare of lichens by caribou (Cringan 1957). Ahti (1959) reported that "*Alectoria jubata*" ranks with *Cladina mitis* and *C. rangiferina* as a preferred winter food eaten on a large scale in Newfoundland; *Alectoria sarmentosa* was only eaten in smaller quantities. In their studies in Ontario, Ahti & Hepburn (1967) describe "*A. jubata*", *Bryoria furcellata* (sub *A. nidulifera*) and *B. simplicior* as "highly palatable." Experiments carried out in Quebec (DesMeules & Heyland 1969) demonstrated

that while *Alectoria* s. lat. (in a mixture with *Evernia* and *Usnea* spp.) was not the favourite food when compared with some *Cladinae*, it was preferred to *Cetraria islandica* and *Stereocaulon* spp. Apparently the terricolous *Alectoria ochroleuca* is avoided by caribou, according to papers cited by Ahti & Hepburn (1967). Whether this is due to a quantitative or qualitative difference in lichen substances in this species as suggested by Ahti & Hepburn (1967) requires investigation.

The food value of *Alectoria* s. lat. seems to be rather high in comparison to that of other lichens eaten by caribou, especially with regard to protein. All lichens are high in carbohydrate but are low in both fat and protein (Scotter 1965). Karev (1956) gives the protein and fat content of "*Alectoria implexa* s. lat." as 7.3% and 1.3%, respectively, compared with 2.6–2.9% protein and 1.8–2.2% fat for the *Cladinae*. Many *Alectoriae* s. lat., especially *A. sarmentosa*, are digested very rapidly by the caribou (Bergerud & Russell 1964) and so are presumably utilized efficiently.

From the foregoing discussion, it is evident that the majority of those working with the brown "*Alectoriae*" (i.e., *Bryoria*) were generally not certain as to the specific identity of their material. Although it would be impossible to "translate" reports of "*Alectoria jubata*" into a list of known *Bryoria* species in any precise way, our revision of the vouchers for many of these studies has enabled us to specify some of the species involved.

Ahti & Hepburn (1967) probably came closest to defining the species they treated under "*A. jubata* s. lat." Based on identifications by Motyka, they reported "*A. americana*", "*A. canadensis*", "*A. glabra*" and "*A. tenerrima*" for northern Ontario. According to our examinations of their material, Ahti & Hepburn were working mainly with *Bryoria trichodes* subsp. *trichodes* with smaller amounts of *B. fuscescens* and *B. lanestris*. Scotter's material from northern Saskatchewan (Scotter 1962, 1964, 1965) was a mixture of *B. lanestris* and *B. simplicior*. The Newfoundland "*A. jubata*" reported by Ahti (1959) and Bergerud (1972) is mainly *B. trichodes* subsp. *americana* (Ahti & Hawksworth 1974, sub *A. americana*), but some *Bryoria trichodes* subsp. *trichodes* and perhaps also *B. fuscescens* were probably also included.

The "*Alectoria jubata*" of Wells Gray Park (Edwards et al. 1960) included "*A. oregana*", "*A. chalybeiformis*", and "*A. jubata*" according to the authors themselves. Based on collections made by Teuvo Ahti in the park in 1961, it would appear that their "*A. jubata*" consisted of *Bryoria pseudofuscescens*, *B. fuscescens*, *B. glabra*, and *B. lanestris*. Since *B. furcellata* is virtually absent in the mountains, their "*A. chalybeiformis*" was probably a spinulose form of *B. fuscescens* (such as f. *pallida*). Since we have seen no specimens of *B. fremontii* from that park, although the species does occur in the Selkirk Mountains and in Yoho National Park, it is likely that the "*Alectoria fremontii*" referred to by Edwards et al. (1960) was largely *B. pseudofuscescens*.

The "*Alectoria* spp." used by DesMeules & Heyland (1969) in Parc des Laurentides was not segregated according to colour group, and probably consisted largely of *Bryoria trichodes* subsp. *trichodes*, *B. nadvornikiana*, *B. fuscescens*, and *Alectoria sarmentosa*, to judge from observations made in the park by one of us (I.M.B.).

Food for man

In parts of interior British Columbia, some tribes of Indians have long been using certain species of *Bryoria* as a traditional food. Some fascinating folk legends have been built up around its use (e.g., "How the Coyote Happened to Make the Black Moss Food", Dove 1933). Nancy Turner of the British Columbia Provincial Museum reports (in press) that members of the Lillooet tribe still use *Bryoria* to make a sort of baked pancake (Fig. 23), often eaten sweetened with sugar. Richardson (1974) describes its preparation in some detail based on the account by Dove (1933).

Samples of the lichens used by the Indians were sent to us by Turner and all are *B. fremontii*. We have also seen herbarium specimens of *B. tortuosa* collected by J. T. Rothrock in "New Caledonia, northern British Columbia" annotated by the collector as "used by Indians and cattle for food in hard winters." It is very unlikely that "New Caledonia" is in the northern part of the province in view of the known distribution of the species. In any case,

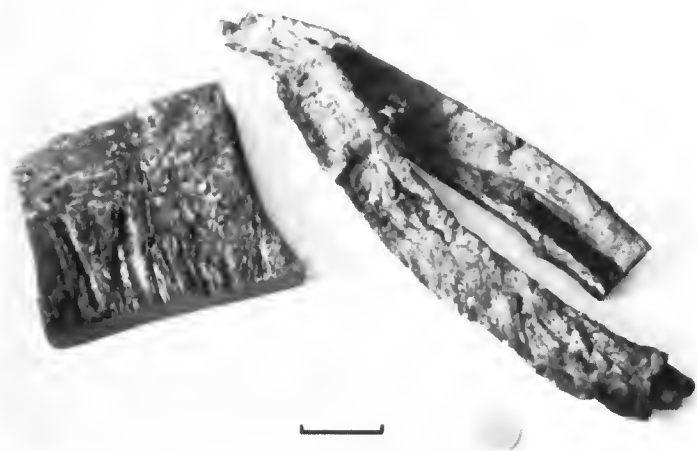


Fig. 23. A type of "pancake" made from *Bryoria fremontii* by Lilloet Indians in British Columbia. Scale 25 mm. Specimen from the B. C. Provincial Museum; photo by R. Turner.

the possible use of *B. tortuosa* as a food is intriguing in view of the fact that it contains vulpinic acid, a substance which appears to be toxic (Llano 1948). *Bryoria fremontii* also can contain vulpinic acid but only on apothecia or in soralia, which are seldom present. If *B. tortuosa* is actually capable of producing illness in man, which has not been established, one wonders if the limits of its use as a food might follow the distribution limits of *B. tortuosa*, since in southwestern British Columbia, the two species grow together and some forms can easily be confused. Fortunately, vulpinic acid is bitter and the Indians always tasted samples of the lichen before collecting large quantities for consumption (Turner in press). They therefore probably never made serious mistakes. The use of *Bryoria* by the Interior British Columbia Indians will be described in detail by Turner (in press).

Insect pests

Recently, a relationship between species of *Alectoria* and *Bryoria* and the life cycle of an extremely destructive insect pest has been discovered. In studying outbreaks of the Hemlock Looper (*Lambdina fiscellaria fiscellaria* [Guen.]) in eastern Canada, Jobin (1973) discovered that this small moth lays its eggs, 90% of the time, on pendent lichens hanging

from the branches of *Abies balsamea*. Almost all these lichens are species of *Alectoria* or *Bryoria*, including *B. trichodes* (both subspecies), *B. fuscescens*, *B. nadvornikiana*, *B. globra*, and *Alectoria sarmentosa*. When the larvae emerge from their eggs, they crawl over the lichen to the branch, and then crawl to the new leaves where they begin to feed. The Hemlock Looper is so successful that in times of outbreaks, it can completely defoliate vast areas of fir forest. On Ile Anticosti in the Gulf of St. Lawrence, this insect destroyed 210,000 acres of timber, with a loss of 3,000,000 cords of wood, within the single year 1971. Jobin (1973) found that the outbreaks centre around islands, lake shores, or along rivers. Whether the insect is responding to the microclimate characteristic of these localities or to the presence of certain lichen species which in turn require these habitats is still not known. Nothing is known concerning any possible specificity for certain species of *Alectoria* or *Bryoria*, nor concerning its response to certain lichen substances, colours, thallus characteristics, branching patterns, age etc. What role the lichen might play in the control of the insect is under study, but wholesale destruction of the lichen vegetation has been ruled out (Jobin in litt.), at least at this stage.

It is interesting that the western Hemlock Looper (*Lambdina fiscellaria lugubrosa*

[Hulst]) also lays its eggs on lichens (Thompson 1958). Thompson found that on Vancouver Island, both "a fine hair-like black lichen" (probably a species of *Bryoria*) as well as "a pale yellow-green branching lichen" (the latter possibly *Alectoria sarmentosa* or *A. vancouverensis* or a mixture of the two) harboured many eggs, although bark crevices were still the preferred site. He also found that along the coast, where lichens are largely replaced by epiphytic mosses, the mosses are the favoured substrate for oviposition. Thus, in the case of this insect, specificity for lichen species or even lichens in general seems to be low.

Lichenometry

Pseudephebe minuscula and *P. pubescens* are rapid colonizers of bare rock following the retreat of glaciers and so have been used in the lichenometric dating of glacial moraines. (For a synopsis and extensive bibliography on this topic see Webber & Andrews 1973.) They have proved particularly valuable on Baffin Island

where isophyses (lines of equal growth) based on them have been constructed (Andrews & Webber 1964, 1969). Because of the taxonomic problems involved in the separation of these two species, Andrews & Webber (1964) combined data from both and used the epithet *minuscula* as that species was the more frequent in the areas they studied. These authors calculated an optimal annual growth rate of 0.52 mm and a mean of about 0.40 mm in diameter assuming a 10 year initial colonization lag; these data are consistent with the 0.56 mm *per annum* rate recorded on Disko, Greenland, by Beschel (1963). Tracings of individual thalli on Baffin Island over the years 1963–67 revealed a tendency for larger thalli to grow more quickly, but, over a period of up to 300 years, a mean annual growth rate of 0.40 mm appears to hold (Andrews & Webber 1969). A more recent study of *P. minuscula* on Baffin Island, using photographic techniques, showed that the growth rate of this species decreases with increases in altitude (Miller 1973).

Taxonomic survey

Key to the genera of Alectorioid lichens

- 1 Ascospores under 16 μm long, colourless at maturity 2
- Ascospores over 19 μm long, yellowish to brown at maturity 3
- 2(1) Thallus closely adpressed to the substrate, attached over almost the whole thallus area, rosette-forming, under 1 cm tall; cortex cellular in part, \pm differentiated at the surface which is smooth or rough; pycnidia common; lichen products absent 4. *Pseudephebe*
- Thallus erect, caespitose to pendent, attached at the base or sometimes secondarily by branches but never over the whole thallus area, not forming rosettes, over 1 cm tall; cortex not distinctly cellular, not or little differentiated at the surface; pycnidia rare; atranorin and/or chloroatranorin, orcinol tridepsides, β -orcinol depsidones and pulvinic acid derivatives known 2. *Bryoria*
- 3(1) Ascospores becoming transversely septate or muriform at maturity 4
- Ascospores remaining simple at maturity, 2–4 per ascus, 20–45 μm long; cortex with much matrix, not differentiated but often disintegrating at the surface; medullary hyphae usually ornamented; usnic acid, and orcinol depsides known 1. *Alectoria*
- 4(3) Ascospores 1(–3)-septate at maturity, 22–40 μm long, 6–8 per ascus; cyphella-like perforations absent; pseudocyphellae present as a single continuous longitudinal furrow; atranorin, β -orcinol depsidones and pulvinic acid derivatives known 5. *Sulcaria*
- Ascospores muriform at maturity, 76–96 μm long, 1 per ascus; cyphella-like perforations present; pseudocyphellae absent; β -orcinol depsides (incl. atranorin) and depsidones, as well as hydroxyanthraquinones known 3. *Oropogon* Th. Fr.

Check-list of the North American species

| Accepted taxa | Selected synonyms |
|--|---|
| Alectoria Ach. | <i>Bryopogon</i> Link |
| 1. <i>A. fallacina</i> Mot. | |
| 2. <i>A. imshaugii</i> Brodo & D. Hawksw. | |
| 3. <i>A. lata</i> (Tayl.) Linds. | |
| 4. <i>A. mexicana</i> Brodo & D. Hawksw. | <i>A. osteina</i> Nyl. |
| 5. <i>A. nigricans</i> (Ach.) Nyl. | |
| 6. <i>A. ochroleuca</i> (Hoffm.) Massal. | |
| 7a. <i>A. sarmentosa</i> (Ach.) Ach. subsp. <i>sarmentosa</i> | <i>A. stigmata</i> Bystr., <i>A. subsarmentosa</i> Stirt. |
| 7b. <i>A. sarmentosa</i> subsp. <i>vexillifera</i> (Nyl.) D. Hawksw. | <i>A. vexillifera</i> (Nyl.) Stiz. |
| 8. <i>A. vancouverensis</i> (Gyeln.) Gyeln. ex Brodo & D. Hawksw. | |

| Accepted taxa | Selected synonyms |
|--|---|
| Bryoria Brodo & D. Hawksw. | <i>Setaria</i> Michx., <i>Bryopogon</i> Th. Fr., non Link |
| sect. Bryoria | |
| 1. <i>B. chalybeiformis</i> (L.) Brodo & D. Hawksw. | |
| 2. <i>B. fuscescens</i> (Gyeln.) Brodo & D. Hawksw. | <i>A. positiva</i> (Gyeln.) Mot. |
| 3. <i>B. glabra</i> (Mot.) Brodo & D. Hawksw. | |
| 4. <i>B. lanestris</i> (Ach.) Brodo & D. Hawksw. | <i>A. tenerrima</i> Mot. |
| 5. <i>B. subcana</i> (Nyl. ex Stiz.) Brodo & D. Hawksw. | <i>A. haynaldii</i> Gyeln. |
| 6a. <i>B. trichodes</i> (Michx.) Brodo & D. Hawksw. subsp. <i>trichodes</i> | <i>A. canadensis</i> Mot., <i>A. delicata</i> Mot. |
| 6b. <i>B. trichodes</i> subsp. <i>americana</i> (Mot.) Brodo & D. Hawksw. | <i>A. americana</i> Mot., <i>A. ambigua</i> Mot., <i>A. sepiacea</i> Mot. |
| 7. <i>B. vrangiana</i> (Gyeln.) Brodo & D. Hawksw. | |
| sect. Divaricatae (DR.) Brodo & D. Hawksw. | |
| 8. <i>B. bicolor</i> (Ehrh.) Brodo & D. Hawksw. | |
| 9. <i>B. carlottae</i> Brodo & D. Hawksw. | |
| 10. <i>B. cervinula</i> Mot. ex Brodo & D. Hawksw. | |
| 11. <i>B. furcellata</i> (Fr.) Brodo & D. Hawksw. | <i>A. nidulifera</i> Norrl. |
| 12. <i>B. nitidula</i> (Th. Fr.) Brodo & D. Hawksw. | <i>A. lanea</i> auct., non (Ehrh. ex Hoffm.) Vain., <i>A. irvingii</i> Llano <i>A. nana</i> Mot. <i>A. bicolor</i> var. <i>subbicolor</i> Mot. |
| 13. <i>B. simplicior</i> (Vain.) Brodo & D. Hawksw. | |
| 14. <i>B. tenuis</i> (Dahl) Brodo & D. Hawksw. | |
| sect. Implexae (Gyeln.) Brodo & D. Hawksw. | |
| 15. <i>B. capillaris</i> (Ach.) Brodo & D. Hawksw. | <i>A. implexa</i> auct., non (Hoffm.) Nyl. p.p. |
| 16. <i>B. friabilis</i> Brodo & D. Hawksw. | |
| 17. <i>B. implexa</i> (Hoffm.) Brodo & D. Hawksw. | |
| 18. <i>B. nadvornikiana</i> (Gyeln.) Brodo & D. Hawksw. | |
| 19. <i>B. pikei</i> Brodo & D. Hawksw. | |
| 20. <i>B. pseudocapillaris</i> Brodo & D. Hawksw. | |
| 21. <i>B. pseudofuscescens</i> (Gyeln.) Brodo & D. Hawksw. | <i>A. norstictica</i> Mot., <i>A. subtilis</i> Mot. |
| 22. <i>B. salazinicola</i> Brodo & D. Hawksw. | |
| 23. <i>B. spiralifera</i> Brodo & D. Hawksw. | |
| sect. Subdivergentes (Mot.) Brodo & D. Hawksw. | |
| 24. <i>B. abbreviata</i> (Müll. Arg.) Brodo & D. Hawksw. | <i>A. oregana</i> auct. p.p. |
| 25. <i>B. oregana</i> (Tuck.) Brodo & D. Hawksw. | |
| sect. Tortuosae (Mot.) Brodo & D. Hawksw. | |
| 26. <i>B. fremontii</i> (Tuck.) Brodo & D. Hawksw. | |
| 27. <i>B. tortuosa</i> (Merr.) Brodo & D. Hawksw. | <i>A. virens</i> sensu R. Howe, non Tayl. |
| Pseudephebe Choisy | |
| 1. <i>P. minuscula</i> (Nyl. ex Arnold) Brodo & D. Hawksw. | <i>Parmelia minuscula</i> (Nyl. ex Arnold) Nyl. |
| 2. <i>P. pubescens</i> (L.) Choisy | <i>Parmelia pubescens</i> (L.) Vain. |
| Sulcaria Bystr. | |
| 1. <i>S. badia</i> Brodo & D. Hawksw. | |

Key to the North American species

- 1 Thallus yellow or yellowish-green; conspicuous pseudocyphellae present (occasional in *Ramalina thrausta*, couplet 7); cortex KC + yellow (usnic acid) 2

- Thallus not yellow or yellowish-green; pseudocyphellate or not; cortex KC- or KC+ reddish (usnic acid absent) 10
- 2(1) Medulla C+ red (olivetic acid) 3
- Medulla C- (olivetic acid absent) 4
- 3(2) Thallus subpendent, bright yellow throughout; cortex clearly delimited, not becoming fibrous internally; known only from the highlands of Mexico and Guatemala 4. *A. mexicana*
- Thallus pendent, often very long, yellow to greyish-green; cortex joined with a fibrous network within the medulla; medulla dense and compact; southern California to British Columbia close to sea level 8. *A. vancoverensis*
- 4(2) Thallus caespitose to subpendent or pendent, usually corticolous 5
- Thallus erect to prostrate, usually terricolous 9
- 5(4) Thallus caespitose, rarely subpendent, usually less than 10 cm long 6
- Thallus pendent to subpendent, 8-20 cm long or longer 7
- 6(5) Isidioid spinules arising from the pseudocyphellae in tufts or along the branches; ascocarps rare; medulla PD+ orange-yellow or PD- (thamnolic or squamatic acid present), medulla KC-, exceptionally KC+ red (alectoronic acid very rare); Idaho, west to B.C. coast, south to central California; locally frequent 2. *A. imshaugii*
- Isidioid spinules absent; ascocarps not uncommon; medulla KC+ red (alectoronic acid); from Washington southwards in mountains to Guatemala 3. *A. lata*
- 7(5) Apices of branches sorediate or granular, often hooked; medulla KC- *Ramalina thrausta* (Ach.) Nyl.
- Apices of branches not sorediate or granular, never hooked; medulla KC+ red or KC- 8
- 8(7) Branches more or less regular, pendent; medulla usually lax, KC+ red or rarely KC-; cortex relatively uniform throughout; a very common boreal-montane species 7 a. *A. sarmentosa* subsp. *sarmentosa*
- Branches recurved and tangled, subpendent; medulla dense, KC- or rarely KC+ red; cortex very uneven in thickness, giving thallus a knobby appearance; Appalachian Mountains, Tennessee to Nova Scotia; rare 1. *A. fallacina*
- 9(4) Thallus usually erect, rarely subdecumbent; main stems more or less terete, usually less than 2 mm diam.; medulla KC-, CK+ golden-yellow (diffractaic acid), or rarely KC+ red (alectoronic acid) especially in the Aleutians and in Central America; a frequent to abundant species in the tundra 6. *A. ochroleuca*
- Thallus prostrate to decumbent; main stems becoming dorsiventrally compressed, expanded and foveolate, usually exceeding 2 mm diam. (to 4 cm wide); medulla KC+ red (alectoronic acid) or infrequently KC-; an occasional subspecies of western alpine and eastern arctic tundra 7b. *A. sarmentosa* subsp. *vexillifera*
- 10(1) Thallus closely adpressed to rock, usually less than 1 cm tall, forming rosettes attached over most parts of the thallus; medulla K-, C-, KC-, PD- 11
- Thallus not closely adpressed to rock, usually exceeding 1 cm in height or length, not forming rosettes attached over most parts of the thallus; medulla PD+ or PD- 12
- 11(10) Branches usually terete, even; internodes long; adpressed only at the margins, becoming bushy, prostrate or erect towards the centre of the thallus; arctic-alpine 2. *P. pubescens*
- Branches becoming dorsiventrally compressed, uneven; internodes short; closely attached to the rock over almost the whole thallus area, becoming closely adpressed to almost crustose or foliose towards the centre of the thallus; arctic-alpine 1. *P. minuscula*
- 12(10) Thallus erect or prostrate to decumbent; on rocks or soil (exceptionally on bark or wood) 13
- Thallus caespitose or pendent; on bark or wood (rarely on rock) 26
- 13(12) Thallus PD+ yellow-orange (diffusing onto filter paper), surface C+ pink to red on pale areas (alectorialic and/or barbatolic acid); thallus some shade of grey, white, yellowish grey or black; branching anisotomic dichotomous 14
- Thallus PD- or PD+ red 15

- 14(13) Pseudocyphellae white, raised and conspicuous, soralia absent; thallus usually pale at the base with at least the tips blackened; apices usually reflexed; common on the ground in arctic-alpine areas (very rarely on bark or wood) 5. *A. nigricans*
- Pseudocyphellae small, dark, plane, generally inconspicuous; soralia usually present; thallus either pale at tips or entirely dark brown to black, at least black at the base; apices pointed and straight, with abundant, divergent, spinulose lateral branches (see also couplet 28) 18. *B. nadvornikiana*
- 15(13) Medulla or only pseudocyphellae C + red or pink (gyrophoric acid); thallus bright to dark red-brown, usually shiny, concolourous; branching isotomic dichotomous, broad, divergent; subarctic to arctic-alpine; common *Cornicularia divergens* Ach.
- Medulla and pseudocyphellae C – 16
- 16(15) Thallus with conspicuous, broadly fusiform, cyphella-like perforations into the hollow medulla; grey to dark red-brown; known from the high mountains of Central America *Oropogon loxensis* (Fée) Th. Fr. s. lat.
- Thallus without cyphella-like perforations 17
- 17(16) Soralia present (sometimes sparse) 18
- Soralia absent 21
- 18(17) Soralia bearing tufts of isidioid spinules; PD + red; branching regularly isotomic dichotomous; branches smooth, not twisted or foveolate, shiny, pale to cervine brown; occasionally on rocks but also known from subarctic heathland in Newfoundland 11. *B. furcellata*
- Soralia not bearing tufts of isidioid spinules; branching often irregular 19
- 19(18) At least main branches very thick, twisted and often foveolate, generally over 0.5 mm diam. 20
- Branches very slender, pendent or subpendent, usually less than 0.2 mm diam.; soralia numerous, virtually all fissural 4. *B. lanestris*
- 20(19) Thallus dark brown to olivaceous black, often shiny; soralia sparse, usually tuberculate, PD + red; medulla and cortex usually PD –; arctic-alpine 1. *B. chalybeiformis*
- Thallus fuscous brown to brown, usually matt; soralia frequent or sparse, fissural and tuberculate types usually present, PD + red; cortex often PD + red; usually coastal 2. *B. fuscescens* var. *positiva*
- 21(17) Thallus uniformly red-brown, small, prostrate, under 3 cm long; main branches conspicuously longitudinally foveolate and flattened; medulla PD –; ascocarps to 2.5 mm diam., red-brown; known with certainty only from tundra in southwest Greenland *B. subdivergens* (Dahl) Brodo & D. Hawksw. (p. 153)
- Thallus not red-brown and foveolate 22
- 22(21) Main branches shiny, black, with numerous grey to pale brown perpendicular side branches and apices; spinules abundant; medulla PD + red at least in parts 23
- Main branches not black with pale side branches and apices; thallus more or less uniformly cervine brown to dark brown or black; medulla PD + red or PD – 24
- 23(22) Thallus forming dense tufts; third order branches common and arising at right angles; coastal or montane 8. *B. bicolor*
- Thallus not forming dense tufts; third order branches sparse and usually arising at acute angles; mainly coastal and montane, very rare in the tundra 14. *B. tenuis*
- 24(22) Thallus erect or frequently decumbent, usually forming compact tufts, uniformly dark cervine brown to black; branching anisotomic dichotomous with lateral branches arising perpendicularly or at acute angles; medulla PD + red (exceptionally PD –); mainly restricted to the tundra where it is often common 12. *B. nitidula*
- Thallus prostrate to decumbent, not forming compact tufts, cervine brown to dark brown, never uniformly brown-black 25
- 25(24) Branching anisotomic dichotomous; conspicuous, stout, lateral spinules present; pale

- fuscous brown to dark brown, or blackened at the base, often appearing variegated; medulla PD + red; pseudocyphellae absent to sparse; ascocarps unknown; known only from Alaska and coastal British Columbia 10. *B. cervinula*
- Branching isotomic dichotomous; lateral spinules, if present, not stout; uniformly cervine brown, often shiny; medulla PD + red or PD -; ascocarps not infrequent; pseudocyphellae often abundant; mainly coastal 6b. *B. trichodes* subsp. *americana*
- 26(12) Thallus K + persistently bright yellow, KC + red (fading) and often C + pink (fading), PD + orange-yellow (barbatolic and/or alectorialic acid) 27
- Thallus K -, or if K + yellow, the yellow is very pale or quickly darkens to brown, orange or red and largely disappears; PD + or - 30
- 27(26) Thallus caespitose to subpendent, often with perpendicular lateral spinulose branches .. 28
- Thallus pendent, without perpendicular lateral spinulose branches; soralia unknown in North American material; basal branches rarely blackened, apices usually concolourous or darker than the basal parts, thallus greyish to fuscous brown or rarely dark brown; widely distributed in Canada and the northern United States (if K + reaction weak, see *B. pikei*, couplet 60) 15. *B. capillaris*
- 28(27) Soralia present; basal branches blackened, apical branches greyish to fuscous brown; pseudocyphellae short, fusiform; boreal forests in Canada and Alaska 18. *B. nadvornikiana*
- Soralia absent 29
- 29(28) Tips of branches and sometimes most of thallus blackened; pseudocyphellae white, short, raised; thallus much branched, caespitose (see couplet 14) 5. *A. nigricans*
- Basal branches and tips concolourous with main branches, not blackened; thallus grey to dull badia-brown, especially on lateral branches; pseudocyphellae elongate, linear, becoming canaliculate; thallus tangled, subpendent; on trees along sea coast, northern California to Oregon 20. *B. pseudocapillaris*
- 30(26) Thallus with soredia 31
- Thallus without soredia 40
- 31(30) Thallus caespitose, pale to dark cervine brown, usually shiny 32
- Thallus subpendent to pendent 33
- 32(31) Soralia white, bearing tufts of isidioid spinules; inner cortex, medulla and soredia PD + red (fumarprotocetraric acid); widely distributed in eastern temperate and boreal regions, infrequent in the west 11. *B. furcellata*
- Soralia greenish black, not bearing tufts of isidioid spinules; all tissues PD -; common in northern boreal forests 13. *B. simplicior*
- 33(31) Soralia bright yellow or greenish yellow (vulpinic acid), tuberculate; medulla and soralia PD - (see couplet 51) 26. *B. fremontii*
- Soralia white, sometimes flecked with black (not bright yellow or greenish yellow), PD + red (fumarprotocetraric acid), tuberculate or fissural; cortex or medulla PD - or PD + red 34
- 34(33) Pseudocyphellae conspicuous; branches usually uneven in diameter, cervine brown throughout; inner cortex PD + red or PD - a morphotype of *B. trichodes*
- Pseudocyphellae absent or very inconspicuous; branches even or uneven in diameter; colour various; cortex or medulla PD + red or PD - 35
- 35(34) Main branches (not base) usually less than 0.2 mm diam.; thallus dark brown to dark olivaceous or black throughout; soralia fissural or very rarely tuberculate, often speckled with black; branches very uneven in diameter, brittle, tending to fragment in herbarium packets; cortex and medulla PD -; common in the northern boreal forests, extending southwards in the western mountains 4. *B. lanestris*
- Main branches (not base) exceeding 0.2 mm diam.; thallus brown or olivaceous, but rarely darkening to black; soralia almost always uniformly white 36
- 36(35) Outer and sometimes inner cortex of branches PD + intense red (fumarprotocetraric acid) 37
- Medulla and cortex of branches PD - 38

- 37(36) Thallus uniformly grey, sometimes becoming pale fuscous brown towards the apices (not pale at the base); soralia tuberculate; west coast, very rare 5. *B. subcana*
- Thallus fuscous brown to brown, usually pale at the base; fissural and tuberculate soralia usually present; scattered throughout Canada and the northern U.S. 2. *B. fuscescens*
- 38(36) Branches even in diameter throughout; thallus shiny, olivaceous to olive-brown, concolourous; angles between the main dichotomies obtuse and rounded; soralia fissural, rarely tuberculate; mainly in the west where it is locally abundant; very rare on the east coast 3. *B. glabra*
- Branches uneven in diameter, at least in part, or if even, not olivaceous; angles between the main dichotomies, if obtuse, then generally not rounded; soralia tuberculate or fissural 39
- 39(38) Thallus shiny olivaceous brown to olive black, concolourous; branching irregular anisotomic dichotomous especially towards the apices; main branches becoming contorted and foveolate, often becoming spinulose; soralia rare 7. *B. vrangiana*
- Thallus usually dull, fuscous brown to dark brown, usually paler at the base; branching isotomic dichotomous; main branches rarely becoming contorted and foveolate; soralia usually abundant, usually fissural and tuberculate 2. *B. fuscescens*
- 40(30) Thallus with conspicuous broadly fusiform cyphella-like perforations opening into the hollow medulla; grey to dark red-brown, shiny (see couplet 16) *Oropogon loxensis* (Fée) Th. Fr. s. lat.
- Thallus without cyphella-like perforations 41
- 41(40) Main branches shiny, black, with numerous, obviously paler, olivaceous grey to light brown, perpendicular side branches and apices; spinules abundant; inner cortex and medulla PD + red at least in apical parts; mainly coastal and montane 23
- Main branches not black with pale olivaceous perpendicular side branches and apices; cortex and/or medulla PD + red or PD - 42
- 42(41) Thallus caespitose to erect, very small, usually less than 3 cm tall; branches longitudinally furrowed, dull and flattened; almost always abundantly fertile 43
- Thallus pendent or subpendent, usually exceeding 3 cm long 44
- 43(42) Thallus dull red-brown; epithecium red-brown, K -; mountainous areas from the Rockies westwards 24. *B. abbreviata*
- Thallus olive brown to greenish black; epithecium greenish to brown black, usually K + violet; California to the Queen Charlotte Islands *Cornicularia californica* (Tuck.) DR.
- 44(42) Scattered elongate yellow pseudocyphellae present; thallus dark red-brown to dusky yellow-brown, occasionally becoming bright greenish yellow in parts; long, pendent; main branches becoming twisted and foveolate; thallus PD - or faintly PD + yellow on filter paper; mainly along the west coast from California to southern British Columbia 27. *B. tortuosa*
- Pseudocyphellae present or absent, but if present, white or brown (never yellow) 45
- 45(44) Branches with very long (at least 4 mm) deep furrows or grooves (sulci) breaking into the medulla; thallus dull chestnut brown to almost yellowish brown in parts; outer cortex K + faintly yellow (at least on filter paper), PD + brownish or PD - (or pale yellow on filter paper) (atranorin present); California and Oregon 1. *S. badia*
- Branches without very long, deep furrows or grooves breaking into the medulla 46
- 46(45) Cortex and medulla PD - (and not producing any colouration on filter paper) 47
- Cortex and/or medulla PD + yellow or red (or producing a colouration on filter paper) 52
- 47(46) Medulla and/or pseudocyphellae C + pink to red, KC + pink (olivetic acid); thallus red-brown, with punctiform, almost tuberculate, white pseudocyphellae; branching mostly isotomic dichotomous; infrequent, along B.C. coast *Cornicularia pseudosatoana* Asah.
- Medulla C -, KC -; cortex C - or C + pink (gyrophoric acid) 48
- 48(47) Cortex C + pink, KC + pink (gyrophoric acid); branches very brittle; thallus pale greyish brown, or rarely pale olive-brown; usually very uneven in diameter and twisted; infrequent on the west coast, and rare in the western mountains and along the east coast 16. *B. friabilis*

- Cortex C-, KC-; thallus usually dark red-brown or yellowish brown to dark brown or olive-black 49
- 49(48) Thallus shiny olivaceous brown to olive-black; branching anisotomic dichotomous especially towards the apices; main branches becoming contorted and foveolate, often spinulose (see couplet 39) 7. *B. vrangiana*
- Thallus dull or shiny, yellow-brown to red-brown or dark red-brown 50
- 50(49) Main branches even in diameter, not foveolate or channelled, cervine brown throughout (see couplet 55) 6b. *B. trichodes* subsp. *americana*
- Main branches foveolate or channelled 51
- 51(50) Thallus very dull, distinctly red-brown; branches foveolate or longitudinally ridged, channelled but not twisted, very brittle, to 0.3 mm diam.; branching irregularly anisotomic dichotomous; ascocarps, if present, red-brown, epruinose, sometimes "ciliate" at margins; hyphae at the surface of the cortex consisting of short, knobby hyphal cells (jigsaw-like in surface view, see Fig. 12A); in the western mountains 25. *B. oregana*
- Thallus shiny or less frequently dull, yellow-brown to red-brown or dark red-brown; main branches foveolate, twisted, not brittle, mainly 0.4-1.5 mm diam.; branching isotomic dichotomous at the base, with slender perpendicular lateral branches; ascocarps, if present, yellow pruinose, not ciliate; cortex in surface view consisting of long, slender, parallel hyphae; mainly along the west coast 26. *B. fremontii*
- 52(46) Cortex and/or medulla PD + red (fumarprotocetraric acid) 53
- Cortex and/or medulla PD + yellow (at least on filter paper) 56
- 53(52) Thallus olive; branching mostly anisotomic dichotomous to submonopodial, with many short perpendicular side branches along the main axes; pseudocyphellae abundant; PD + red in inner cortex only (not diffusing onto filter paper); rare, known only from the Queen Charlotte Islands 9. *B. carlottae*
- Thallus pale greyish brown to cervine brown (not olive) 54
- 54(53) Thallus pale grey to greyish brown; outer cortex PD + intensely red (diffusing out onto filter paper); rare (see couplet 38) 5. *B. subcana*
- Thallus pale to dark cervine brown; inner cortex and sometimes medulla PD + red (rarely producing a red colouration of filter paper) 55
- 55(54) Branches even in diameter throughout; pseudocyphellae usually sparse, dark and depressed; thallus usually dark; mainly along east and west coasts 6b. *B. trichodes* subsp. *americana*
- Branches very uneven in diameter; pseudocyphellae usually abundant, white and raised; thallus often pale; mainly with an Appalachian-Great Lakes distribution, but also on the west coast 6a. *B. trichodes* subsp. *trichodes*
- 56(52) Thallus dull red-brown or badius, often becoming paler in parts; pseudocyphellae linear, white, often exceeding 4 mm long and spiraling around the main branches; perpendicular side branches frequent; contains abundant norstictic acid; known only from coastal northern California 23. *B. spiralifera*
- Thallus grey to pale olive-brown or pale to dark brown to black, not red-brown or badius; pseudocyphellae never exceeding 1.5 mm in length; perpendicular side branches absent or very sparse, mainly north of California 57
- 57(56) Thallus dark olive-brown to black, often shiny; pseudocyphellae fusiform, white or dark, to 1 mm long, sometimes sparse; contains norstictic acid; common in Rocky and Selkirk Mountains southward into Oregon 21. *B. pseudofuscescens*
- Thallus pale olive-brown to olive-grey, often variegated; pseudocyphellae abundant and obvious 58
- 58(57) Norstictic acid present Infrequent morphotype of *B. pseudofuscescens*
- Norstictic acid absent 59
- 59(58) Salazinic acid present; thallus pale olive to olive-brown, loosely branched and entangled; rare, known only from the northeast coast 22. *B. salazinic*

- Salazinic acid absent 60
- 60(59) Thallus generally smooth, even, shiny, olive to olive-grey or pale olive-brown; cortex sometimes KC + pink (contains alecortalic acid); infrequent along the west coast and rare on the east coast 19. *B. pikei*
- Thallus generally uneven, dull, twisted, pale fuscous to pale olive-brown; cortex always KC - (contains psoromic acid); rare, scattered throughout the northern boreal forest region 17. *B. implexa*

Notes on the presentation of the species

(1) In the case of taxa for which a detailed account of the synonymy has been presented elsewhere by one of us (D.L.H.), the lists of synonyms included in this section have been limited to names based on North American collections. The identity of unlisted synonyms not included here, which have appeared in the North American literature, can be traced through the Index, and full particulars of them located through the literature references appearing under the accepted name. Where a detailed account of the taxon has not been provided elsewhere, an attempt has been made to determine the full synonymy (i.e., including names not based on North American material).

(2) Descriptions are based *only* on North American material examined in the course of this study. Any major departures from previously published descriptions are mentioned under "Discussion".

(3) The observations on "Ecology" similarly refer only to the autecology of the species in North America unless otherwise indicated.

(4) In the course of the present survey we have not endeavoured to trace collections supporting

literature records except in the case of a few extremely rare species and some species reported as important to man or caribou. Comments on known and suspected erroneous reports in the literature have been confined to ones from well outside the range of the species.

(5) In the case of species known from a relatively small number of localities, all collections from North America examined during this study are listed under "Specimens". Where species are extremely common, because of limitations of space, it has not proved possible to cite all those studied and only "Selected specimens" are listed. This selection has been designed to cite at least one specimen from each state or province. A full listing of the specimens examined (with abbreviated localities) is available at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ontario K 1 A 0S2, Canada. Individual record cards prepared in the course of the production of the distribution maps are preserved in the Botany Division of the Museum of Natural Sciences, National Museums of Canada (CANL) in Ottawa and are available for consultation by those working on the floristics of a particular region.

Alectoria Ach.

in Luyken, Tent. Hist. Lich.: 95 (1809). – *Evernia* sect. *Alectoria* (Ach.) Fr., Syst. Orb. 1: 237 (1825). – *Cornicularia* sect. *Alectoria* (Ach.) Duby, Bot. Gall. 2: 616 (1830). – *Parmelia* sect. *Alectoria* (Ach.) Spreng., Fl. Halen., ed. 2, 2: 521 (1832). – *Bryopogon* Link, Grund. Kräut. 3: 164 (1833); nom. illegit. (Art. 63). – *Alectoria* subgen. *Eualectoria* Th. Fr., Lich. Scand. 1: 19 (1871); nom. illegit. (Art. 63). – *Eualectoria* Gyeln., Ann. Mus. Nat. Hung. 28: 283 (1934); nom. inval. (Art. 34), nom. illegit. (Art. 63). – *Alectoria* sect. *Phaeosporae* Hue, Nouv. Arch. Mus. Paris, Sér. 4, 1: 93 (1899); nom. illegit. (Art. 63). – *Alectoromyces* Cif. & Tom., Atti Ist. Bot. Lab. Critt. Pavia, Ser. 5, 10: 44, 70 (1953); nom. illegit. (Art. 63).

Ceratocladia Del., in Schwendener, in Naegeli, Beitr. Bot. 2: 149 (1860); nom. inval. (Art. 34); type: *C. luteola* (Mont. ex de Not.) Schwend. [= *Alectoria sarmentosa* (Ach.) Ach.], holotype.

Alectoria sect. *Ochroleuca* Gyeln., Feddes Repert. 38: 243 (1935); type: *A. ochroleuca* (Hoffm.) Massal., holotype.

Non *Alectoria* Link, Grund. Kräut. 3: 163 (1833); nom. illegit. (Arts. 63, 64); type: *A. articulata* (L.) Link [= *Usnea articulata* (L.) Hoffm.], holotype.

Type species: *Alectoria sarmentosa* (Ach.) Ach. (syn. *Lichen sarmentosus* Ach.; lectotype designated by Clements & Shear 1931 p. 322).

Thallus fruticose, erect, caespitose, decumbent, subpendent or pendent; branching variable, branches generally terete but becoming compressed and angular to foveolate near the base and axils, in a few taxa becoming markedly expanded and dorsiventrally compressed; greenish-yellow to yellow in most species, fuscous black to black and pinkish below in one.

True lateral spinules absent, spinules arising through the pseudocyphellae in some species. Isidia absent. Soralia large and tuberculate, very rare, unknown in most species. Pseudocyphellae always present, abundant, conspicuous, fusiform, white, markedly raised, sometimes becoming sorediate and bearing spinules. Cortex composed of periclinial, arachnoid, con-

glutinate hyphae, the hyphae immersed in a relatively large amount of matrix, not disintegrating and not differentiated at the surface. Medullary hyphae usually ornamented.

Apothecia lateral, sometimes appearing geniculate owing to the death of the branch distal to them, rare and unknown in some species, common in others; excipulum thallinum concolourous with the thallus, persistent and often markedly incurved, not ciliate; disc brown to dark brown or black. Asci clavate, thick-walled, arrested bitunicate, 2–4-spored. Ascospores ellipsoid, with a distinct hyaline epispore, brown at maturity, simple, 20–45 μ m long. Pycnidia usually rare.

Usnic acid present in all but one species, usually abundant; atranorin and chloroatranorin absent; orcinol depsides abundant; β -orcinol depsides (excluding atranorin and chloroatranorin) frequent; orcinol tridepsides, β -orcinol depsidones, pulvinic acid derivatives and hydroxyanthraquinones absent. An unidentified K + red, C + green-black compound occurs in the cortex of the basal parts of the thalli of most species.

Discussion

As interpreted here *Alectoria* comprises eight species all of which are known from North America. The genus shows its greatest diversity in western North America where all but one species (*A. fallacina*) occur. Species of this genus are widely distributed throughout the world and occur in both hemispheres; three have bipolar tendencies and three are circum-boreal and widely distributed in the Northern Hemisphere.

Alectoria is readily separable from the other genera accepted here, even in the absence of

apothecia, by virtue of the characteristic chemistry, cortical structure and pseudocyphellae.

The nomenclature and typification of *Alectoria* are discussed under *Bryoria*.

1. *Alectoria fallacina* Mot.

Fragm. Florist. Geobot. 6: 447 (1960); type: U.S.A., Tennessee, Great Smoky Mountains, near Alum Cave, on *Picea rubra*, alt. 1575 m, G. Degelius, 13 September 1939 (US holotype! herb. Degelius, US isotypes!).

Thallus subpendent to almost caespitose, rarely pendent, having a tangled appearance, 6–8(–20) cm long; branching variable, broad and obtuse to narrowly acute, with perpendicular lateral branches not uncommon, basically isotomic dichotomous; branches uneven in thickness, knobby due to large differences in cortical thickness, usually 0.2–0.4 mm diam.; grey-green to greenish yellow, rarely yellow; medulla dense, filling medullary cavity; cortex becoming extremely thick in places, commonly up to 120 μ m and reaching 160 μ m in thickness.

True lateral spinules absent; soralia absent, or very rarely present (see discussion below). Pseudocyphellae punctiform to short fusiform, often inconspicuous, commonly raised, white, without spinules.

Apothecia not seen. Pycnidia common, usually in raised, darkened tubercles; conidia bacillariform, c. $2.0 \times 0.8 \mu$ m.

Cortex K–, C–, KC+ yellow, PD–; medulla K–, KC– or KC+ red, C–, PD–. Contains usnic acid, and sometimes alectoronic acid, plus an unknown substance which is barely visible in thin layer chromatography. The unknown is not visible in UV light and produces only a light yellow colour after development with H_2SO_4 . It has relative positions of 1, 1, 3, in the standard solvents (see C. Culberson 1972).

Ecology. On *Picea rubens*, *Abies fraseri*, and *Quercus* spp. on mountain trails and along the seashore.

Distribution. Along the Appalachian mountains (Fig. 24A). It might well be considered as a vicariad of *A. sarmentosa*, having speciated in the southern Appalachians. The two species are almost entirely allopatric.

The report of *A. fallacina* from Alaska (Krog 1968) is erroneous being based on a specimen of *A. sarmentosa*.

Discussion

This Appalachian population, very closely related to *A. sarmentosa*, is being tentatively recognized at the species level following Motyka (1960), but a study of more material may prove it to be more properly ranked as a subspecies. Its knobby, uneven appearance, sparse, punctiform pseudocyphellae, conspicuous raised pycnidial tuberculae, variable but generally very thick cortex, dense medulla, grey-green colour and tangled habit all serve to distinguish it from *A. sarmentosa*. Specimens showing all these characters most distinctly are invariably deficient in alectoronic acid (i.e., medulla KC–). Specimens which are KC+ red, including the holotype, are somewhat yellower, and their cortices are less variable and slightly thinner; the other distinguishing characters usually remain. The presence of a few soralia on a single specimen from Tennessee (Iltis & Sharp, 1942 [CANL]) is not regarded as taxonomically important.

Although the holotype is entirely KC+ red, the isotypes are either KC– (US) or a mixture of KC– and KC+ red plants (herb. Degelius).

The description of *A. fallacina* as given by Motyka (1964) agrees with our observations in most points (e.g., the irregular appearance, the presence of "swellings", the indistinct pseudocyphellae). However, Motyka surprisingly found the cortex to be exceptionally thin ("only 35 μ m thick").

Motyka (1964) compared this species with *Alectoria pellucida* Mot., a lichen first described from Bulgaria, and which Bystrek placed in *Bryopogon*. Motyka (1962) and Bystrek (1971) placed *B. pellucidus* in its own section (*Pellucidae*) within the subgenus and genus *Bryopogon*, respectively. Later, Bystrek (1974) again referred it to the genus *Alectoria*, comparing it this time with *A. stigmata* Bystr., which appears to be a morphotype of *A. sarmentosa* (see Discussion under *A. sarmentosa* subsp. *sarmentosa*). Bystrek, in the latter paper, mentioned that the soralia of *A. pellucida* are PD+ red, a very unusual characteristic for an *Alectoria* s. str. and one which persuaded

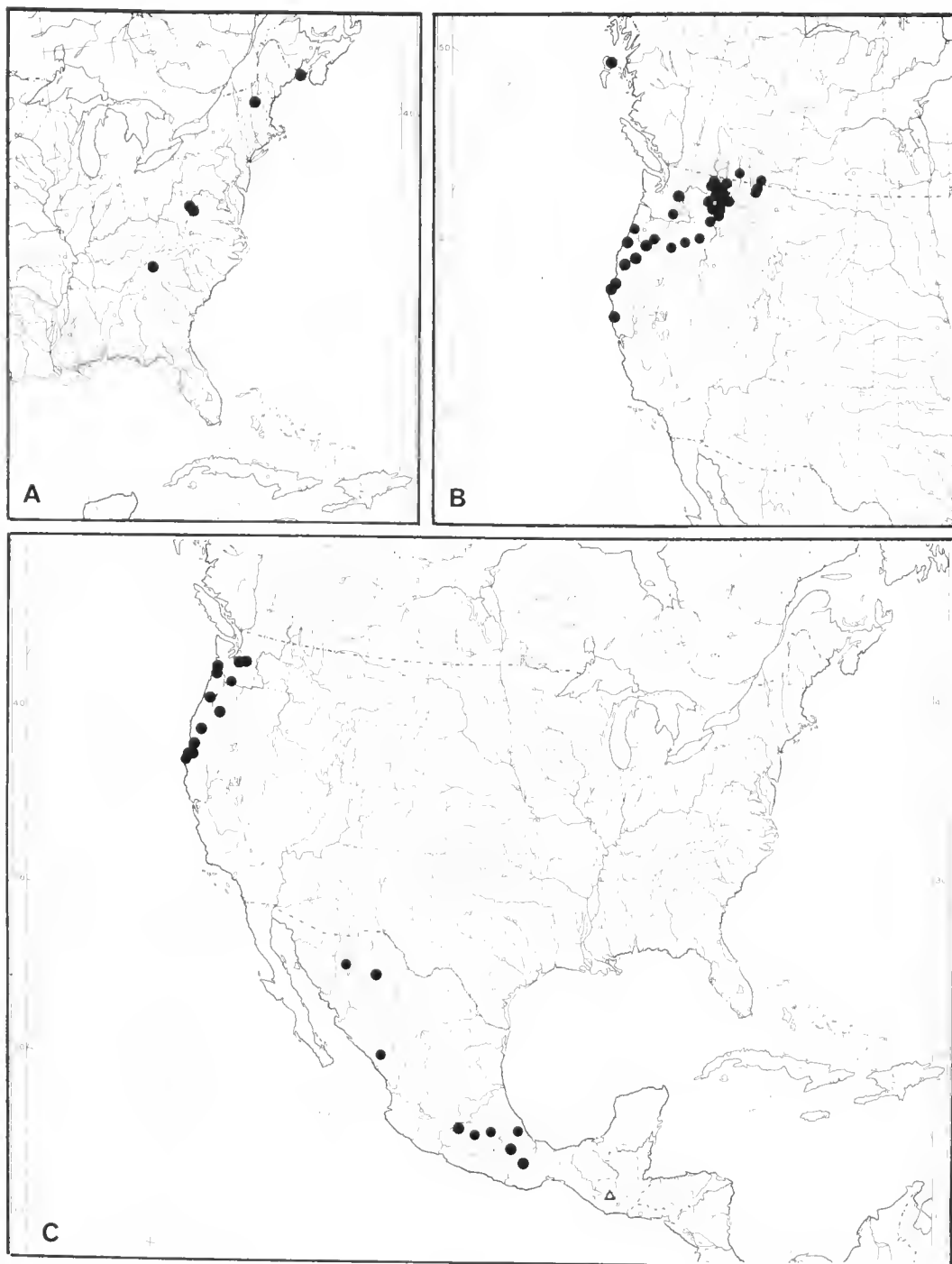


Fig. 24. A: *Alectoria fallacina*. Known distribution. – B: *A. imshaugii*. Known distribution. – C: *A. lata*. N. American distribution. Δ uncertain locality.

us to request the type from Lublin thinking that the name might refer to one of our thamnolic-containing *Alectoriae*. Bystrek very kindly sent us a Polish specimen named as *A. pellucida* (Montes Tatry, Wotoszyn Mt., ad ramos *Picea* in *Piceeto primitivo*, J. Bystrek, 12 June 1964 [LBL]), which he said was identical with the holotype of that species. This specimen is clearly a *Bryoria*, with conspicuous fissural pseudocyphellae and very sparse fissural soralia. The thallus is entirely devoid of cortical pigments leaving it pale greenish and translucent, as described by Bystrek (1971). A chemical analysis of the thallus by TLC showed it to have trace amounts of psoromic acid. Thus it would seem that at least this specimen is very close to, if not conspecific with, *Bryoria osteola*, as suggested by Hawksworth (1972 p. 250). The soralia of this thallus give a PD+ yellow rather than PD+ red reaction, as reported by Bystrek, and so the holotype should be reexamined by TLC.

Specimens

Canada. New Brunswick, Charlotte County: Grand Minan (sic) (Manan), Willey s.n., 1879 (US).

U.S.A. New Hampshire, Coos County: Mt. Washington, Burkholder 43 (CANL) – North Carolina, Swain County: Great Smoky Mountains, Mt. Kephart, Degelius s.n., 15 Sept. 1939 (DEGELIUS) – Tennessee, Sevier County: Great Smoky Mountains, Alum Cave, Degelius s.n., 13 Sept. 1939 (US, DEGELIUS) – Clingman's Dome, Degelius s.n., 12 Sept. 1939 (DEGELIUS) – Great Smoky Mountains National Park, Iltis & Sharp s.n., 16 May 1942 (CANL) – West Virginia, Randolph County: Winchester, Millsbaugh 769 (NYBG) – Locality unknown, Hale 10998 (US) – Pendleton County: Panther Knob, Hale 14386 (US).

2. *Alectoria imshaugii* Brodo & D. Hawksw., sp. nov.

Thallus caespitosus vel subpendulus, rigidulus, plerumque 5–8 cm longus; rami aniso-dichotomiter vel iso-dichotomiter fastigiati, frequentes e baso emergentes, uno loco ad substratum affixi, in angulos acutos divergentes, irregulariter compressi et angulares, diametro inaequales, 0.4–0.7 mm diam. basi; tota planta viridi-fulva vel straminea.

Rami laterales spiniformes veri et soralia desunt. Pseudocyphellae copiosae, conspicuae, albae, elongato-fusiformes, planiusculae vel convexae, amplitudine variabiles, spinulis isidiiformibus eis *Bryoria furcellatae* similibus, copiose instructae, interdum leviter sorediosae.



Fig. 25. *Alectoria imshaugii*. Holotype. Scale 0.5–1.0 mm.

Apothecia rarissima, lateral, ad circa 3 mm diam., excipulum thallinum thallo concolor et incurvatum, discus concavus, brunneus. Ascospores non visae. Pycnidia ignota.

Cortex K– vel leviter flavescens, C–, CK–, KC+ flavescens, PD–; medulla K+ flavescens vel –, C–, CK–, KC– vel rarissime rubescens, PD– vel flavescens-aurantiacus. Thallus acidum usneicum continens una cum acido thamnolico vel squamatico et duas substantias chemicas ignotas (rarissime etiam acidum alectoronicum).

Holotypus: America septentrionalis, U.S.A., Idaho, circa 4.5 mls ad boreo-occidentalem a St Joe, in summo monte St Joe Baldy, 116° 25' W et 47° 22' N, G. L. Schroeder L 1944, 19 July 1971 (CANL 38827). Fig. 25.

Thallus caespitose to subpendent, rigid, usually 5–8 cm long; branching anisotomic to isotomic dichotomous, frequent from the base, attached to the substrate at a single point, angles between the dichotomies acute, branches irregularly flattened and angular, uneven in diameter, 0.4–0.7 mm diam. at the base; greenish yellow to straw yellow throughout.

True lateral spinules and soralia absent. Pseudocyphellae abundant, conspicuous, white, elongate fusiform, plane to convex, variable in size, bearing numerous isidiiform spinules similar to those of *Bryoria furcellata*, sometimes becoming sparsely sorediate (Fig. 2B).

Apothecia very rare, lateral, to c. 3 mm diam.; excipulum thallinum concolourous with the thallus, incurved, disc concave, brown. Ascospores not seen. Pycnidia unknown.

Cortex K- or slightly yellow, C-, CK-, KC+ yellow, PD-; medulla K+ yellow or -, C-, CK-, KC- or very rarely KC+ red, PD- or PD+ yellow to orange. Contains usnic acid and two unidentified compounds together with either thamnolic or squamatic acid (plus accessory alectoronic acid in a small population in California).

Ecology. Mostly on coniferous trees (especially *Pseudotsuga* and *Pinus*) and lignum, rarely on rock; either in plateau or mountain areas (750–1750 m elevation) or close to sea level (2–85 m elevation); usually in dry, well-lighted conifer stands. On the coast it occurs in "pine barrens" of *Pinus contorta*.

Distribution. Western intermontane, centered to the east of the Columbia Plateau in eastern Washington, northern Idaho, and north-western Montana with a westward extension along the montane Ponderosa pine – Douglas fir forest zones to the mixed pine forests of central Oregon and northern California (Fig. 24B). A specimen morphologically identical to *A. imshaugii* but containing alectoronic rather than thamnolic or squamatic acid was seen from the mountains of Venezuela (Hale 43,198 [US]) and may be distinct. The disjunct specimen from the Queen Charlotte Islands (see below) is not morphologically identical to the others and may represent a distinct taxon.

Discussion

This extremely well-defined species has been recognised as distinct by some students of western North American lichens for many years (notably, H. A. Imshaug in whose honour it is named) but does not appear to have been described previously. Its characters are generally very uniform throughout its range but with two interesting exceptions. First, the species is capable of producing either thamnolic acid or its corresponding para-depside, squamatic acid; the thamnolic acid chemotype is the more frequently encountered. No morphological differences are correlated with the differences in chemistry and in many instances both chemotypes have been found to occur mixed in the same herbarium packet. We detected, however, no

thallus containing both thamnolic and squamatic acids.

Secondly, a departure from the uniform morphology is seen in a specimen of the disjunct population from the Queen Charlotte Islands (Brodo 18224 [CANL]). In this collection the spinules are rather long and scattered along the branches or arising from short raised pseudocyphellae in contradistinction to plants from its main distributional area which have rather short and clustered spinules arising from elongate and generally sorediate pseudocyphellae. It is possible that the Queen Charlotte population merits taxonomic recognition, perhaps at the rank of subspecies, but with only a single collection at hand we are reluctant to accord it any status. This specimen belongs to the thamnolic acid chemotype.

Selected specimens

Canada. British Columbia. Kootenay District: Moyie Lake Area, Schroeder L1864 (SCHROEDER) – *Alberta.* Waterton Lakes National Park, Imshaug 6088 (MSC).

U.S.A. California. Humboldt County: Manila, Brodo 20502 (CANL) – Mendocino County: 8.4 miles W of junction Hwy 1 and 101, Tavares 345A (UC) – Mendocino, Brodo 20489 (CANL) – *Idaho.* Benewah County: Plummer, Schroeder L1324 (SCHROEDER) – Bonner County: Priest River Exp. Forest, Esslinger 1157 (ESSLINGER) – Boundary County: Kaniksu National Forest, Schroeder & Anderegg L2104 (SCHROEDER) – Latah County: Moscow, Schroeder L1157 (SCHROEDER) – Shoshone County: Calder, Schroeder L1160 (SCHROEDER) – *Montana.* Glacier County: Glacier National Park, Imshaug 5966 (MSC) – *Oregon.* Douglas County: Leuthner 175 (US) – Grant County: Malheur National Forest, Schroeder & Anderegg L2102 (SCHROEDER) – Josephine County: Selma, Becking 6909108 (BECKING) – Lane County: Florence, Pike 1475 (CANL, DUKE) – Union County: Camp Elkanah, Schroeder & Anderegg L2109 (SCHROEDER) – Wheeler County: Ochoco National Forest, Schroeder & Anderegg L2111 (SCHROEDER) – *Washington.* Asotin County: Fields Spring State Park, Imshaug 16480 (MSC) – Chelan County: Wenatchee National Forest, Hoffman OP-26 (US) – Pend Oreille County: Newport, Schroeder L1065 (SCHROEDER) – Spokane County: Mt. Spokane State Park, Esslinger 2555 (ESSLINGER) – Stevens County: Colville National Forest, Schroeder L2118 (SCHROEDER) – Whitman County: Kamiak Butte, Imshaug 16444 (MSC) – Yakima County: Deadhorse Hill, Howard 982 (COLO).

Venezuela. Merida: Above La Aquada, Sierra Nevada de Merida, alt. ca. 3500 m, Hale 43,198 (US).

3. *Alectoria lata* (Tayl.) Linds.

Trans. Roy. Soc. Edinb. 22: 135 (1859). – *Cornicularia lata* Tayl., Hook. Lond. J. Bot. 6: 190 (1847); type: Mexico, ex herb. Hooker (FH holotype!). – *Bryopogon latus* (Tayl.) Müll. Arg., Flora, Jena 71: 130 (1888).

Alectoria osteina Nyl., Flora, Jena 41: 378 (1858); type: Mexique, Pic Orizaba, 10,000 ft, Galeotti 6947 (H-Nyl. 35983 holotype!). – *Alectoria ochroleuca* f. *osteina* (Nyl.) Nyl., Syn. Lich. 1: 282 (1860).

Alectoria japonica Tuck., Am. J. Arts Sci., ser. 2, 28: 202 (1859); type: Japan, Ayan, hillsides, on dead pine trees, C. Wright (FH holotype!).

Alectoria ochroleuca f. *gracilis* Kremp., Verh. Zool.-Bot. Ges. Wien 18: 314 (1868); type: Mexico, Vulcan Toluca, 10,000 ft, C. Heller 325 (M holotype! ZT isotype!).

Alectoria lata f. *subfibrillosa* Gyeln., in Sato, J. Jap. Bot. 10: 19 (1934); type: Saghalien, Sisuka, on the bark of *Larix dahurica* var. *japonica*, M. Sato 73 (not traced; no material with Prof. M. Sato and none located in BP). – *Bryopogon latus* f. *subfibrillosus* (Gyeln.) Gyeln., Feddes Repert. 38: 249 (1935).

Thallus caespitose to subpendent, occasionally prostrate and entangled, stiff, usually 5–8(–15) cm long; branching mainly isotomic dichotomous from the base, sometimes becoming anisotomic dichotomous towards the apices, angles between the dichotomies mainly acute, sometimes with short perpendicular lateral branches; branches usually somewhat angular, even to uneven in diameter, 0.5–1.5(–2.0) mm diam.; yellow to yellowish green, sometimes becoming blackened in parts, especially towards the base, so as to assume a striately blackened appearance.

True lateral spinules and soralia absent. Pseudocyphellae abundant, conspicuous, raised, elongate fusiform, white, mainly 0.5–1.0 mm long, not bearing isidiiform spinules.

Apothecia common, occasionally absent, lateral but sometimes appearing geniculate due to the death or disintegration of the branch distal to the ascocarps; excipulum thallinum concolourous with the thallus, incurved; disc concave, brown to black, 2–4(–10) mm diam. Spores 2(–24) per ascus, ellipsoid, with a hyaline epispore, becoming brown at maturity, simple 35–45 × 18–24 μm. Pycnidia not seen.

Cortex K– or sometimes K+ red, C– or sometimes C+ green-black, KC+ yellow, PD–; medulla K–, C– or slowly becoming yellow, KC+ red or –, PD–. Contains usnic and alectoronic acids, and occasionally, the K+ red unknown referred to on p. 29.

Ecology. On conifer branches, soil, and rocks, usually at high altitudes.

Distribution. Central Mexican highlands northward along the Sierra Madre Occidental, then disjunct to the Cascade range in northern California, Oregon and Washington (Fig. 24C). Having seen the luxuriant and typical growth of this species in northern California in stands of *Pinus jeffreyi* which probably resemble the montane Mexican pine forests closely, it seems probable to us that the species occurs elsewhere in the California mountains in suitable habitats. It should be noted that the range of *Pinus jeffreyi* extends without interruption into northern Baja California.

The record of this species from British Columbia (Räsänen 1933, Gyelnik 1935) was based on a fragmentary specimen in H filed under this name; it is most probably *A. sarmentosa* subsp. *vexillifera* (Hazelton, ad terram, 8–10 August 1931, V. Kujala).

Outside North America, *A. lata* is essentially a species of eastern Asia but also occurs in Central America in Guatemala (Huehuetenango, summit of Cuchumatanes Mts. above Chiantla, 3090 m, corticole, C. W. Dodge, 13 May 1941, herb. Dodge). A map of its known world distribution has been published by Hawksworth (1972 p. 242). The possible origin of such a disjunction is discussed in the general section Distribution, category 15.

Discussion

Alectoria lata is a well-defined species which may be distinguished from other yellow species of the genus by the more caespitose habit and generally abundant ascocarps. On Horse Mountain (California) this species has been seen by one of us (I.M.B.) growing with *A. sarmentosa* subsp. *sarmentosa* where their habits render them easily separable in the field.

Specimens at the northern edge of the range of the species in North America tend to be somewhat more slender than those in the central parts of its range. A sterile collection from the Queen Charlotte Islands (Graham I., Newton Point, R. Taylor 126 [COLO]) may also belong here, but it is unusually long in part.

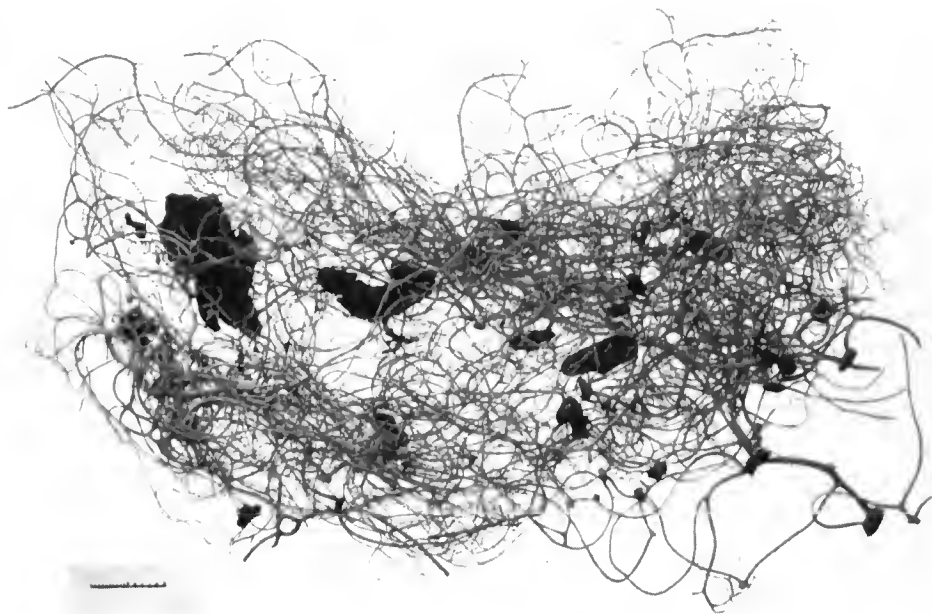


Fig. 26. *Alectoria mexicana*. Holotype. Scale 0.5–1.0 mm.

Selected specimens

Exsiccatae. Weber, Lich. Exs. 417: *California*, Humboldt County: summit of Horse Mountain, Pike & Becking (CANL).

U.S.A. California. Del Norte County: Bear Basin, Tucker 6433 (MSC) – *Oregon*. Josephine County: Selma, Becking 6908108 (BECKING) – Benton County: Corvallis, Mary's Peak, Brodo 20952 (CANL) – Clatsop County: Saddle Mtn. State Park, Pike 3817 (OSC) – *Washington*. Pacific County: South Bend, Herre s.n., 20 Aug. 1939 (F). – Pierce County: Mt. Rainier National Park, Van Trump Peak, Howard 4428 (LAM) – Skamania County: Gifford Pinchot Nat. Forest, Pechanec 1023 (COLO) – Kittitas County: Stampede Pass, Thiers 35180 (SFSU).

Mexico. Chihuahua. San Pedro Springs, Gooding s.n., Jan. 1907 (F, US) – *Durango*. El Salto, Bell s.n., June 1965 (DUKE) – *Guerrero*. Mt. Popocatepetl, Moore 4942 (US) – *Mexico*. Nevado di Toluco (sic), Pringle s.n., 25 Sept. 1892 (FH, COLO, FH:Riddle) – *Michoacan*. Tancitaro region. Leavenworth 9 (US) – *Oaxaca*. Cerro San Felipe, Beharrel s.n., 14 Aug. 1975 (CANL 55341) – *Vera Cruz*. Pic Orizaba, Galeotti 6947 (H:Nyl).

Guatemala. Sacatepéquez. Volcán de Agua, Kellerman s.n., 15 Feb. 1905 (US) – Huehuetenango,

summit of Chucumatanes Mts., C. W. Dodge s.n., 13 May 1941 (DODGE).

4. *Alectoria mexicana* Brodo & D. Hawksw., sp. nov.

Thallus subpendulus vel pendulus, 10–12(–22) cm longus; rami plerumque e baso iso-dichotomiter fastigiati, praecipue in angulos obtusos divergentes, teretiusculi vel leviter compressi et angulares, aequales vel inaequales diametro, 0.5–1.5 mm diam.: tota planta straminea.

Rami laterales spiniformes veri desunt. Soralia aliquando producta, conspicua, alba, tuberculata, latoria quam rami ex quibus orientia, ad 1–1.5 mm diam. Pseudocyphellae copiosae, conspicuae, albae, depressae vel elevatae, elongato-fusiformes vel ovales, plerumque circa 0.5–0.7 mm longae, rarissimo spinulis isidiiformibus instructae. Medulla alba, lata, ubique densa.

Apothecia vulgaria, lateraliter sed interdum apparenter geniculata, plerumque 3–4 mm diam., excipulum thallinum thallo concolor, primo incurvatum sed gradatim fere exclusum, discus planiusculus vel convexus, brunneus vel niger. Asci 2(–4)-spori. Ascospores ellipsoideae, episporio

hyalino, gradatim brunneae, simplices, $35-43.5 \times 21-27 \mu\text{m}$. Pycnidia ignota.

Cortex K-, C-, CK-, KC+ flavescens, PD-; medulla et soralia K-, C+ rubescentes, CK+ rubescentes, KC+ rubescentes, PD-. Thallus acidum usneicum et acidum olivetoricum continens.

Holotypus: Nova Hispania, provincia Oaxacae, Sierra de San Felipe, in pino, alt. 10,500 ft, C. G. Pringle 195, 3 June 1894 (CANL 16582). Isotypi: ALA, BM, COLO, DUKE, LE, MINN, MSC, NYBG, UC, WIS. Fig. 26.

Thallus subpendent to pendent, 10-12(-22) cm long; branching mainly isotomic dichotomous from the base, angles between the dichotomies mainly obtuse, branches terete to slightly flattened and angular, even to uneven in diameter, 0.5-1.5 mm diam.; straw yellow throughout.

True lateral spinules absent. Soralia rare, conspicuous when present, white, tuberculate, broader than the branches on which they arise, to 1-1.5 mm diam. Pseudocyphellae abundant, conspicuous, white, depressed to elevated, elongate-fusiform to oval, mainly c. 0.5-0.7 mm long, rarely bearing isidiiform spinules. Medulla white, thick and dense throughout.

Apothecia common, lateral but sometimes appearing geniculate (due to the death and disintegration of the branch distal to the apothecium), mainly 3-4 mm diam., excipulum thallinum concolourous with the thallus, at first incurved but tending to become excluded with age, disc plane to convex, brown to black. Asci 2(-4)-spored. Ascospores ellipsoid, with a hyaline epispore, brown at maturity, simple, $35-43.5 \times 21-27 \mu\text{m}$. Pycnidia unknown.

Cortex K-, C-, CK-, KC+ yellow, PD-; medulla and soralia K-, C+ red, CK+ red, KC+ red, PD-. Contains usnic and olivetoric acids.

Ecology. On trees at high altitudes, probably in pine forests (2850-3500 m).

Distribution. Known only from two localities in the Central American highlands (Fig. 27), and possibly limited to the high altitude pine forests.

Discussion

This previously unrecognized species, which is most closely related to *A. vancouverensis* in its chemical components, differs from that species in its habit, colour, ability to produce



Fig. 27. *Alectoria mexicana*. Known distribution.

soralia, and frequent apothecia. Soralia have only been seen in a few of the duplicates of Pringle 195 examined and so cannot be regarded as a diagnostic character for this species; they are probably of sporadic occurrence here as they are in other members of this genus. Studies of populations of this species in the field are needed before a more detailed account of its variability and affinities can be produced.

Specimens

Mexico. Oaxaca, Sierra de San Felipe, Pringle 195 (ALA, NYBG, WIS, MSC, CANL, COLO, UC, DUKE), S 21,157 (DUKE) - Cerro San Felipe, Beharrel s.n., 14 Aug. 1975 (CANL 55334, 55342, 55335).

Guatemala. Totonacapan, Santa Maria Tecum, 30 km from Totonacapan, C. W. Dodge 11551 (DODGE).

5. *Alectoria nigricans* (Ach.) Nyl.

Lich. Scand.: 71 (1861). - *Cornicularia ochroleuca* *β. nigricans* Ach., Lich. Univ.: 615 (1810); type: Lapponia (H-Ach. lectotype!).

Alectoria boryana Del., in Th. Fr., Nova Acta Reg. Soc. Sci. Upsal., Ser. 3, 3: 28 (1860) [Reprint]; type: Newfoundland, 1828, Despréaux, ex herb. Delise (BM lectotype! FH isoelectotype!); nom. inval. (Art. 34).

For further synonyms see Hawksworth (1972 p. 224). *Alectoria arctica* Elenk. & Savicz (Acta Horti Petrop. 32: 73, 1912) was tentatively placed as a

synonym of *A. nigricans* by Hawksworth (1972 p. 224) on the basis of the original description and illustration. We examined the holotype in 1975 (Novaya Zemlya, sinus Krestovaja, in terra inter alios lichenes, J. V. Palikin, 1901 [L.E]) and concluded that it is a species of *Evernia*. Its medulla is more-or-less dense throughout, and the cortex is scarcely differentiated; TLC of a fragment showed it to contain usnic and what appears to be divaric acid. We are thus in agreement with Lyngby (1928), who transferred the species into *Evernia* (as *E. arctica* (Elenk. & Savicz) Lyngby), and Llano (1951), who, because *E. arctica* is a later homonym of *E. arctica* (Hook.) Tuck. (= *Dactylina arctica* (Hook.) Nyl.), created the new name, *Evernia perfragilis* Llano, for the taxon.

Thallus erect, sometimes becoming decumbent to prostrate (in f. *subchalybeiformis* Räs.), usually 3–8 cm tall; branching anisotomic dichotomous from the base, often appearing submonopodial towards the apices; angles between the dichotomies variable but usually mainly acute; branches terete at first but becoming compressed and sometimes slightly foveolate towards the base, to 2.5 mm diam.; thallus dull, rarely shining in parts, mottled grey-fuscous to black or entirely black, often pale brown or pinkish below, discolouring herbarium paper reddish after about 10 years; dying from the base.

True lateral spinules absent. Soralia (f. *sorediata* Dahl) unknown in North America. Pseudocyphellae abundant, conspicuous, usually slightly raised, fusiform to fissural, mainly 0.5–1.0 mm long.

Apothecia infrequent (most commonly seen on corticolous specimens), lateral but sometimes appearing geniculate; excipulum thallinum thin, concolourous with the thallus, becoming excluded; disc concave at first, becoming plane and then convex with age, yellowish brown to pale reddish brown, (1.0–)1.5–4.0(–9.0) mm diam.; thecium 80–90 μ m tall. Spores 2(–4) per ascus, ellipsoid, hyaline at first but becoming reddish brown when mature, with an hyaline epispore, simple, (21–)30–39(–41) \times (12–)20–23 μ m. Pycnidia not seen.

Cortex and medulla K faintly + yellowish (rarely K + red), C + rose-red, KC + red, PD + yellowish. Contains alectoralic acid, usually traces of barbatolic acid, and sometimes an unidentified K + red (PD –) substance.

Ecology. On rocks and soil, frequently calcareous, and over ground vegetation; often also

on the low branches of spruce or fir trees. In highly exposed habitats, this lichen is often restricted to cracks and spaces between rock fragments.

Distribution. Circumpolar arctic-alpine to northern boreal, especially common in the Ungava Peninsula (Fig. 28). It is apparently rare in the Rocky Mountains, and more common in the Coast Range. *A. nigricans* has a classical bipolar distribution (see Hawksworth 1972 p. 227 for a map of its world distribution).

Discussion

The identification of this frequently abundant species generally presents few problems. Particularly dark specimens have sometimes been confused with *Bryoria chalybeiformis* or *B. nitidula* in herbaria but these can be readily separated on the basis of chemical criteria.

The frequent occurrence in the genus *Alectoria* of a K + red, C + green-black substance in the dying basal portions of the thallus has already been referred to in the general section on Chemistry. In one specimen from Southampton Island (Parker SP-70-14 [CANL]), however, the whole thallus contained this substance. The thallus of this specimen was also shiny rather than dull and more divergently branched than is usual of this species. Having seen only a single specimen of this chemotype, we have been unable to make a reliable assessment of its taxonomic importance.

Despite the very broad world distribution of this species, apothecia are only known from North American specimens. Apothecia are especially frequent in the eastern part of the species' range.

Selected specimens

Canada. *British Columbia.* Chilkat River Basin: Haines Road, mile 60, Szczawinski 1259/5 (US) – Coast District: Terrace, Ohlsson 2817 (CANL) – Fraser River Basin: Wells Gray Provincial Park, Ahti 14278 (H) – Islands North District: Moresby Island: Takakia Lake, Brodo 10967 (CANL) – Kootenay River Basin: Gold Range, Macoun 4, Aug. 1889 (CANL) – Skeena River Basin: E of Hazelton, Ohlsson 2986 (MSC) – *Alberta.* Banff National Park, Silvertip Mountain, Lamb 6444 (MSC) – *Manitoba.* Churchill, J. W. Thomson 3712 (CANL, DUKE) – *Ontario.* Kenora District: Cape Henrietta Maria, Ahti 4995 (H) – Fort

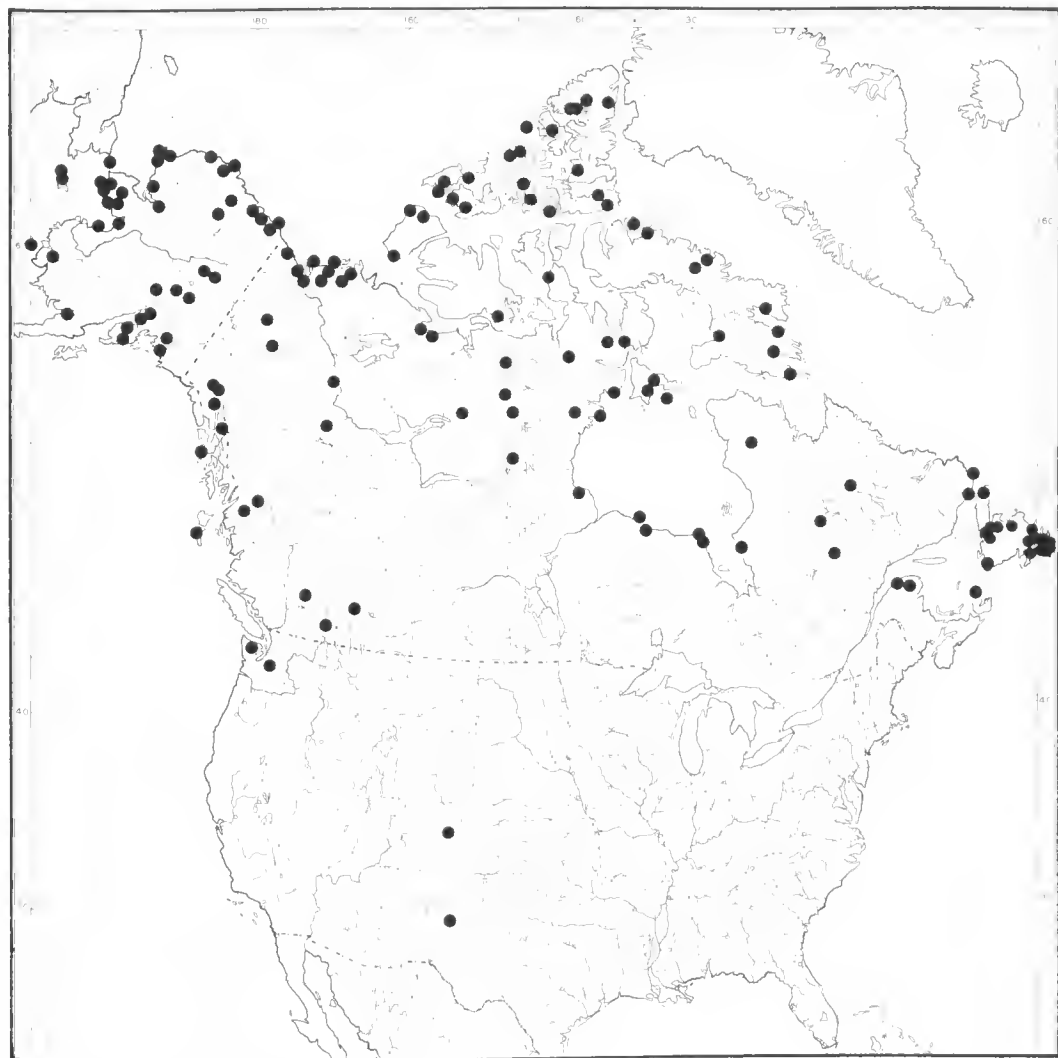


Fig. 28. *Alectoria nigricans*. N. American distribution.

Seyern, Ahti 4220 (H) – Pen Island, Kershaw s.n. (CANL 36003) – *Quebec*, Cte Gaspé-Ouest: Parc de la Gaspésie, Mont Albert, Brodo 18537 (CANL) – Territoire de la Baie de James: Goose Bay, Kucyniak & Tuomikoski 361 (CANL) – Territoire de Mistassini: Otish Mountains, Mont du Lagopède, Shchepanek 71-1.-50 (CANL) – *Nova Scotia*, Victoria County: Cape Breton Highlands National Park, Scotter 6280 (H) – *Newfoundland*, Labrador South District: Battle Harbor, Waghorn s.n., 25 Aug. 1891 (NYBG). (See also Ahti & Hawksworth 1974.) – *Yukon*, British Mountains, Trout Lake, J. W. Thomson & Larsen 14756 (p.p.) (WIS) – *Northwest Territories*,

District of Franklin: Baffin Island: Barnes Ice Cap, Hale 480 (CANL) – District of Keewatin: Coral Harbor, Southampton Island, Weber S 23,628 (CANL, COLO, NYBG) – Mackenzie District: Artillery Lake, J. W. Thomson & Larsen 11334 (WIS).

U.S.A. Alaska, Aleutian Islands: Agattu Island, Townsend 78 (US) – Unalaska, Setchell s.n., 1899, June–Aug. (FH) – Alaska Range District: Mt. McKinley National Park, Mt. Eielson, Weber & Viereck S7084 (CANL, COLO, DUKE, US, FH) – Bering Sea District: St. George Island, J. M. Macoun 38 (CANL) – St. Lawrence Island, Geist s.n., 1933 (US) – St. Paul Island, J. M. Macoun 39

(CANL) – Eastern Pacific Coast District: Mt. Juneau, Imshaug 28714 (MSC) – *Colorado*. Summit County: North Star Mountain, Weber 6531 (COLO) – *New Mexico*. Otero County: Sierra Blanca Peak, Sacramento Mountains, Egan El-1560 (MSC) – *Washington*. Clallam County: Olympic National Park, Obstruction Peak, Brodo 14409 (CANL) – *Jefferson County*: Moose Lake Trail, Imshaug 17588 (WIS) – *Pierce County*: Mt. Rainier National Park, Burroughs Mountain, Imshaug 17354 (MSC).

6. *Alectoria ochroleuca* (Hoffm.) Massal.

Sched. Crit. Lich. Ital.: 47 (1855). – *Usnea ochroleuca* Hoffm., Descr. Adumbr. Pl. Lich. 2(1): 7 (1791); type: Funck, Crypt. Gew. Ficht. no. 420 (MW-Hoffm. 8562 neotype!).

For a detailed treatment of the nomenclature of this epithet see Laundon (1970) and for further synonyms see Hawksworth (1972 p.p. 231–233).

Thallus erect, usually 5–8(–12) cm tall or, less frequently, decumbent; branching anisotomic dichotomous appearing submonopodial and of the *Cladina* type, apices often falcate and drooping; branches terete, often straight, even to uneven in diameter, sometimes becoming compressed towards the base, usually 0.5–2.0 mm diam.; yellow to yellowish green, the apices often becoming striately blackened and the blackening sometimes extending down the main stems; dying from the base.

True lateral spinules absent. Spinules rarely arising from old pseudocyphellae. Soralia absent. Pseudocyphellae abundant, conspicuous, raised, elongate fusiform to ovoid, white, mainly about 1 mm long.

Apothecia occasional, sometimes abundant, lateral, sometimes appearing geniculate; excipulum thallinum concolourous with the thallus, thick, often incurved and persistent; disc usually plane to concave, rarely becoming convex, orange-yellow to reddish brown or black, 3–6 mm diam. Spores 2(–4) per ascus, ellipsoid, with a hyaline epispore, becoming dark brown when mature, simple, (26–)28–35 (–42) × (12–)16–22(–28) μm. Pycnidia occasional, apical or subapical, minute, black and shining, to 0.15 mm diam.; conidia 7–8 × 0.8 μm.

Cortex K – (sometimes K + reddish at the base), C –, KC + yellow, PD –; medulla K –, C –, PD –, KC –, CK + yellow-orange; rarely KC + red, CK –; or very rarely KC –, CK –. Contains diffractaic or alectoronic acid, and usnic acid and sometimes an unidentified K +

reddish substance in the base. The diffractaic race (med. KC –, CK + yellow-orange) is much more widespread than the alectoronic race (KC + red, CK –). Acid deficient specimens are also known (KC –, CK –) but are extremely rare.

Ecology. On dry, or less frequently, wet tundra soil; characteristically found on or between non-calcareous or calcareous rock fragments on talus and fel-fields. It is infrequently found on the lower branches of spruce or willow in the northern subarctic region.

Distribution. Arctic to northern boreal, with scattered alpine localities in the western Canadian mountains, and in Quebec's Gaspé Peninsula (Fig. 29). It appears again in the very high Mexican ranges, the Andes of South America, and Tierra del Fuego. In view of their isolation it is interesting that the Mexican populations tend to contain alectoronic rather than diffractaic acid. The plants that we analyzed from Tierra del Fuego, on the other hand, contained diffractaic acid. *A. ochroleuca* is much more widespread in North America than is *Bryoria nitidula*, being fairly common in the northern boreal zone, especially on exposed, alpine-like ridges. In fact, it is the most widespread North American *Alectoria*. This species is widely distributed in other parts of the world as well (e.g., all the European mountain ranges, Japan, China, India, Nepal, New Zealand) although it is not very common in the British Isles (Hawksworth 1972).

Discussion

Several collections from the Mexican highlands referred to this species were unusually slender and delicate and provided a strong KC + red medullary reaction (shown to be due to alectoronic acid by TLC). It is possible that such plants belong to the taxon termed var. *variegata* (Samp.) Zahlbr. (syn. *Bryopogon guatemalensis* Gyeln.) by Hawksworth & Moore (1969). In many cases, it proved difficult to distinguish this morphotype from slender, terricolous specimens of *A. lata*. A rare alectoronic acid race with a typical morphology is also present in the American arctic (e.g., Aleutian Islands, Alaska; Churchill, Manitoba).

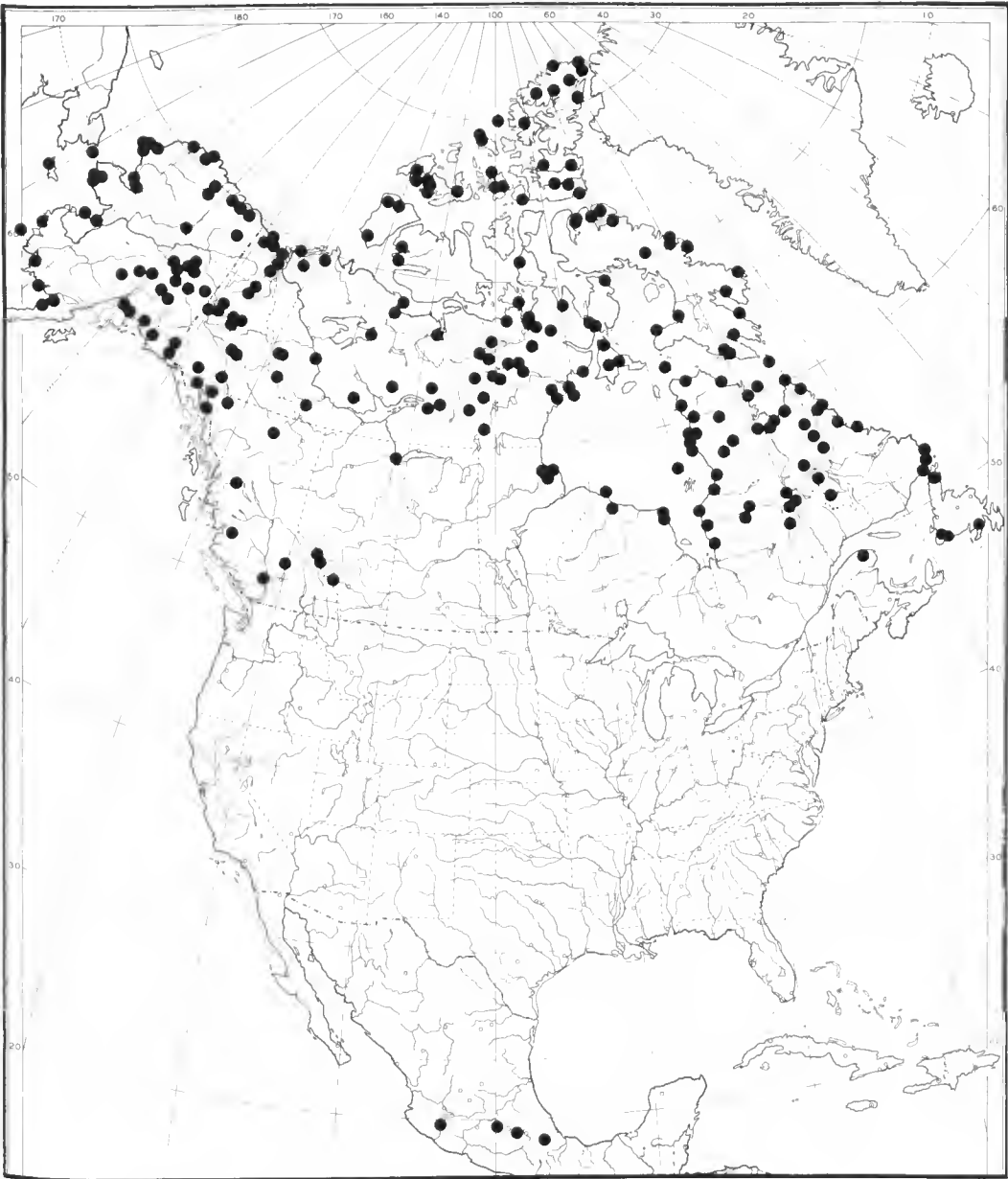


Fig. 29. *Alectoria ochroleuca*. Central and N. American distribution.

Specimens with alectoronic acid were also seen from Uruguay and Venezuela.

In general the North American material of this species contains diffractaic acid as does all European and Asian material so far examined. It can thus be distinguished from rather similar morphotypes of *A. sarmentosa* subsp. *vexillifera* lacking alectoronic acid (medulla KC-) by TLC (and also the CK+ test noted under Spot tests in the general section Chemistry).

The neotype in the Hoffmann herbarium has a typical erect habit and apparently contains only diffractaic and usnic acids as determined by TLC (although we were unable to demonstrate good diffractaic crystals in GE solution).

Motyka's (1964) reference to the occurrence of a sorediate morphotype of *A. ochroleuca* in North America (treated as "*f. sorediosa* Lynge") appears to be erroneous; Lynge's epithet belongs to *A. sarmentosa*, as pointed out by Hawksworth (1972 p. 240).

Selected specimens

Exsiccatae. Merrill, Lich. Exs. Ser. II, 106: *Alaska*, Cantwell, Palmer (ALA, BM, COLO, DUKE, F, MSC, NYBG, US, WIS) – Thomson: Lich. Arct. 59: *N.W.T.*, District of Keewatin: Rossby Lake, J. W. Thomson (CANL, COLO, DUKE, LAM, MSC) – Thomson: Lich. Arct. 90: *N.W.T.*, District of Mackenzie: Artillery Lake, J. W. Thomson & Larsen (CANL, COLO, DUKE) – Weber: Lich. Exs. 220: *N.W.T.*, District of Mackenzie: Mackenzie Mts., O'Grady Lake, Cody 16815 (BM, CANL, COLO, US).

Canada. British Columbia. Chilkat River Basin: Mile 77, Haines Road, Szczawinski 28/62 (US) – Coast District: Mt. Walker, E of Bella Coola, Ohlsson 2240 (CANL) – Fraser River Basin: Wells Gray Provincial Park, Battle Mountain, Ahti 14277 (H) – Liard River Basin: Summit pass, Alaska Highway, Szczawinski 177/1 (US) – Skeena River Basin: E of Hazelton on Nine Mile Mountain, Ohlsson 2979 (CANL) – Yukon River Basin: Altin Lake Region, Anderson 925 (MSC) – *Alberta*. Banff National Park, Snow Creek Pass, Weber S23,486 (COLO, CANL, FH, DUKE) – *Manitoba*. Fort Churchill, J. W. Thomson 3589 (CANL) – *Ontario*. Kenora District: Cape Henrietta Maria, Courtin 7 (CANL) – *Quebec*. Clé Gaspé-Nord: Mont Jacques-Cartier, Gauthier 2578 (CANL) – Territoire du Nouveau Québec: Gérin Mountain, Viereck 702 (BM, ALA, CANL, COLO, DUKE) – *Newfoundland*. St. Barbe North District: Highlands of St. John, Fernald 2271 (FH, US) – Labrador North District: Crater Lake vicinity, Gillett 8765 (CANL) – Labrador South

District: Battle Harbor, Waghorne s.n., 25 Aug. 1891 (NYBG) – *Yukon*. Stewart Plateau, Porsild 5B (CANL) – *Northwest Territories*. Mackenzie District: Vicinity of Lake-on-the-Mountain, Thieret & Reich 5910 (CANL, FH, NYBG, WIS, US) – Keewatin District: Parsons Lake, J. W. Thomson & Larsen 5933 (COLO, US) – Franklin District: Strathcona Sound, Admiralty Inlet, Soper 381 (CANL, DUKE, NYBG, US).

U.S.A. Alaska. Aleutian Islands: Amchitka Island, Reich & McCann 60 (F, CANL, WIS) – Amlia Island, Eyerdam s.n., 10 July 1932 (NYBG) – Attu Island, Hardy 14 (COLO) – Kiska Island, McCarthy & Kellas 5 (CANL) – Unalaska, Bean 3 (US) – Alaska Range District: Mt. McKinley National Park, Mt. Eielson, Weber S7061 (ALA, BM, CANL, COLO, DUKE, FH).

Mexico. Mexico. Nevado de Toluca, Kiener 30894 (WIS, MIN, COLO) – Volcan de Toluca, Iltis 3127 (WIS) – *Puebla*. Mt. Popocatepetl, Kiener 18585 (WIS, COLO, MIN) – *Vera Cruz*. Orizaba, J. G. Smith 1? (US, MIN).

7a. *Alectoria sarmentosa* (Ach.) Ach. subsp. *sarmentosa*

Lich. Univ.: 595 (1810). – *Lichen sarmentosus* Ach., K. Vet. Acad. Handl. 16: 212 (1795); type: Suecia (H-Ach., upper specimen, lectotype!).

Alectoria luteola Mont. ex de Not., Giorn. Bot. Ital. I: 206 (1846); type: Newfoundland, 1828. Depréaux, herb. Montagne ex herb. Delise (RO lectotype! FH isotype!).

Alectoria subsarmentosa Stirt., Trans. Proc. Bot. Soc. Edinb. 14: 358 (1883); type: Newfoundland, from rocks near Brigus, A. Gray, August 1878 (E holotype! BM isotype!).

Alectoria sarmentosa var. *gigantea* Räs., Ann. Missouri Bot. Gard. 20: 10 (1933); type: British Columbia, Longworth, ad corticem *Thuja occidentalis*, V. Kujala, September 1931 (H holotype! H two isotypes!).

Alectoria sarmentosa var. *hypocyphellata* Gyeñl., Ann. Mus. Nat. Hung. 28: 283 (1934); type: Oregon, Crater Lake, on limbs [of trees], F. P. Sipe 680, August 1930, (ORE lectotype!); nom. inval. (Art. 32). – *Eualectoria sarmentosa* var. *hypocyphellata* Gyeñl., Ann. Mus. Nat. Hung. 28: 283 (1934); nom. inval. (Arts. 32, 34).

Alectoria sarmentosa var. *alaskana* Mot., in Krog, Norsk Polarinst. Skr. 144: 138 (1968); type: Alaska, Eastern Pacific Coast District, Sitka, Harbour Mt., H. Krog 6255, 31 August 1957 (O lectotype!); nom. inval. (Arts. 32, 36, 37).

Alectoria sarmentosa var. *brevior* Mot., in Krog, Norsk Polarinst. Skr. 144: 139 (1968); type: Alaska, Eastern Pacific Coast District, Ketchikan, Deer Mt., H. Krog 6263, 3 September 1957 (O lectotype!); nom. inval. (Arts. 32, 36, 37).

Alectoria sarmentosa var. *macra* Mot., in Krog, Norsk Polarinst. Skr. 144: 139 (1968); type: Alaska, Eastern Pacific Coast District, Juneau, Loops Road,

H. Krog 5565, 24 August 1957 (O lectotype!); nom. inval. (Arts. 32, 36, 37).

Alectoria stigmata Bystr., Frag. Flor. Geobot. 22: 255 (1973); type: Alaska, Central Pacific Coast District, Kenai Peninsula, Creek Ridge, H. Krog s.n., 28 May 1957 (LBL holotype!).

For further synonyms see Hawksworth (1972 p.p. 238–239).

Thallus pendent, flaccid except at the base, commonly 20–40 cm long, exceptionally to 80 cm; branching mainly isotomic dichotomous, frequent from the base, angles between the dichotomies variable, acute or obtuse, often rounded; branches terete often becoming compressed and angular to foveolate towards the base and at the axils, 0.5–2.0(–2.5) mm diam.; greenish grey to bright golden yellow, sometimes becoming striately blackened in parts; base of the thallus persistent.

Lateral spinules absent. Soralia irregularly tuberculate, rare in North American material (see Discussion). Pseudocyphellae abundant, conspicuous, raised, elongate fusiform to ovoid and tuberculate, clearly delimited, white, usually c. 1 mm long.

Apothecia often abundant (especially in the west), lateral; excipulum thallinum concolourous with the thallus, usually persistent; disc orange-yellow to dark brown or black, 2–3(–5) mm diam. Spores 2–3(–4) per ascus, ellipsoid, with a hyaline epispore, becoming dark brown at maturity, simple, 23–35(–48) × (12–)15–20(–25) μ m. Pycnidia sometimes frequent, mainly apical, to c. 2.0 mm diam., black and shining; conidia not seen.

Cortex K–, C–, KC+ yellow, PD– (sometimes K+ red, C+ green-black near the base); medulla K– (rarely K+ yellow), C– or slowly becoming yellow, KC+ red or –, CK–, PD– (rarely PD+ yellow). Contains usnic acid, \pm alectoronic acid, rarely thamnolic, [squamic,] or barbatic acids, and occasionally an unidentified K+ red, C+ green-black substance.

Ecology. On a variety of trees, but especially conifers, in *Picea-Tsuga heterophylla* forests. Most collections are from *Picea* (especially *P. sitchensis*), *Tsuga heterophylla*, *Abies* spp., *Pseudotsuga menziesii*, and *Pinus contorta*. Rarely, collections are made from the ground or rocks. The species grows most luxuriantly along the edges, or in glades, of the tall, moist, lowland forests along the west coast.

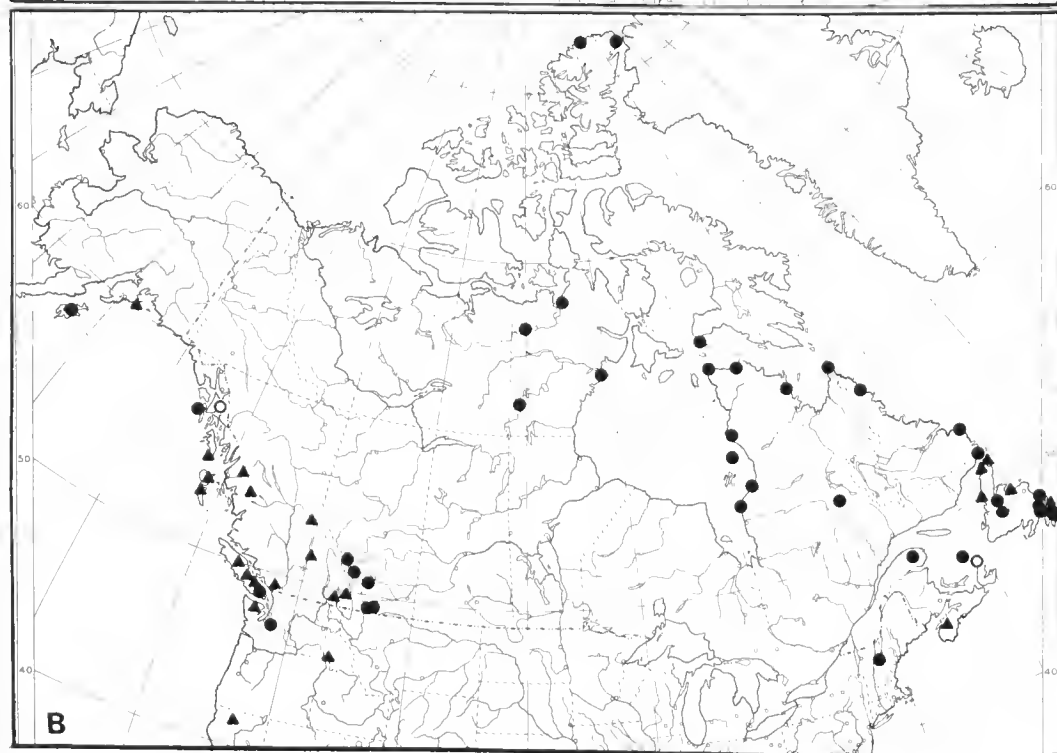
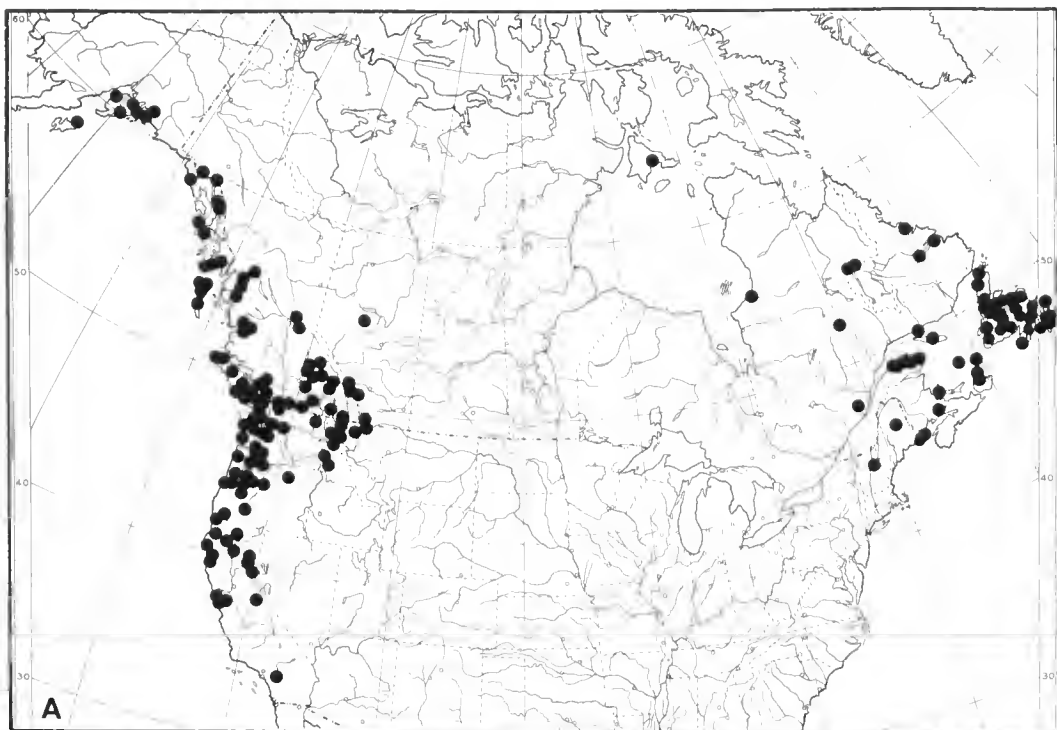
In Wells Gray Park, British Columbia, *A. sarmentosa* was found to be largely confined to lower tree branches within 30 feet of the ground, apparently requiring more moderate levels of light, moisture, and temperature than the brown species (Edwards et al. 1960).

Distribution. Mainly along the west and east coasts in humid coniferous forests (Fig. 30). Its close association with the more mesic western hemlock forests both along the coast and in the Rocky and Selkirk Mountains, avoiding the drier inter-montane regions, is apparent in the distribution map. Ahti (1964) suggests that, rather than lower humidity, the colder winters of the interior (e.g., northern Ontario) may be a critical factor in largely restricting it to the coasts. In the Appalachian mountains, *A. sarmentosa* is replaced by its vicariad, *A. fallacina*. The arctic localities may be based on unusually slender forms of subsp. *vexillifera*; the two taxa intergrade to some extent (see Discussion under the latter).

The alectoronic acid-deficient race can be found scattered throughout the range of the species and appears to be of no taxonomic importance, although its particularly high frequency in Newfoundland should be noted (Ahti & Hawksworth 1974). The world distribution of this circumboreal species has been mapped by Hawksworth (1972 p. 242). Poelt (1969) reports that it is common in the boreal and subalpine forests in mountainous regions of northern, southern and central Europe. Although *A. lata* appears to replace *A. sarmentosa* in Japan (loc. cit.) the two species grow side by side in the montane Jeffrey pine forests of northern California.

Discussion

Specimens of this subspecies containing abundant quantities of thamnolic acid in addition to alectoronic acid, were seen from California. These specimens were often robust, having a dense medulla very much like that of *A. vancouverensis*. Less robust specimens with small amounts of thamnolic acid were also seen from this area and from the Queen Charlotte Islands. We regard these collections as representing only a chemical race of *A. sarmentosa*, although further collecting and



more careful study may result in a reevaluation of their taxonomy.

A reading of the descriptions of *A. imshaugii*, *A. vancoverensis*, and *A. sarmentosa* will reveal the immense complexity of the morphological and chemical variation in this species group, especially along the west coast, and in particular, in California. No explanation for this complexity can be offered at this time. One simply must accept the fact that the variation exists and hope that closer attention to the *Alectoriae* of California will clarify the situation.

While the distinctiveness of these three taxa, at some taxonomic level, can hardly be questioned, one must grapple with the undeniable fact that clear morphological and chemical intermediates exist between all possible combinations of them. There is even one excellent specimen (Tavares 371) which combines the chemical characters and many of the morphological features of all three taxa (see also Discussion under *A. vancoverensis*). If one may put aside for the moment the possibility that the variation might be produced by environmental factors (since no obvious ecological or distributional correlations were apparent), one is left with two possible explanations: (a) the enzyme systems leading to the production of lichen substances in the genus *Alectoria* are somewhat plastic, and that a certain amount of variation should be expected in all the taxa, and (b) that some sort of genetic recombination or "hybridization" is occurring among the taxa.

If we were dealing with possibility "a", we would expect a certain amount of chemical variation in plants showing little or no morphological intermediacy. Such might be the case for the many "typical" *A. sarmentosa* specimens found to contain traces or large amounts of thamnolic acid in addition to alectoronic acid. It should be noted that these thamnolic-alectoronic-containing *A. sarmentosa* plants can be found over a very large range: from the Queen Charlotte Islands to central California. As stated previously (see p. 28), the

ability for squamatic acid production has been well-documented in *A. sarmentosa* (although not the North American specimens). The occasional appearance of the corresponding meta-depside, thamnolic acid, would therefore not be altogether surprising and probably has nothing to do with the presence of this substance in *A. imshaugii*.

On the other hand, the very complex combination of chemical and morphological characters, especially in central and northern California where all three taxa converge in the same forests, can best be explained by postulating some kind of genetic exchanges (i.e., possibility "b"). The genetic exchanges may be occurring through sexual mechanisms as species in the genus *Alectoria* are frequently fertile. Kristinsson (1969) suggested such an explanation for the morphological and chemical variation in *Cetraria islandica* s. lat. in Iceland. In that case, one is dealing with a simpler system: the presence or absence of a single chemical substance and correlating morphological features. Even in the absence of sexual reproductive bodies, however, it is possible to have genetic exchange in certain non-lichenized fungi by parasexual mechanisms such as somatic heterokaryon formation. It may be that under environmental stress, there is more of a tendency for such a phenomenon to occur.

Perhaps it is significant that northern California is close to the distributional limits for all three *Alectoria* species while at the same time, they grow close together.

A true heterokaryon, moreover, although haploid, might produce a phenotypic expression of both parents, acting almost like a heterozygotic diploid. Thus, while an exchange of characters might best be explained by sexual reproduction and crossing-over, the addition of certain chemical or morphological characters might suggest heterokaryosis. C. Culbertson & Hale (1973) found that they could account for the occurrence of compounds in addition to the compounds found in one parental species by postulating a hybridization which involved

Fig. 30. N. American distribution. — A: *Alectoria sarmentosa* subsp. *sarmentosa*, KC + red chemotype. — B: ▲ *A. sarmentosa* subsp. *sarmentosa*, KC— chemotype. ● *A. sarmentosa* subsp. *vexillifera*. ○ *A. sarmentosa*, sorediate morphotype.

a partial exchange of enzyme systems such that new compounds were formed. It would be extremely interesting to see a detailed analysis of the chemical, morphological, and geographical correlations of this complex similar to that of Culberson & Hale for *Parmelia* sect. *Hypotrachyna*.

There is, however, another possible mechanism for the addition of chemical constituents. Henssen & Jahns (1973 p. 221) recently suggested the possibility that two closely related mycobionts might grow together and form a single lichen thallus, sharing the phycobiont. Presumably, such a chimera would produce the chemical products of both mycobiont races. This is an attractive hypothesis and deserves considerable attention. As discussed in the section Taxonomic concepts: Species, any possible role of the phycobiont is difficult to assess at the present time.

How to deal with this variation taxonomically is another problem. Kristinsson (1969) concluded, in agreement with Imshaug (1957), that perhaps using the rank of subspecies for *C. ericetorum* was the most realistic solution to the *C. islandica* problem. We decided, however, to regard *A. vancouverensis*, *A. imshaugii*, and *A. sarmentosa* all as equivalent species, at least for the present. *A. vancouverensis* maintains its distinctiveness more than 90% of the time even in areas where it grows very closely associated with *A. sarmentosa*: in the field, we have had no difficulty in distinguishing one from another. *A. imshaugii* has such a remarkably distinct morphology it would be clearly incorrect to consider it merely as a subspecies. At first we were tempted to recognize the Tavares specimen (see Discussion under *A. vancouverensis*) as nomenclaturally distinct, but, in the final analysis, we decided to consider it as just another strange variation of *A. vancouverensis*.

The variability in the morphology of *A. sarmentosa* has led to the recognition of numerous infraspecific taxa by Motyka (in Krog 1968). We have examined Krog's collections studied by Motyka and feel these are of little or no taxonomic importance since intergradations between all of them occur. Motyka's names are typified here by the packets which he annotated "*typus varietas*", etc. Two collections (Krog 2212 and 6255) were labelled

as the type of var. *alaskana* by Motyka; the latter is designated as lectotype here as it is larger and better developed.

Alectoria stigmata Bystr. is another species based on one of Krog's specimens from Alaska which we feel should be placed into synonymy with *A. sarmentosa* subsp. *sarmentosa*. The holotype, a portion of which was generously sent to us by Dr. Bystrek, appears to be a broadly pseudocyphellate morphotype; it contains usnic and alectronic acids.

An abundantly sorediate morphotype of this species, var. *sorediosa* (Lång ex Räs.) DR. (see Hawksworth 1972 p. 240), occurs rarely in North America (Fig. 30 B) as it does in Europe (Ahlner 1948). It seems to be of relatively minor taxonomic importance.

Selected specimens (KC +, C -)

Exsiccatae. Brodo: Lich. Can. Exs. 1: *British Columbia*, S of Princeton, Brodo 8508 (CANL) - Hale: Lich. Amer. Exs. 126: *Oregon*, Lane County: Willamette National Forests, Shushan sl-1876 (CANL, WIS) - Lojka: Lich. Univers. 218: *Insula Miquelon*, Delamare (H) - Merrill: Lich. Exs., Ser. I, 13: *Idaho*, (no locality mentioned), Tower 1902 (BM [KC-], CANL, DUKE, NYBG, US) - Rel. Tuck. 4: *Oregon* (no locality), E. Hall (DUKE, F, FH, LAM, NYBG) - Univ. California: Lich. Oregon 1126: *Oregon*, Linn County: Tombstone Pass, Tavares & Chisaki 125 (BM, COLO, DUKE, F, MSC, US) - Weber: Lich. Exs. 132: *California*, Humboldt County: Hoopa, Weber (CANL, COLO, DUKE, US).

Canada. *British Columbia*. Coastal District: Burke Channel in Crayden Bay, Ohlsson 2034 (MSC, CANL) - Columbia River Basin: Revelstoke, Shaw 851 (NYBG, US), Deen River Basin: Tweedsmuir Provincial Park, Ohlsson 2207 (CANL) - Fraser River Basin: Blue River, Brodo 15792 (CANL) - Islands North District: Graham Island: Boulton Lake, Brodo 9954 (CANL) - Islands South District: Tofino, Ohlsson 1080-A (MSC) - Kootenay River Basin: Glacier National Park, Ohlsson 310 (MSC) - Okanagan District: Rock Creek, Brodo 15127 (CANL) - Skagit River Basin: Manning Provincial Park, Bird 15417 (CANL) - Skeena River Basin: W of New Hazelton, Ohlsson 2893A (CANL) - *Alberta*. Oldman River Watershed, Waterton Lakes National Park, Bird 16925 (CANL) - *Quebec*. Cte Gaspé-Nord: Mont Albert Nord, Gauthier 2640 (CANL) - Parc des Laurentides: Junction of Highway 54A and 54B, Scotter 6872B (H) - Territoire de Mistassini: Otish Mountains on Mont du Lagopède, Shehepanek 71-L-17 (CANL) - Territoire du Nouveau Québec: Poste-de-la-Baleine, Brisson & Forest 20485 (CANL) - Schefferville, Brodo 9239 (CANL) - *New Brunswick*. Albert County: Fundy National Park, Ireland 10979B (CANL) - Charlotte County: Campobello, collector unknown, July 1902 (FH) -

Nova Scotia. Inverness County: French Mountain, Brodo 19002 (CANL) – Victoria County: St. Paul Island, Erskine 53C2402 (CANL) – *Prince Edward Island*. Prince County: Richmond, Ireland 10297D (CANL) – *Newfoundland*. Labrador North District: Goose Bay, Judd GB-52 (CANL) – Labrador South District: Backway, Tanner s.n., 5 July 1937 (H). (See also Ahti & Hawksworth 1974.) – *Northwest Territories*. District of Keewatin: Coral Harbor, Southampton Island, Brown 33 (CANL).

U.S.A. Alaska. Aleutian Islands: Nazan Bay, Atka, Van Dyke 232 (FH) – Amchitka Island, Reich 201 (CANL) – Salteny Cove, US Bureau Soils Kelps Expedition s.n. (F) – Eastern Pacific Coast District: Juneau, Auke Lake, Imshaug 28505 (MSC) – Central Pacific Coast District: Evans Island, Port San Juan, Eyerdam 560 (LAM, ALA) – *California*. Humboldt County: Horse Mountain, Brodo 20515 (CANL) – San Bernardino County: San Bernardino Mountains, Arrowhead Lake, Bonnie & Templeton s.n., 29 Dec. 1929 (LAM) – Siskiyou County: Sissou, region of the Upper Sacramento, Howe 139 (NYBG) – *Colorado*. County unknown: Austin s.n., no date (FH) – *Idaho*. Idaho County: Selway Falls, Selway River, Imshaug 16408 (CANL, MSC) – *Maine*. Washington County: Head Harbor, Norton s.n., 3 May 1921 (FH) – *Piscataquis County*: Mt. Katahdin, Degelius s.n., 31 Aug. 1939 (DEGELIUS) – *Montana*. Glacier County: Avaleneh Lake, Glacier National Park, Mains 6036 (FH) – *Nevada*. Humboldt County: Paradise Valley, Britton s.n., 10 Aug. 1904 (FH) – *New Hampshire*. Coos County: Mt. Washington, Merrill s.n., Sept. 1904 (CANL, FH) – *Oregon*. Deschutes County: Doris Lake in the Deschutes National Forest, Pike L-390 (OSC) – *Washington*. Clallam County: Hurricane Ridge, Olympic National Park, Brodo 13213 (CANL).

Selected specimens (KC–)

Canada. British Columbia. Columbia River Basin: Selkirk Mountains near Emerald Lake, Petersen 65 (NYBG) – Dean River Basin: Young Creek, Tweedsmuir Provincial Park, Ohlsson 1899 (MSC) – Fraser River Basin: Wells Gray Provincial Park, Battle Mountain, Ahti 6529 (H) – Islands North District: Graham Island: Dinan Bay, Brodo 18387 (CANL) – Islands South District: Vancouver Island: Mount Arrowsmith, Shchepanek 312A (CANL) – Kootenay District: East Kootenay (sic) (Kootenay), from Fort Colville to Rocky Mountains, Lyall s.n., 1861 (FH) – Skeena River Basin: Dorren (sic) (Dorreen), Kujala s.n., Aug. 1931 (H) – *Nova Scotia*. Annapolis County: Albany Crossing, Darrow s.n., 30 Aug. 1959 (LAM) – *Newfoundland*. Lewisporte District: Notre Dame Bay, Pyke Island, Riewe P-50 (CANL, ALA).

U.S.A. Alaska. Eastern Pacific Coast District: Dall Island, Augustine Bay, Foster s.n., 7 July 1913 (LAM) – Central Pacific Coast District: Evans Island, Prince William Sound, Eyerdam 560 (F) – *California*. County unknown: Sacramento Canyon, near Sima, Sisson (collector? or "Sissou", locality in Siskiyou County), July 1902 (F) – *Idaho*. Idaho

County: Selway Falls, Imshaug 16408 (CANL) – *Oregon*. County unknown: Cascade Mountains, Hogg Pass, Britton s.n., 19 June 1952 (LAM) – *Washington*. Clallam County: Olympic National Park, Hurricane Trail, Herre 5171 (F).

Specimens (sorediate morphotype)

Canada. Nova Scotia. Victoria county: Cape Breton Highlands National Park, Scotter 6212B (H).

U.S.A. Alaska. Eastern Pacific Coast District: Windham Bay, Culbertson 118 (F, FH) – Aleutian Islands: Amlia Island, Eyerdam s.n., 10 July 1932 (FH).

7b. *Alectoria sarmentosa* subsp. *vexillifera*

(Nyl.) D. Hawksw.

Taxon 19: 241 (1970). – *Alectoria ochroleuca* [subsp.] *vexillifera* Nyl., in Kihlman, Medd. Soc. Fauna Fl. Fenn. 18: 48 (1891); type: U.S.S.R., Murmansk District, Lapponia ponojensis, ad promontorium Orlov, in apertis glareosis, A. O. Kihlman, 15 May 1889 (H-Nyl. 35997 holotype! ZT isotype!).

For further synonyms see Hawksworth (1972 p. 243).

Plants differing from subsp. *sarmentosa* in having prostrate thalli to 8–15 cm long which are rigid, more sparsely branched; branching becoming anisotomic dichotomous towards the base, main stems becoming dorsiventrally compressed, expanded, and foveolate, sometimes with spinulose side branches, usually 2–4(–40) mm wide (Fig. 31); basal parts dying, attached to the surrounding vegetation or substrates by hapteres.

Apothecia very rare (see Discussion).

Chemical reactions and components as in subsp. *sarmentosa* but thamnolic acid is always absent.

Ecology. On well-drained rocky or gravelly soil at various pH levels; rarely on peaty soils; usually on rocky ridges or mounds; high alpine (2150–2800 m) in the Rocky Mountains to sea level in the arctic. However, one coastal rock outcrop on Vancouver Island had what appears to be this subspecies.

Distribution. Eastern Canadian arctic, Aleutian Islands, and the Canadian Rocky Mountains, with scattered high alpine localities along the west coast, and in the White, Shickshock and Otish Mountains of the east (Fig. 30B). The strikingly dissected distribution of this

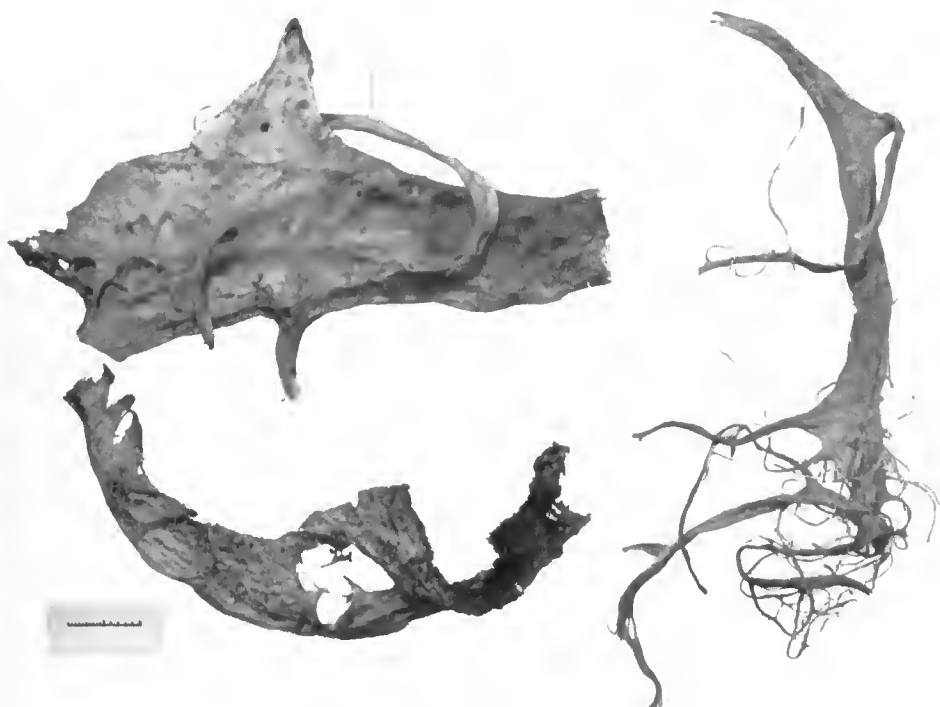


Fig. 31. *Alectoria sarmentosa* subsp. *vexillifera*. An unusually broad specimen. Quebec, Iles Doremeuses, Payette s.n. (CANL). Scale 0.5–1.0 mm.

subspecies requires some comment. *A. sarmentosa* subsp. *vexillifera* is a common plant in southwest Greenland, the mountains of Scandinavia, and the Scottish highlands (Dahl 1950, Hawksworth 1972), but is virtually absent from eastern Greenland (Dahl et al. 1937) and is very uncommon in the central European mountains (Poelt 1969). It is apparently absent from Asia and the Southern Hemisphere (Hawksworth 1972). Such a distribution pattern probably had its origin as a pre-glacial, continuous, amphi-atlantic distribution dissected during the Pleistocene. Remnant populations could then have radiated from coastal refugia (as in Greenland) and from refugia south or north of the ice sheets as evidenced, for example, by the isolated localities in northern Ellesmere Island (see the comments of Dahl 1950). The eastern population corresponds almost exactly with Porsild's (1958) "Amphi-atlantic southern element" matching the distribution of the willow *Salix herbacea* very closely.

The western localities also suggest a pushing of the population southward during the Ice Age with limited subsequent reinvasion northward. The persistence of the subspecies in the Aleutians and coastal mountains almost certainly is due to the presence of coastal refugia along the headlands and fiords (see Calder & Taylor 1968). The entire absence of the subspecies from the northwestern arctic despite the many well-documented refugia of that area, together with its absence from Asia, would argue strongly against its ever having had an amphi-Beringian distribution.

The distinctive distribution of *A. sarmentosa* subsp. *vexillifera* is good evidence for its genetic basis.

Discussion

The present taxon has been treated by recent authors as a variety (James 1965), a subspecies

(Hawksworth 1970, 1972, 1973), and a species (Krog 1968); Motyka (1964) regarded it as having no taxonomic importance. The situation here is certainly complex since while transitional morphotypes can be found at least in parts of Europe (Hawksworth 1973) and Newfoundland (Ahti & Hawksworth 1974), they appear to be absent in subarctic regions. Indeed a comparison of the distribution of *vexillifera*-morphotypes with that of *sarmentosa*-morphotypes lends considerable support to the distinctness of the two taxa (see above). The changes in thallus morphology seen in this subspecies are clearly adaptive in serving to present the maximum thallus area to the incident sunlight when growing with a prostrate habit, but it seems difficult to determine with any high degree of certainty that this is always genotypic in origin rather than phenotypic. In North America particularly, the two taxa are generally well defined and only very exceptionally show any tendency to intergrade. These exceptions might be due to (a) gene exchange taking place where the morphotypes are sympatric thus producing large series of intermediates, or (b) *sarmentosa*-genotypes exhibiting phenotypic convergence with *vexillifera*-genotypes, thus forming thalli morphologically similar to them. In the absence of transplant experiments it is not possible to say which of these explanations is the more nearly correct, but the evidence currently available tends to support the thesis of two genetically distinct populations occasionally intergrading where they are sympatric. As these populations have different distributional tendencies, the rank of subspecies appears to be the most appropriate at the present time.

As pointed out by Hawksworth (1973), a number of other Alectorioid species occasionally produce *vexillifera*-like morphotypes although in all but a few cases (e.g., *A. ochroleuca* var. *ecuadorensis* Zahlbr., *Sulcaria virens* var. *forrestii* (D. Hawksw.) D. Hawksw.) the degree of flattening and expansion is much less than is seen in subsp. *vexillifera*.

Apothecia are exceedingly rare in subsp. *vexillifera* and have been noted only in a single North American collection (Newfoundland, Despreaux, 1828 [FH]) which was given an herbarium name by Delise. In contrast, subsp. *sarmentosa* is frequently found fertile

and some populations have numerous apothecia on individual thalli.

Selected specimens

Canada, British Columbia. Flat-Head River Basin: Flat-Head Provincial Forest, NW of Mt. Rowe, Bird & Lakusta 17257 (UAC) – Islands South District: Vancouver Island: Victoria, Ahti 15134 (H) – *Alberta.* Waterton Lakes National Park, Bird & Lakusta 16751 (CANL, US, UAC) – *Quebec.* Cte Gaspé-Ouest: Mt. Albert, Collins 2656 (US) – Cte Iles-de-la-Madeleine: Grande Entrée, Le Gallo 2999 (US) – Territoire du Nouveau Quebec: 53°20'N, 69°54'W, Guimont QFB-E 4446 (CANL) – Deception Bay, Eskimo Hill, Gardner 281 (WIS) – Iles Dorneuses, Payette s.n., Aug. 1970 (CANL) – *Newfoundland.* Labrador North District: Hebron, Oldenburg 30A (WIS). (See also Ahti & Hawksworth 1974) – *Northwest Territories.* Franklin District: Diggs (sic) (Digges) Island, Hudson Strait, Bell 342 (CANL, FH) – Ellesmere Island, 82°24'–32'N, 62°00'–32'W, Schuster 35523 (CANL) – Keewatin District: Dubawnt Lake, J. W. Thomson, Larsen & Foote 14395 (WIS).

U.S.A. Alaska. Aleutian Islands: Amchitka Island, Reich 111 (CANL, F) – Attu Island, Van Schaack 293 (US) – Oumak (sic) (Umak Island), Stevenson s.n., 24 Nov. 1920 (US) – Unalaska Island, Eyerdam s.n., 24 May 1932 (ALA, FH, LAM) – Eastern Pacific Coast District: Sitka, Harbour Mountain, Krog 6265 (O) – Western Pacific Coast District: Kodiak Island (sic) (Kodiak Island), Trelease s.n., 2 July 1899 (US) – *New Hampshire.* Pierce County: Mt. Rainier National Park, Burroughs Mt., Imshaug 17371 (US).

8. *Alectoria vancouverensis* (Gyeln.) Gyeln. ex Brodo & D. Hawksw., comb. nov.

Bryopogon vancouverensis Gyeln., Feddes Repert. 38: 245 (1935); type: Canada, Vancouver Island, J. Macoun, 22 July 1897 (UPS holotype!); basionym. – *Alectoria vancouverensis* Gyeln., Feddes Repert. 38: 245 (1935); nom. inval. (Art. 34).

Thallus pendent, commonly 15–20 cm, but sometimes to 1–2 m long (Pike in litt.); branching mainly isotomic dichotomous, angles between the dichotomies mainly acute; branches very uneven in diameter, often flattened (especially at the axils) and becoming very twisted and foveolate, 0.4–0.9 mm diam.; straw-yellow to yellowish green or greyish green, usually concolourous.

Medulla compact and dense.

True lateral spinules and soralia absent. Pseudocypellae abundant, conspicuous, mostly raised, often elongate fusiform and twisting around the branches to give them a conspicuous

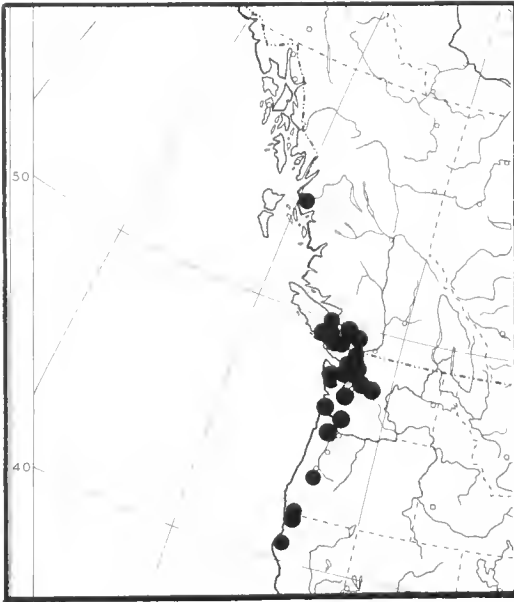


Fig. 32. *Alectoria vancoverensis*. Known distribution.

striped appearance, sometimes confluent, white, rarely with spinules arising from them.

Apothecia not uncommon, lateral, to 2.6 mm diam.; excipulum thallinum concolourous with the thallus, persistent, incurved; discs concave, dark brown to black. Spores 2–4 per ascus, ellipsoid, with a hyaline epispore, becoming brown at maturity, simple, $23\text{--}35 \times 16\text{--}23 \mu\text{m}$. Pycnidia not seen.

Cortex K–, C–, KC+ yellow, PD–; medulla K–, C+ red or rarely C–, KC+ red, PD–. Contains olivetoric and usnic acids and some unidentified accessory substances; rarely contains alectoronic acid or barbatic acid in addition to, or instead of, olivetoric acid.

Ecology. On well-lighted tree limbs, especially *Pseudotsuga menziesii* and *Tsuga heterophylla*, from an elevation of 30 to 1000 m along the coast, particularly in humid zones.

Distribution. West coast, lowland, mainly from southern British Columbia to northern California (Fig. 32). Its centre of distribution appears to be the moderately humid to dry *Pseudotsuga*–*Quercus* forests in the southern

Vancouver Island and northern Washington region corresponding to a “dry summer, subtropical or mediterranean” climate (“Csb”, of Köppen’s classification; Atlas of Canada 1958 map 30), although it was found in some localities in the very moist coastal *Thuja*–*Tsuga* forests as well.

Alectoria vancoverensis is endemic to North America.

Discussion

This species closely resembles *A. sarmentosa* in several respects, but differs from the latter in chemistry, thallus anatomy, colour and size. Rare specimens can be found which are morphologically more like *A. sarmentosa* s. str. (i.e., with even, straw-coloured branches having a more-or-less lax medulla). Specimens also occur which appear to be *A. vancoverensis* due to a dense medulla and twisted branches, but which have alectoronic rather than olivetoric acid.

We saw two very odd chemotypes from California. In addition to alectoronic acid, one contained abundant thamnolic acid and the other contained barbatic acid. We named these specimens *A. vancoverensis* on morphological grounds, and because other specimens of *A. vancoverensis* exist which have olivetoric-barbatic, olivetoric-alectoronic, and olivetoric-thamnolic combinations, giving one the impression that the chemistry is more plastic than one would expect.

The vast majority of specimens, however, are easily separated on chemical as well as morphological grounds. In the field the species is usually easily spotted as being distinct from *A. sarmentosa*.

Two rather odd forms are worth mentioning. A small caespitose and strigose specimen in FH collected by John Macoun in June 1915 “on old fences” was given a herbarium name by G. K. Merrill but the name was apparently never published. Its medulla was very dense and C+ red and we are regarding it as an aberrant form of *A. vancoverensis*.

A specimen which presented us with a more serious problem was Tavares 371 collected in Humboldt Co., California. This robust specimen was so clearly intermediate between *A. vancoverensis* and *A. imshaugii* that for a long

time we considered naming it as new. The discussion under *A. sarmentosa* subsp. *sarmentosa* will explain why we did not take this step here. A more complete description of the specimen is worthwhile, however, in the possibility that it may be rediscovered elsewhere.

Thallus subpendent, 8–20 cm long, stiff, branching mostly anisotomic dichotomous, with frequent perpendicular side branches giving parts of the thallus a “strigose” appearance; main branches very uneven and twisted, with an irregular surface, 0.3–0.45 mm diam.

True lateral spinules, isidia, and soredia absent; pseudocyphellae white, raised, very conspicuous, often twisting around the filaments on ridges.

Apothecia and pycnidia unknown.

Cortex K+ yellow, C–, KC+ yellow, PD+

orange-yellow; medulla K+ yellow or K–, C+ red, KC+ red, PD– or PD+ yellow in part. Contains alectoronic, olivetoric, thamnolic, and usnic acids, the first two in the medulla and the latter two mainly in the cortex.

Selected specimens

Canada. British Columbia. Coastal District: Earl's Cove, Brodo 8320 (CANL) – Islands South District: Saltspring Island, Bird 23770 (UAC) – Skeena River Basin: Skeena River, J. M. Macoun 164 (CANL).

U.S.A. California. Del Norte County: 24 miles E of Gasquet, Tucker 6426 (UC) – Humboldt County: Near Manila, Stone 37 (HSC) – Pepperwood, Tavares 371 (FH) – *Oregon.* Josephine County: Between Cave Junction and O'Brien, Weber 8032 (COLO) – Lane County: W of Creswell, Pike L-453 (OSC) – Washington County: Forest Grove, Lloyd s.n., 1894 (F) – *Washington.* Jefferson County: Olympic National Park, Hoh Rain Forest, Brodo 13222A (CANL).

Bryoria Brodo & D. Hawksw., nom. nov.

Nom. nov. for *Setaria* Michx., Fl. Bor.-Amer. 2: 331 (1803); nom. rejic. (Art. 14). Etymology: *Bry*(-opogon) and (*Alect*-) *oria*.

Non *Setaria* Beauvois, Agrost.: 51, 178 (1812); nom. cons.; type: *S. viridis* (L.) Beauvois [Gramineae].

Bryopogon Th. Fr., Nova Acta Reg. Soc. Sci. Upsal., Ser. 3, 3: 25 [repr.] (1860); nom. illegit. (Art. 64); type: *B. jubatum* (L.) Th. Fr., lectotype. – *Alectoria* subgen. *Bryopogon* Th. Fr., Lich. Scand. 1: 23 (1871). – *Alectoria* sect. *Bryopogon* (Th. Fr.) Zahlbr., Cat. Lich. Univ. 6: 375 (1930). – *Alectoria* sect. *Hyalosporae* Hue, Nouv. Archs. Mus. Paris, Sér. 4, 1: 86 (1899).

Non *Bryopogon* Link, Grund. Kräut. 3: 164 (1833); nom. illegit. (Art. 63); type: *B. sarmentosus* (Ach.) Link [= *Alectoria sarmentosa* (Ach.) Ach.], holotype (Art. 63).

Type species: *Bryoria trichodes* (Michx.) Brodo & D. Hawksw. (syn. *Setaria trichodes* Michx.; holotype).

Thallus fruticose, erect, caespitose, decumbent, subpendent or pendent; branching variable, branches generally terete but becoming somewhat compressed, angular and foveolate in a few species, not becoming markedly expanded and dorsiventrally compressed; greenish grey to brown, dark brown or black (and shades of these colours), some species characteristically bicoloured.

True lateral spinules with constricted bases arising at right angles to the main stems in some species, absent in others. Isidia absent but isidiiform spinules arising in tufts from soralia in a few species. Soralia absent to abundant, tuberculate or fissural, sometimes bearing sprouts of secondary branches or tufts of isidiiform spinules. Pseudocyphellae absent to abundant, usually rather sparse and inconspicuous, elongated and spiralling around the main stems in a few species, fusiform, white, yellow or brownish, depressed in most species but somewhat raised in a few, not becoming sorediate or bearing spinules. Cortex

composed of periclinal conglutinate hyphae immersed in moderate or relatively little matrix, not disintegrating, and smooth or knobby at the surface. Medullary hyphae not ornamented.

Apothecia lateral, sometimes appearing geniculate owing to the death of the branch distal to them, rare or unknown in many species, frequent to common in others; excipulum thallinum concolours with the thallus, becoming excluded in most species, or if persistent, not markedly incurved; margin ciliate in a few species; disc reddish brown to dark brown, rarely white, never black, sometimes yellow-pruinose. Asci clavate, thick-walled, arrested-bitunicate, 8-spored. Ascospores ellipsoid, lacking a distinct hyaline episporc, hyaline at maturity, simple, 4.2–15 μm long. Pycnidia usually rare.

Usnic acid absent; atranorin and chloro-atranorin frequent; orcinol tridepsides rare; β -orcinol depsidones abundant; pulvinic acid derivatives rare; orcinol depsides, β -orcinol depsides (excluding atranorin and chloro-atranorin) and hydroxyanthraquinones absent.

Discussion

With some 46 accepted species, *Bryoria* is by far the largest segregate of *Alectoria* s. lat. and includes species occurring on all continents of the world in montane, north temperate and boreal to arctic regions. Some individual species are very widely distributed and common whilst others are more localized and rare.

As pointed out above, it is with some regret that we are introducing here a new generic name for so many species. As the original account of *Bryopogon* Link included both *A. jubata* and *A. sarmentosa*, whether the earlier name *Alectoria* Ach. is lectotypified

by *A. jubata* or *A. sarmentosa*, Link's name is superfluous and illegitimate under Art. 63. That is, *Bryopogon* Link must be lectotypified by one of these two species selected as the lectotype of *Alectoria* Ach. as prescribed in Art. 7. This would be, in fact, *A. sarmentosa*, as pointed out by Hawksworth (1972 p. 197). As Th. Fries (1860) specifically excluded *A. sarmentosa* from *Bryopogon*, *Bryopogon* Th. Fr. has to be lectotypified by one of the species he included in it, and *A. jubata* has been selected by almost all subsequent authors. *Bryopogon* Link and *Bryopogon* Th. Fr. are thus nomenclaturally distinct as they are based on different type species. The latter name is a later homonym of Link's and thus illegitimate under Art. 64. The employment of *Bryopogon* Th. Fr. for the genus named *Bryoria* here in the manner proposed by Bystrek (1971) is thus contrary to the Code and unacceptable.

In our view, it would not be possible to make a sound case for conserving *Bryopogon* Th. Fr. against *Bryopogon* Link since it could not be argued that "*Bryopogon*", at the generic rank, had actually been widely used in the sense of *Bryoria*. Most authors in the past using this name as a genus have applied the name to *Alectoria* s. lat. (including *A. sarmentosa*); Rabenhorst (1845), Körber (1855) and Gyelnik (1935) are examples. Some Soviet authors, however, have followed the usage of Fries (1860), e.g., Oxner 1956, and Elenkin and Savicz in many papers. Even if *Bryopogon* Th. Fr. was eventually conserved, a large number of new combinations would still have to be made since many of the transfers made by Bystrek (1971) into that genus are invalid under Article 33.

We decided that the species formerly called *Alectoria americana* Mot. would be most appropriate as the type species of the new genus in that it exhibits most features of it well and is not uncommonly fertile. The earliest epithet available for this species, in fact, proves to be *Setaria trichodes* Michx., the type species of *Setaria* Michx. nom. rej. As pointed out by Hawksworth (1972 p. 197), although Michaux's name was based on *Lichen tribus Setaria* Ach. (Acharius 1798 pp. 4, 219) it must not be cited as "*Setaria* (Ach.) Michx.", as was done, for example, by Lanjouw (1966 p. 259), since it has been typified by

S. trichodes Michx., a species quite unknown to Acharius in 1798. We are introducing the name *Bryoria* as a *nomen novum* for *Setaria* Michx. nom. rej. typified by the holotype (monotype) of Michaux's name, as authorized by Art. 72.

Setaria Beauvois was first added to the list of conserved generic names after the Cambridge Congress of 1930 (Briquet 1935 p. 131) but no type was designated there for the rejected *Setaria* "(Ach.)" Michx. The first selection of a type for the latter name appears to be that of Rickett & Stafleu (1959 p. 224) whose choice of *S. trichodes* Michx. has been adopted in all subsequent editions of the Code. Acharius (1798 pp. 219–221) definitely accepted three species in his tribe *Setaria*, viz. *Lichen jubatus* L., *L. chalybeiformis* L. and *L. hippotrichodes* G. Web. As the first two are definitely *Bryoria* species (the third probably being a non-lichenized fungus), even if the selection of *S. trichodes* were to be considered a "lapsus" and "corrected" in a future edition of the Code, the name would still conform to our concept of *Bryoria* although the type would require "correction".

Most authors since Du Rietz (1926) have endeavoured to recognize a number of infrageneric units within *Bryoria* as we have circumscribed it. On the basis of morphological, anatomical and chemical characteristics, we are accepting five groups at the rank of section. In general these sections are quite distinct, and are based on several unrelated characters (Table 3). That some of these sections have geographically separate regions of maximum diversity suggests that they are indeed natural groupings. We do not feel that there are, as yet, adequate distinctions within the sections to merit their further subdivision.

Bryoria sect. *Bryoria*

Bryopogon sect. *Eujubatae* subsect. *Lanestres* Gyeln., Feddes Repert. 38: 223 (1935); type: *B. lanestris* (Ach.) Gyeln. [= *Bryoria lanestris* (Ach.) Brodo & D. Hawksw.], holotype.

Bryopogon sect. *Subfibrillosae* subsect. *Subfibrillosae* Bystr., Ann. Univ. Mariae Curie-Skłodowska, C. 26: 271 (1971); type: *B. fuscescens* (Gyeln.) Gyeln. [= *Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksw.], holotype; nom. illegit. (Art. 66).

? *Alectoria* subgen. *Bryopogon* sect. *Jubatae* DR., Ark. Bot. 20A (11): 5 (1926); type: *A. jubata* (L.) Ach. [= *B. sp.*, see Excluded taxa], holotype. – *Alectoria* sect. *Bryopogon* subsect. *Jubatae* (DR.) Keissl., Rabenh. Krypt.-Fl. 9, 5(4): 97 (1958). – *Bryopogon* sect. *Eujubatae* Gyeln., Feddes Repert. 38: 223 (1935); nom. illegit. (Art. 63).

Table 3. Diagnostic characters separating the five sections of *Bryoria*. Included are characters of non-North American species.

| Character | <i>Bryoria</i> | <i>Divaricatae</i> | <i>Implexae</i> | <i>Subdivergentes</i> | <i>Tortuosae</i> |
|--|----------------------|---------------------------------|-------------------------|-------------------------------------|-----------------------|
| Apothecia | | | | | |
| Presence | Occasional | Rare | Rare | Common | Occasional |
| Margins | Eciliate | Eciliate | Eciliate | Ciliate | Eciliate |
| Yellow pruinose discs | Absent | Absent | Absent | Absent | Present |
| Vegetative structure | | | | | |
| Cortex | | | | | |
| Surface texture | Smooth | Smooth to \pm rough | Smooth | Rough and knobby | Smooth to \pm rough |
| Differentiated superficial layer | Absent | Absent or virtually so | Absent | Present | Absent |
| Matrix, relative to hyphae | Moderate to abundant | Moderate to abundant | Very little to moderate | Moderate | Moderate |
| Lateral spinules or spinulose branches | Rare | Present and constricted basally | Rare | Present but not constricted basally | Absent |
| Pseudocypbellae | Present or absent | Present or absent | Always present | Absent | Present or absent |
| Soralia | Frequent | Occasional | Occasional | Absent | Occasional |
| Pigmentation | Superficial crust | Superficial crust | Superficial crust | In tips of cortical cells | Superficial crust |
| Chemical components | | | | | |
| Atranorin and (or) chloroatranorin | Occasional | Usually absent | Rare | Absent | Absent |
| Fumarprotocetraric acid | Present | Usually present | Very rare | Absent | Absent |
| Other β -orcinol depsidones | Absent | Absent | Rare | Absent | Absent |
| Orcinol tridepsides | Absent | Absent | Rare | Absent | Absent |
| Pulvinic acid derivatives | Absent | Absent | Absent | Absent | Present |
| Number of species | 10 | 20 | 12 | 4 | 2 |

Type species: *Bryoria trichodes* (Michx.) Brodo & D. Hawksw. (holotype species of *Bryoria* Brodo & D. Hawksw.).

Thallus decumbent, subpendent or pendent; greyish, fuscous, brown to dark brown, not becoming blackened except in fragmentation areas. True lateral spinules absent. Isidia absent. Soralia frequent, fissural or tuberculate, white or brownish. Pseudocypbellae present or absent, usually inconspicuous, fusiform, depressed or elevated, brown or white. Cortex with a moderate quantity of matrix material, the hyphae not markedly fasciculate. Apothecia frequent in some species, unknown in others; margins not ciliate; discs orange-brown to reddish brown. Atranorin and/or chloroatranorin occasionally present in some species; fumar-

protocetraric acid present in almost all species; other β -orcinol depsidones and pulvinic acid derivatives absent.

Discussion

Bryoria sect. *Bryoria* comprises eight currently described species and at least two non-North American species awaiting description. One may recognize two distinct elements within it, one represented by *B. trichodes* and the other by the *B. fuscescens* group. The differences between these groups are much less than those separating sections but a treatment in the rank of subsection perhaps could be justified on the basis of the presence or absence of pseudocypbellae.

Alectoria subgen. *Bryopogon* sect. *Jubatae* DR. has been included as a synonym of this section with some hesitation in view of the uncertain identity of its type species.

1. *Bryoria chalybeiformis* (L.) Brodo & D. Hawksw., comb. nov.

Lichen chalybeiformis L., Sp. Pl. 2: 1153 (1753); type: sine loc., herb. C. Linnaeus (LINN 1273.90 lectotype!); basionym. - *Alectoria chalybeiformis* (L.) Gray, Nat. Arr. Brit. Pl. 1: 408 (1821).

For further synonyms see Hawksworth (1972 pp. 213-216).

Thallus prostrate or decumbent, usually 8-15(-20) cm long; branching irregular, often sparse towards the base, isotomic dichotomous towards the base but becoming anisotomic dichotomous towards the apices, often entangled, angles between the dichotomies mainly obtuse; main branches even in diameter, sometimes straight but usually becoming twisted and foveolate and sometimes channelled, (0.3-)0.5-1.0(-2.0) mm diam.; brown to dark brown or olivaceous-black, usually shiny, sometimes paler in colour towards the base.

True lateral spinules absent but irregular spinulose branches sometimes present. Soralia absent or sparse, usually tuberculate, occasionally becoming spinulose, usually narrower than the branches on which they occur. Pseudocyphellae absent.

Apothecia and pycnidia unknown.

Cortex K-, C-, KC-, PD-; soralia K-, C-, KC-, PD+ red; medulla K-, C-, KC-, PD- (or exceptionally PD+ red in parts). Contains fumarprotocetraric acid.

Ecology. Growing over calcareous or non-calcareous rocks and soil, and on tundra vegetation. It is occasionally found on lignum, and rarely on trees.

Distribution. Hemi-arctic to arctic tundra west and north of Hudson's Bay; rare in the east, mainly in exposed and alpine localities (Fig. 33). The occurrence of the species on the Lake Superior shore is still doubtful, and may be based on an exceptionally olivaceous specimen of *Bryoria fuscescens* var. *positiva* which occurs in the same area. Disjunct alpine occurrences are common in the western mountains at high altitudes. Hawksworth (1972)

comments on the world distribution of this circumboreal and apparently bipolar, arctic-alpine species.

Discussion

Bryoria chalybeiformis in North America can usually be reliably recognized on the basis of its stout, very dark and often almost olivaceous black, shiny main stems, and the failure of the medulla to react with PD whilst the soralia are generally PD+ red. At least some PD+ soralia are generally present on a thallus but in some plants a few may fail to provide a positive reaction. Some morphotypes of *B. fuscescens* var. *positiva* may approach it in habit but can in most instances be distinguished by the duller and paler colour of the thallus, and by the fact that quite often, both the medulla and the soralia react readily with PD. The separation of these taxa is discussed further by Hawksworth (1972 pp. 214-215).

A further difficulty has arisen in Europe over the separation of this species and *Bryoria intricans*, a taxon of somewhat doubtful validity (see Excluded taxa). Material corresponding to *B. intricans* does not seem to occur in North America.

In the past North American authors have widely misapplied the name *B. chalybeiformis* when referring to *B. furcellata*, a very different species.

Selected specimens

Exsiccatae. Weber: Lich. Exs. 125: Colorado, Larimer County: Rocky Mt. National Park, Mount Chapin, R. A. Anderson 3523 (CANL, COLO, DUKE, US, WIS).

Canada. British Columbia. Islands South District: Vancouver Island: Mt. Benson, Macoun 207 (NYBG) - Coast Area: Garibaldi Park, Krajina 351-4 (CANL) - Fraser River Basin: Spences Bridge, Macoun s.n., 28 May 1889 (CANL) - Skeena River Basin: Hazelton, Ohlsson 2936 (MSC) - Alberta. Morely, Bird 18510 (CANL) - Saskatchewan. Cypress Hills, Macoun 448 (CANL) - Manitoba. Kasmere Lake, Scotter 2857A (WIS) - Ontario. Kenora District: Pen I., Kershaw s.n., July 1971 (CANL) - Quebec. Cte lles-de-la-Madeleine: Grand Entrée, Le Gallo 3004 (US) - Cte de Matapédia: Lac au Saumon, Le Gallo 2157A (US) - Nova Scotia. Halifax County: Halifax, Taylor 1118 (MSC) - Newfoundland. Humber East District: Sheffield Lake, Ahti 558 (H) - Labrador North District: Chidley Peninsula,

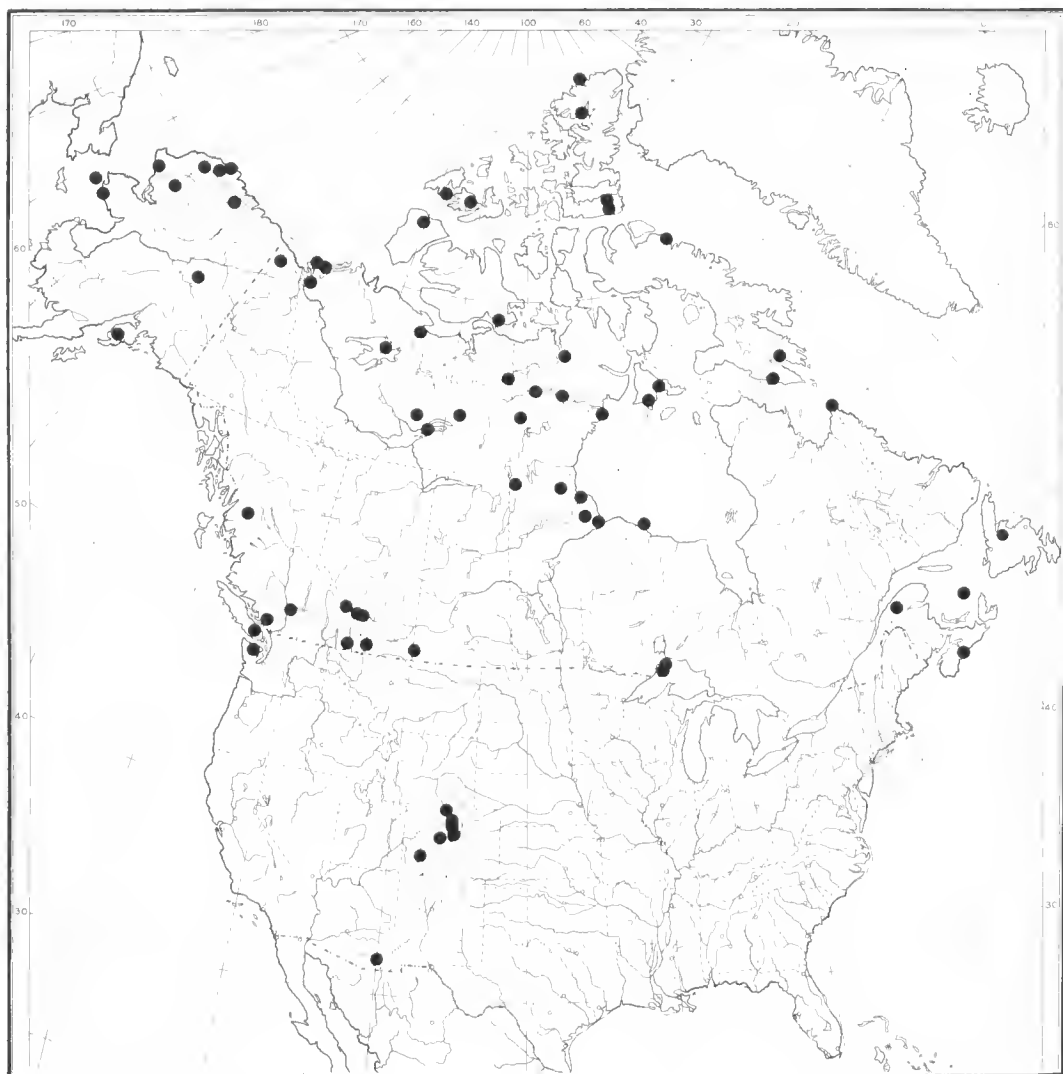


Fig. 33. *Bryoria chalybeiformis*. N. American distribution.

MacGregor s.n., 1905 (BM) – *Yukon*. British Mountains: Trout Lake, J. W. Thomson 14782 (WIS) – *Northwest Territories*. District of Franklin: Victoria Island: Cambridge Bay, Weber S 23,810 (COLO, CANL) – District of Keewatin: Aberdeen Lake, Scotter 3973 (WIS).

U.S.A. *Alaska*. Aleutian Islands: Amchitka Island, Schacklette 8013 (COLO) – *Unalaska*, J. M. Macoun 202 (CANL) – *Arctic Coast District*: Colville R. at Umiat, J. W. Thomson & Shushan 6198 (WIS) – *Arizona*. Graham County: Mt. Graham, Nash 4211 (NASH) – *California*. County unknown:

Packlow Hills, Blander 161 (US) – *Colorado*. Boulder County: Summit of Rollins Pass, Shushan & Anderson S 25,716 (COLO) – *Michigan*. Keweenaw County: Isle Royale, Raspberry Island, J. W. Thomson 17233 (WIS) – *Washington*. Clallam County: Hurricane Ridge, Olympic National Park, Brodo 13197 (CANL).



Fig. 34. *Bryoria fuscescens* var. *positiva* showing the pale basal area. Newfoundland, Ahti 560 (CANL). Scale 0.5–1.0 mm.

2. *Bryoria fuscescens* (Gyeln.) Brodo & D. Hawksw., comb. nov.

Alectoria fuscescens Gyeln., Nyt Mag. Naturvid. 70: 55 (1932); type: Finland, Tavastia austr., Hollola, ad truncos *Pini* locis apricioribus in silva, J. P. Norrlin, September 1882, Nyl. & Norrl., Lich. Fenn. Exs. no. 466 (BP 33,947 lectotype! BM, CANL, H isoelectotypes!); basionym.

Bryopogon pacificus Gyeln., Acta Geobot. Hung. 2: 166 (1937); type: Oregon, Benton Co., on apple trees in old orchard, F. P. Sipe (ORE lectotype!).

For further synonyms see Hawksworth (1972 pp. 217–219).

Thallus pendent (to prostrate in some morphotypes of var. *positiva*), usually 5–15(–30) cm long; branching anisotomic or isotomic dichotomic at the base, often becoming anisotomic dichotomous towards the apices, frequent from the base, angles between the dichotomies acute or obtuse, sometimes with lateral spinulose branches; branches even to uneven in diameter, usually straight but sometimes becom-

ing twisted and occasionally foveolate (in var. *positiva*), (0.2–)0.3–0.4(–0.6) mm diam.; pale fuscous to brown or blackish, the basal parts usually much paler in colour than the apices (Fig. 34); black fragmentation regions often present.

True lateral spinules and pseudocyphellae absent (note that young fissural soralia may resemble pseudocyphellae). Soralia abundant to sparse, tuberculate or fissural, some fissural soralia always present, usually broader than the branches on which they occur, sometimes becoming spinulose.

Apothecia and pycnidia not seen in North American material.

Cortex K–, C–, KC–, PD+ red or –; soralia K–, C–, KC–, PD+ red; medulla K–, C–, KC–, PD+ red at least in parts or –. Contains fumarprotocetraric acid, with chloroatranorin as an accessory substance (only in specimens east of the Rocky Mountains). The

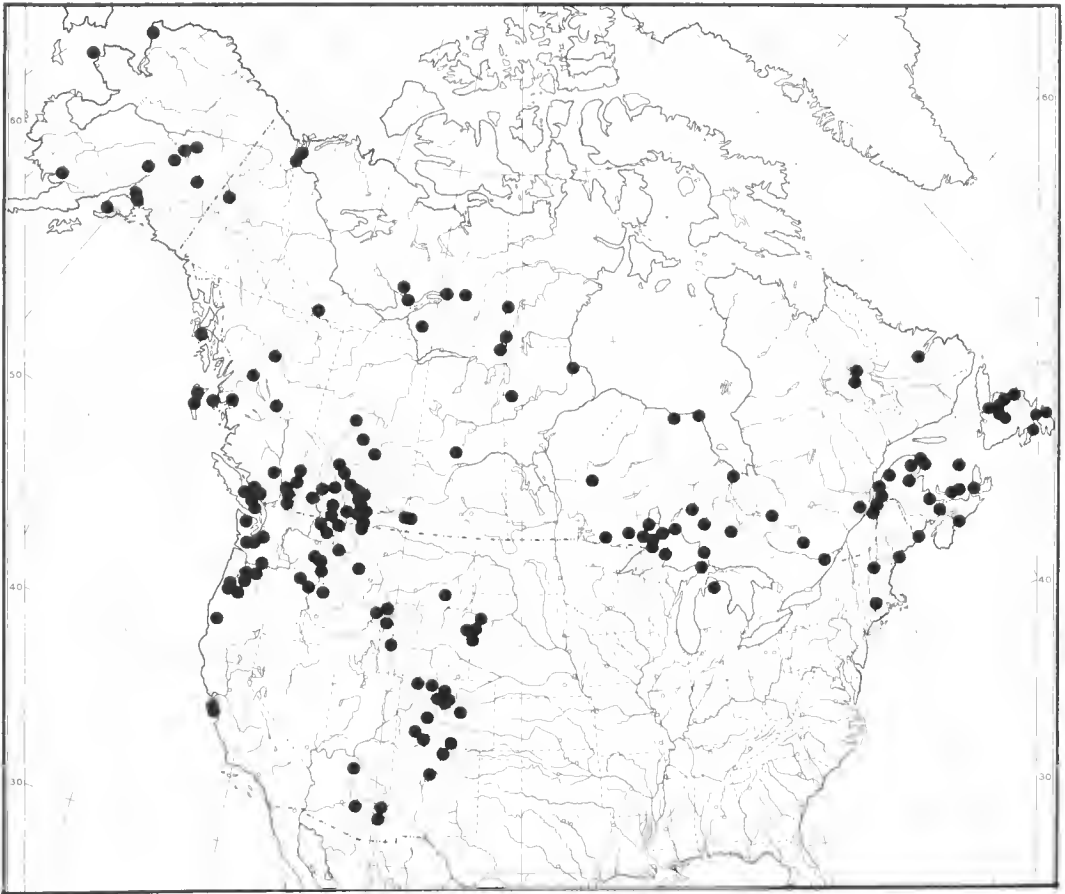


Fig. 35. *Bryoria fuscescens* s. lat. N. American distribution.

isotype in CANL contained fumarprotocetraric acid and atranorin s. lat., and the cortex of the filaments was PD+ red in part.

Ecology. On trees, mostly coniferous, in *Picea glauca*–*Abies balsamea* forests in the east; *Picea mariana* forests in the north; *Pinus contorta*, *P. ponderosa*, and *Pseudotsuga* forests in the west. Well developed on *Betula papyrifera* in northern Michigan.

The var. *positiva* occurs on rocks, lignum, and trees, generally in highly exposed habitats.

Distribution. Throughout the boreal forest zones of North America from Newfoundland to Alaska, north to the tree-line (Fig. 35). It ranges southward in the west along the Rocky Moun-

tains to New Mexico and into the Arizona mountain systems, and, to some extent, along the Coast Range. In the east, it shows a preference for the more humid coastal localities and milder central Newfoundland forests.

B. fuscescens is widespread in the Northern Hemisphere, and is the most common *Bryoria* in the lowland areas of northern Europe and the British Isles (Hawksworth 1972). It also occurs in the East African mountains (Hawksworth 1971 a, Krog & Swinscow 1975).

Discussion

There is no species group in which there are more problems in delimiting taxa than those

species of the section *Bryoria* which generally have PD+ red soralia. "Intermediate" specimens can be demonstrated from almost any pair within the group, although the distinctness of the taxa is unquestioned in most cases. Few characters of any of the taxa are constant for all specimens and variability is exceptionally broad. Environmental modifications may be the cause of at least some of this variability.

Most plastic in morphology and chemistry is *Bryoria fuscescens* (Bystrek 1963, Hawksworth 1972, 1973). Its "forms" and "varieties" are so abundant that there is a danger of circumscribing it in a way similar to the former use of the name "*Alectoria jubata*", with almost every puzzling *Bryoria* being conveniently placed within its all-encompassing boundaries.

The most easily identified specimens of *B. fuscescens*, those having all the most characteristic features of the species, are as follows: pendent; dark fuscous brown except at the base which is much paler, often almost white; having a mixture of fissural and tuberculate soralia; the outer portion of the cortex PD+ red; the branches about 0.2–0.4 mm in diameter, more or less even except for the basal branches which can be flattened and somewhat twisted. *Bryoria glabra* is "typically" dark olivaceous and shiny with very even, broadly angled, and strictly dichotomous branches (especially at the base), about 0.2–0.4 mm in diameter; soralia are small, oval, and fissural. In southern Alberta and southern British Columbia, the two seem to intergrade to some extent.

In the western mountains, *B. fuscescens* develops a morphotype with abundant fissural, often quite spinulose, soralia. It is usually pale fuscous, although sometimes extremely dark, and has a paler base. Otherwise, it resembles *B. vrangiana* in many ways. This pale, spinulose *B. fuscescens* probably can be assigned to f. *pallida* (Savicz) D. Hawksw. (Hawksworth 1972 p. 218). We are tentatively regarding *B. vrangiana* as a distinctly dark, olivaceous species with sparse fissural soralia (which often are absent altogether). The plant is quite thick at the base (often over 0.5 mm diam.) and is strongly foveolate, twisted, and spinulose. Räsänen's Lich. Fenn. Exs. no. 23 is slightly more pendent and slender than the North American specimens, but is a good match in other respects. Brown (non-olivaceous) speci-

mens named as *B. vrangiana* in Europe as well as North America due to their foveolate, twisted branches and spinulose soralia are usually either *B. fuscescens* f. *pallida* or var. *positiva*.

As can be seen from the above circumscription of *B. vrangiana*, the species comes very close to resembling *B. chalybeiformis*. In fact, *B. chalybeiformis* and *B. vrangiana* differ largely in their habitat and distribution with predictable differences in growth form and habit. *B. vrangiana* is found on trees and stumps in subalpine and subarctic localities, and is pendent with branches forming acute angles; *B. chalybeiformis* grows over soil, vegetation, and rocks mainly in alpine and arctic localities, and is, not surprisingly, prostrate with branches forming broad, obtuse angles. The only other distinction worthy of note is that the soralia of *vrangiana* are largely or entirely fissural, and those of *B. chalybeiformis* are commonly tuberculate.

In any discussion of *B. chalybeiformis*, one must return to *B. fuscescens* for a consideration of its variety *positiva*. These two taxa have already been compared in Britain by Hawksworth (1972) but a reexamination of the problem is warranted in view of the distinctive and abundant North American material. Whereas in the British Isles, var. *positiva* could be distinguished from *B. chalybeiformis* by basal colour, branch diameter, and type of soralia, this cannot be done with the North American specimens. Both taxa here commonly have pale bases, thick (over 0.5 mm) branches and both fissural and tuberculate soralia. *B. fuscescens* var. *positiva* is largely a temperate taxon occurring on rocks and frequently on trees. It is always brown to pale fuscous (especially the pendent form) and commonly has a PD+ red cortex or medulla. *B. chalybeiformis* is almost always olive-black to olive-brown, at least in part, and is a terricolous and saxicolous species of arctic-alpine situations. The cortex and medulla is PD– with very rare exceptions.

For discussions of the distinctions between *B. fuscescens*, *B. lanestris* and *B. subcana*, see the comments under the latter two species.

As regards its chemistry, *B. fuscescens* is not entirely uniform throughout its range. Chloroatranorin occurs fairly regularly in material east of the Rocky Mountains but appears very rarely in Europe and in the west. On the other hand, neither the intensity nor the anatomical

position of the PD reaction has any geographical correlation.

Unfortunately, it appears that the taxonomic problems in this group cannot be resolved on the basis of the North American material alone and must await a critical study of the group on a world scale.

Selected specimens (var. fuscescens)

Canada. British Columbia. Columbia River Basin: Revelstoke, Shaw 977 (US) – Coastal Region: Alice Lake Provincial Park, Ohlsson 740B (MSC) – Fraser River Basin: S of Clearwater, Brodo 15767 (CANL) – Islands North District: Graham Island: Marian Lake, Brodo 18474 (CANL) – Islands South District: Vancouver Island: Ladysmith, Ahti 15384 (H) – Kootenay River Basin: Fernie, Brodo 15076 (CANL) – Okanagan District: Princeton, Brodo 7815 (p.p.) (CANL) – Skeena River Basin: 30 miles W of New Hazelton, Ohlsson 2887B (MSC) – *Alberta.* Bow River Watershed, Wildcat Hills, Bird 9924 (WIS) – *Saskatchewan.* Cypress Hills, Lamb 6128 (DUKE, CANL, WIS, NYBG) – Waskesiu, Jesberger 745 (SASK) – *Manitoba.* Zed Lake, Larsen s.n., 10 Aug. 1959 (CANL) – *Ontario.* Cochrane District: Moosonee, Brodo 14784 (CANL) – Winisk, Webber W 22B (CANL) – Thunder Bay District: Sibley Provincial Park, Denison 645 (US, CANL) – *Quebec.* Bonaventure Island, Brodo 18691C (CANL) – Cte Pontiac: Parc de la Verendrye, Brodo 17028 (CANL) – *New Brunswick.* Albert County: Fundy National Park, Ireland 11332 (p.p.) (CANL) – *Nova Scotia.* Halifax County: Peggy's Cove, Taylor 1487 (MSC) – *Prince Edward Island.* Queens County: West Barkley Beach, Fabiszewski s.n., 20 July 1970 (CANL) – *Newfoundland.* Humber East District: Upper Humber Big Falls, Ahti 572 (H) – Labrador West District: Menihik Lake, Brodo 8825-5B (WIS, CANL) – *Yukon.* Dawson, Williams 71 (NYBG) – *Northwest Territories.* Mackenzie District: Mosquito Lake, Oldenburg 46-1534 (WIS).

U.S.A. Alaska. Central Yukon River District: White Mts., Krog 2767 (O) – *Arizona.* Apache County: Trail to Mt. Baldy, Nash 7838 (p.p.) (CANL) – Coconino County: San Francisco Peaks, Nash 7489 (CANL) – Graham County: Pinatino Mts., Darrow 1780 (WIS) – Pima County: Santa Catalina Mountains, Nash 4010 (CANL, ASU) – *California.* San Mateo County: Pilarcitos Creek Canyon, Herre & Doty 3348 (NYBG, F) – Santa Cruz County: Santa Cruz Mts., Black Mt., Herre s.n. (NYBG) – *Colorado.* Latimer County: Rocky Mt. National Park, Bierstadt Lake, Anderson 2507 (COLO) – *Idaho.* Latah County: N of State Route 8, Cooke 23047 (WIS) – *Maine.* Washington County: Quody Head near Lubec, Taylor 1073B (MSC) – *Massachusetts.* Hampden County: Springfield, Farlow s.n., May 1878 (NYBG) – *Michigan.* Chippewa County: 1 mile E of Makina County, Imshaug 3351 (MSC) – *Montana.* Granite County: Clinton, Norris 2072C (HSC) – *New Hampshire.* Crafton County: White Mts., Faxton s.n., 12 June 1879 (FH) – White Mt. Region, Tuckerman s.n.

(NYBG) – *New Mexico.* Sandoval County: Sandia Mt., Ellis s.n., 1914 (FH) – Taos County: Tres Piedras, Shushan & Weber S-6533 (COLO, ABSL) – *Oregon.* Josephine County: Rough and Ready Creek Botanical Wayside, Pike L-234 (PIKE) – *South Dakota.* Lawrence County: Bower Intake, Wetmore 9020 (MSC) – *Washington.* Pierce County: Mt Rainier National Park, Burroughs Mt., Imshaug 170C (LAM) – *Wyoming.* Pennington County: Black Hills, 4 miles W of US 385, Wetmore 8865 (BM).

Selected specimens (var. positiva)

Canada. Alberta. Cypress Hills Provincial Park, MacNeil 1274 (CANL) – *Manitoba.* Fort Churchill, J. W. Thomson 3822 (CANL) – *Ontario.* Kenora District: Cape Henrietta Maria, Cowell 1287 (CANL) – Thunder Bay District: Longcroft I., Garton 6251 (WIS) – *Quebec.* Cte Gaspé-Est: Bonaventure Island, Cain 27403 (US) – *New Brunswick.* Charlotte County: Campbell, collector unknown, July 1902 (FH) – *Newfoundland.* Grand Falls District: Great Rattling Brook road, Ahti 578 (H) – Labrador South District: Red Bay, Waghorne s.n., 6 Aug. 1894 (BM).

U.S.A. Alaska. Bering Sea District: St. Paul Island, J. M. Macoun 447? (624?) (CANL) – Bering Strait District: King Island, Krog s.n., 27 Aug. 1969 (O) – *Arizona.* Coconino County: Mt. Agassiz, Brodo 20350 (CANL) – *Maine.* Hancock County: Salisbury Cove (sic) (Salsburg Cove), Mount Desert Isl., Plitt 26a (US) – *Massachusetts.* Hampden County: Springfield, Herb. W. G. Farlow s.n., May 1878 (FH) – *Michigan.* Keweenaw County: Sand Bay, W of Eagle Harbour, J. W. Thomson 2799 (WIS) – *Oregon.* Benton County: Corvallis, Plitt? 19 (US) – *Washington.* Kittitas County: Easton, Howard 837 (FH).

3. *Bryoria glabra* (Mot.) Brodo & D. Hawksw., comb. nov.

Alectoria glabra Mot., Fragm. Florist. Geobot. 6: 448 (1960); type: U.S.A., Washington, Olympic Peninsula, Clallam Co., Hurricane Ridge, alt. 5,800 ft, on trunk of *Abies lasiocarpa*, B. I. Brown & W. C. Muenscher 129, 24 July 1950 (US holotype!); basionym. – *Bryopogon glaber* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 271 (1971); nom. inval. (Art. 33).

Thallus pendent, usually 10–15 cm long; branching regularly isotomic dichotomous, angles between the dichotomies usually obtuse and rounded; branches even in diameter, straight, not becoming twisted or foveolate, 0.2–0.4 mm diam.; olive brown to greenish black throughout, shiny, often with a translucent appearance.

True lateral spinules and pseudocypheallae absent. Soralia present, fissural or very rarely tuberculate, sparse to abundant, usually narrower than the branches on which they occur, white, to 1.0 mm long.

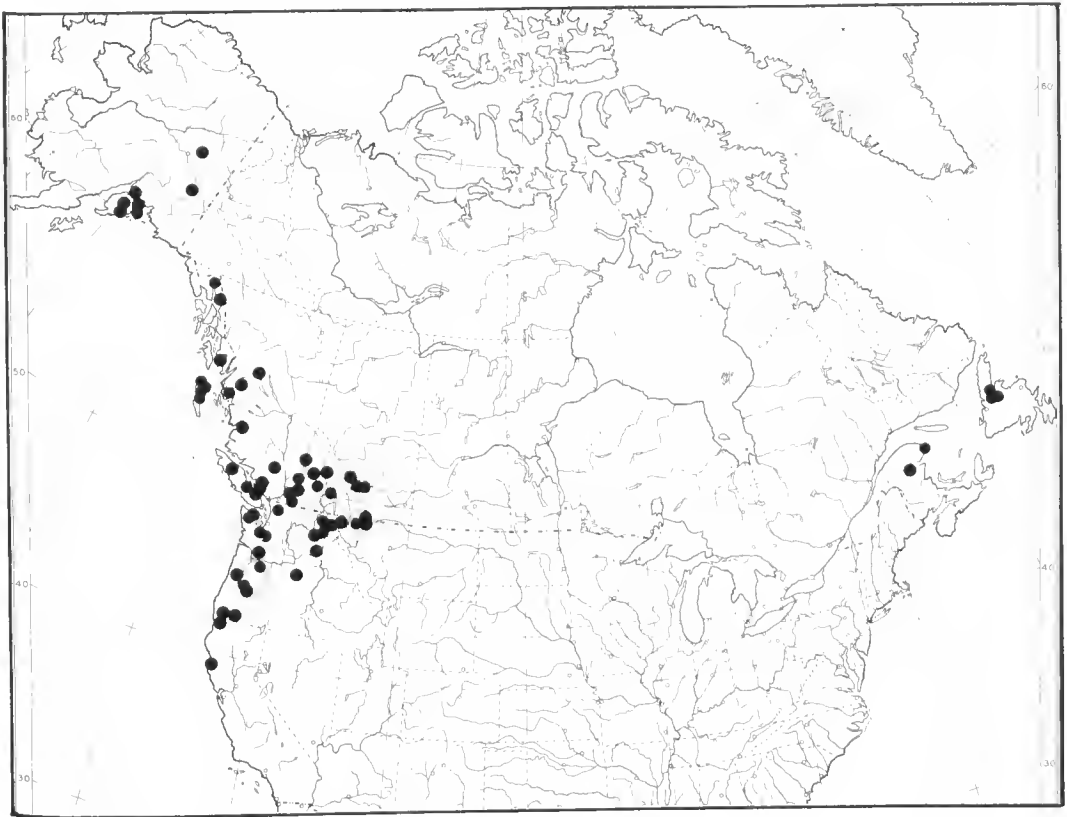


Fig. 36. *Bryoria glabra*. Known distribution.

Apothecia rare, lateral 0.65–1.15 mm diam.; excipulum thallinum concolourous with the thallus or darkening to disc colour, persistent, even, smooth, becoming somewhat reflexed in age; disc concave to plane, becoming convex when old, pale red-brown to dark fuscous. Asci 27–30 × 9–10 μm ; no mature spores seen. Pycnidia unknown.

Cortex K–, C–, KC–, PD–; soralia K–, C–, KC–, PD+ red; medulla K–, C–, KC–, PD–. Contains fumarprotocetraric acid.

Ecology. On coniferous trees, especially *Abies lasiocarpa* and *Picea* in the subalpine zone of mountains; also on *Picea sitchensis*, *Tsuga heterophylla*, and *Pinus contorta* and associated trees on the coast, typically around bogs.

Distribution. Along the west coast from northern California to Alaska, extending eastward into the

northern Rocky Mountains (Fig. 36). Disjunct populations exist in the Gaspé area and central Newfoundland (see general section on Distribution, category 11). Like *B. friabilis* and *B. pikei*, with bicoastal disjunctions, *B. glabra* is a North American endemic.

Discussion

Although only proposed relatively recently, this name has been used in a rather broad sense by North American lichenologists, and has often included plants clearly referable to *B. fuscescens*. In the course of the present investigation we have restricted the name "*glabra*" to specimens with shiny, smooth branches which have regularly isotomic dichotomous branching with broadly rounded axils, and have fissural soralia. Such specimens are



Fig. 37. *Bryoria lanestris* on a spruce twig, showing rather typical "wool-like" appearance. Quebec, Schefferville, Brodo 9125a (CANL). Scale 0.5–1.0 mm.

mainly confined to an area from the Rocky Mountains westwards, with their greatest abundance in the Coast Range and along the British Columbia coast; they are extremely rare on the east coast.

Bryoria glabra is usually fairly regularly sorediate but rare specimens have been found with very few or no soralia. Such specimens superficially resemble *B. trichodes* subsp. *americana* except in colour. They can be easily distinguished, however, by the consistently PD – medulla of *B. glabra* and the presence of pseudocyphellae in subsp. *americana* (although these may be rare in some specimens and easily overlooked). The separation of *B. glabra* from *B. fuscescens* can present a number of difficulties; these are discussed with the latter species.

A peculiar specimen found in Washington, containing gyrophoric acid but with some characters of *B. glabra*, is discussed under *B. friabilis*.

Selected specimens

Canada. British Columbia. Columbia River Basin: Columbia R. below Revelstoke, Macoun 53 (CANL) – Coastal Region: Garibaldi, Brodo 8182 (CANL) – Fraser River Basin: Wells Gray Provincial Park, Ahti 13044 (H) – Islands North Region: Port Clements,

Brodo 9780 (CANL) – Islands South District: Powell River, Tusko 8015 (H) – Okanagan Region: Tulameen, Ahti 10307 (H) – Skagit River Basin: Manning Park, Ahti 15387 (H) – Skeena River Basin: 9 Mile Mountain, east of Hazelton, Ohlsson 2962A (MSC, CANL) – *Alberta.* Banff National Park, trail to Lake Agnes, Imshaug 6866 (MSC) – *Quebec.* Cte Gaspé-Est: Bonaventure Island, Shushan S 23,039 (NYBG) – *New Brunswick.* Restigouche County: Dalhousie, Reijonen s.n., 16 Nov. 1930 (H) – *Newfoundland.* (See Ahti & Hawksworth 1974.)

U.S.A. Alaska. Eastern Pacific Coast District: Juneau, Mt. Roberts, Krog 5530 (O) – Central Yukon River District: White Mts., Lion Peak, Krog 2758 (O) – Indian Village, Krog s.n., 17 June 1969 (O) – *California.* Del Norte County: Near Bear Basin, Tucker 6435 (COLO) – *Idaho.* Bonner County: Gisborne Mt., Priest R. Experimental Forest, Esslinger 377B (COLO) – *Montana.* Glacier County: Glacier National Park, near Anaconda Creek, Imshaug 7591 (WIS) – *Oregon.* Klamath County: O'Dell Lake, Howard 4733 (COLO) – *Washington.* Clallam County: Hurricane Ridge, Muenscher 129 (NYBG, US).

4. *Bryoria lanestris* (Ach.) Brodo & D. Hawksw., comb. nov.

Alectoria jubata ζ . *lanestris* Ach., Lich. Univ.: 593 (1810); type: Helvetia (H-Ach. holotype!); basionym. – *Alectoria lanestris* (Ach.) Gyeln., Nyt Mag. Naturvid. 70: 58 (1932).

Bryopogon negativus Gyeln., Acta Geobot. Hung. 2: 164 (1937); type: Oregon, Crater Lake, on trees, F. P. Sipe 682, August 1930 (ORE lectotype!).

Alectoria tenerrima Mot., Bryologist 67: 31 (1964); type: British Columbia, Southern Caribou Mts., Wells Gray Park, south-west end of Turtle Lake, on old branches of *Picea engelmannii* in swamp, T. Ahti 6512, 25 June 1961 (H holotype!). – *Bryopogon tenerrimus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 274 (1971); nom. inval. (Art. 33).

For further synonyms see Hawksworth (1972 p. 222).

Thallus pendent to subpendent, 5–10(–15) cm long; branching irregularly isotomic dichotomous to anisotomic dichotomous, frequent from the base, angles between the dichotomies usually acute; branches usually very uneven in diameter, straight, sometimes becoming compressed toward the base, very brittle and tending to fragment in herbarium packets, 0.1–0.25(–3.0) mm diam.; brown-black to olivaceous black or black, usually concolourous, dull or rarely becoming shiny (often in parts). Fig. 37.

True lateral spinules and pseudocyphellae absent. Soralia sparse to abundant, fissural, white or white speckled with black, to 0.3 mm long.

Apothecia and pycnidia unknown.

Cortex and medulla K–, C–, KC–, PD–; soralia K–, C–, KC–, PD+ red. Contains fumarprotocetraric acid.

Ecology. On coniferous trees, especially *Picea mariana*, *P. glauca*, *Pinus banksiana*, and *Larix laricina* (rarely on willows and birches) in boreal black spruce forests, fens and bogs, and *Pinus contorta* or *Picea engelmannii* in the western mountains. (See comments under *Bryoria simplicior*.) Rarely, it is found on rocks or even soil.

Distribution. Mainly in the northern boreal zone from Alaska to Labrador, and in the western mountain ranges south to Colorado, New Mexico and Arizona (Fig. 38). *B. lanestrus* seems to prefer the more continental forest regions, although there are a number of occurrences in the coastal ranges, especially in British Columbia. This is evidently a circumboreal species. Although not confirmed for Asia by Hawksworth (1972), we have now seen it from several sites in northern Mongolia collected by Nina Golubkova in 1972 and 1974 (e.g., Golubkova 138, 787, 789 [LE]) and it is undoubtedly also present in Kamchatka and Siberia. We have seen a collection from Hawaii (Maui, Haleakala

National Park, Bowler 1645 [BM, CANL, IMI]) which appears to belong to *B. lanestrus*. Gyalnik's (1935) reports of this species from Algeria and Mexico must be treated as dubious; Japanese references to *B. lanestrus* mainly refer to *B. trichodes* subsp. *trichodes*.

Discussion

Bryoria lanestrus is normally a well-marked species which can be separated from *B. fuscescens* by its very dark colour, narrower branches which are characteristically uneven in diameter and extremely brittle (readily fragmenting in herbarium packets); the cortex in *B. lanestrus* is also always PD–, whilst in *B. fuscescens*, the outer cortex sometimes reacts PD+ red.

B. lanestrus often grows mixed with *B. simplicior* and the two thalli can be intricately entangled. *B. simplicior* is readily separable by the greenish black colour of the soralia, more even branches, and the failure of the soralia to react with PD.

In North America *B. lanestrus* usually has frequent fissural soralia. Tuberculate soralia, which occur in some European collections, appear to be absent here. Specimens which are almost esorediate also sometimes occur. These variations appear to be of little taxonomic importance.

Selected specimens

Exsiccatae. Merrill: Lich. Exs., Ser. II, 129 (mixed collection): Alaska, Fairbanks, Palmer (US) – Thomson: Lich. Arct. 88: Northwest Territories, District of Mackenzie: Artillery Lake, J. W. Thomson & Larsen (ALA, CANL, COLO, DUKE) – Weber: Lich. Exs. 431: Wyoming, Park County: Silver Gate, Weber (CANL).

Canada. British Columbia. Columbia River Basin: Glacier National Park, Ohlsson 395 (MSC, CANL) – Coastal Region: Pemberton, Garibaldi Mountains, Brodo 8269 (CANL) – Dean River Basin: Tweedsmuir Provincial Park, Ohlsson 1899 (MSC, CANL) – Fraser River Basin: Kamloops Tearsdale 3 (WIS) – Okanagan District: Okanagan Lake, Maslin s.n., 14 Aug. 1952 (COLO) – Skagit River Basin: Manning Park, Otto 105A (H) – Skeena River Basin: 30 miles W of New Hazelton, Ohlsson 2887B (MSC) – Alberta. Bragg Creek, Bird 10015 (WIS) – Saskatchewan. South Black Lake, Scotter 66 (WIS) – Charcoal Lake, Scotter 2684 (WIS) – Prince Albert National Park, Jesberger 1171 (SASK) – Manitoba. Churchill, Masson 9854 (QUE, WIS) – Ontario. Cochrane District: Gardiner, Wetmore 5765 (US) – Thunder Bay District: Niblock, Cain 26417 (CANL, TRTC) – Quebec. Parc des

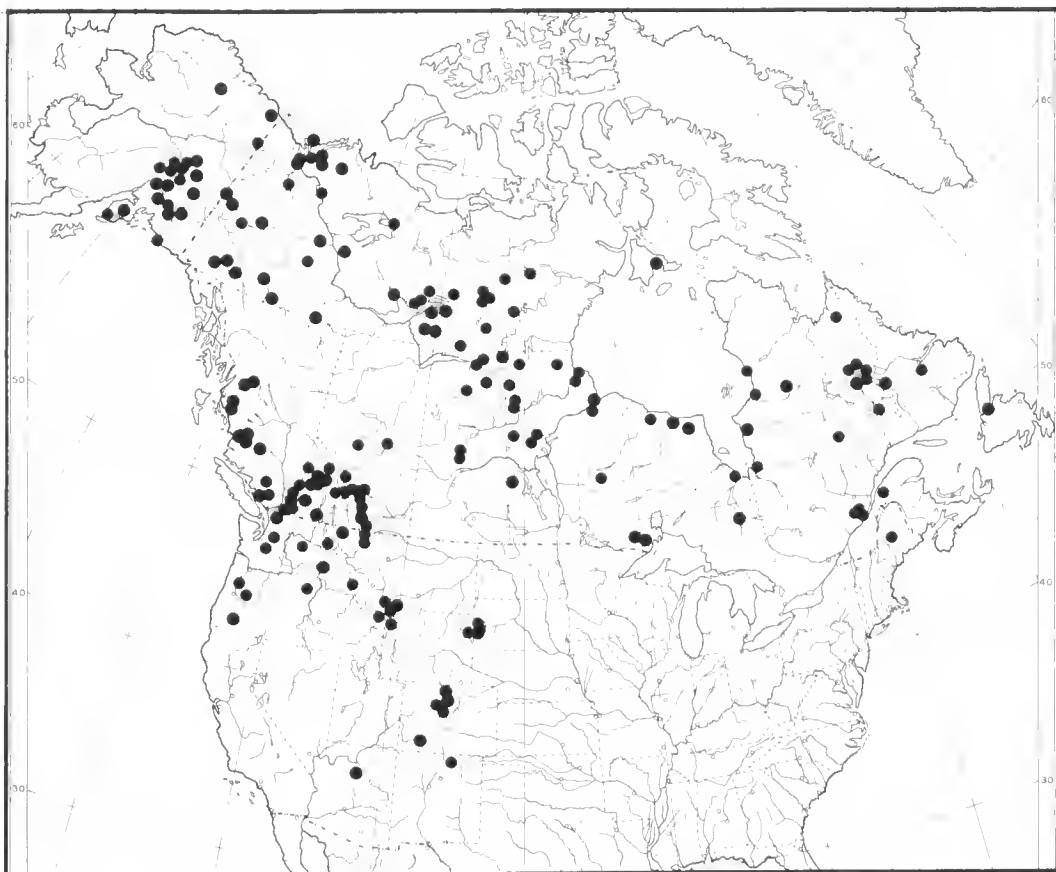


Fig. 38. *Bryoria lanestrís*. N. American distribution.

Laurentides: Riv. Montmorency, Masson 9982 (WIS) – Territoire de Mistassini: Rupert House, Kucyniak & Tuomikoski 51A (H) – *Newfoundland*. Central Labrador: Mary River, Hustich s.n., 26 Aug. 1937 (H) – Labrador North District: Goose Bay, Murray & Pruitt 1652 (ALA, H) – *Yukon*. Mt. Sheldon, Porsild & Breitung 2297 (DUKE, WIS, US, NYBG, CANL) – Semenof Hills, Scotter 19744 (CANL) – *Northwest Territories*. District of Mackenzie: W shore of Liard R., Fort Liard, Cody 11617 (CANL) – Keewatin District: Coral Harbor, Southampton Island, Weber S23, 687 (p.p.) (US) – Thelon River, Aberdeen Lake, Scotter 4236 (WIS).

U.S.A. *Alaska*. Alaska Range District: Wonder Lake, Mt. McKinley Nat. Park, Weber & Viereck S 7259 (DUKE, COLO, MSC, ORE, WIS) – Arctic Coast District: Valley of Mancha Creek and Firth River, Sharp 6532 (DUKE, US, MSC, WIS) – *Arizona*. Coconino County: San Francisco Peaks, Nash 7525

(CANL, NASH) – *Colorado*. Grand County: Fraser Exp. Forest, Weber & Dahl s.n., 1 Aug. 1953 (COLO) – Hinsdale County: trail to Upper Powderhorn Lakes, Weber s.n., 28 July 1964 (COLO) – Larimer County: Rocky Mt. Nat. Park, Wild Basin, Kiener 1695 (COLO) – *Idaho*. Fremont County: Targhee Pass, Cain 26415 (US) – *Maine*. Penobscot County: Bangor, Merrill s.n., 23 May 1896 (US) – *Montana*. Gallatin County: Above Gallatin R. on US 191, Norris 2054D (HSC) – *New Mexico*. Taos County: Tres Piedras, Shushan S6533 (US) – *Oregon*. Benton County: Near Corvallis, Plitt s.n., Mar. 1925 (US) – Klamath County: Crater Lake, Sipe 682 (ORE) – Lane County: Salt Creek Falls, Doty 5271 (NYBG) – *South Dakota*. Pennington County: 24 miles SW of Lead, Wetmore 11702 (MSC) – *Washington*. Whitman County: Steptoe Butte, Esslinger 1737b (WIS) – *Wyoming*. Teton County: Moran, Cain 26034 (US).

5. *Bryoria subcana* (Nyl. ex Stiz.) Brodo & D. Hawksw., comb. nov.

Alectoria prolixa var. *subcana* Nyl. ex Stiz., Ann. Naturhist. Mus. Wien 7: 129 (1892); type: Scotland, J. M. Crombie, 1875 (H-Nyl. 35835 lectotype! BM isoelectotype!); basionym. – *Alectoria subcana* (Nyl. ex Stiz.) Gyeln., Magy. Bot. Lapok 30: 54 (1931).

For further synonyms see Hawksworth (1972 pp. 249–250).

Thallus pendent to subpendent, to 5 cm long (in North American material); branching isotomic dichotomous, angles between the dichotomies mainly rounded, 80–90°; branches terete, even in diameter, straight, often brittle, 0.15–0.3 mm diam.; basal parts pale fuscous brown, usually matt but occasionally slightly shiny, apical parts very pale fuscous to greenish white or whitish, sometimes becoming variegated (probably an insolation effect); base persistent.

True lateral spinules absent. Pseudocypheae often present, sparse, inconspicuous, fusiform, white. Soralia usually abundant, tuberculate, as wide as or slightly broader than the branches on which they occur, occasionally becoming spinulose, to 0.8 mm diam.

Apothecia and pycnidia not seen in North American material.

Outer cortex, medulla and soralia K–, C–, KC–, PD+ bright red (rapid). Contains large amounts of fumarprotocetraric acid.

Ecology. On *Picea* along coastal bays and streams in the north, and on conifers and lignum on ridges and sand hills in California.

Distribution. Along the coasts of Alaska and British Columbia, with a disjunct population in the Santa Cruz area of California (Fig. 39). This basically oceanic species has a European distribution very similar to that of *B. smithii* (see maps in Hawksworth 1972 p. 248). The species is unknown outside North America and Europe.

Discussion

Bryoria subcana is most closely allied to *B. fuscescens* from which it can be distinguished by its paler colour and generally extremely strong PD+ cortical reaction. These two species were also found to differ by Hawksworth (1972) in that *B. subcana* never tends to be paler at the base, often has blackened fragmentation

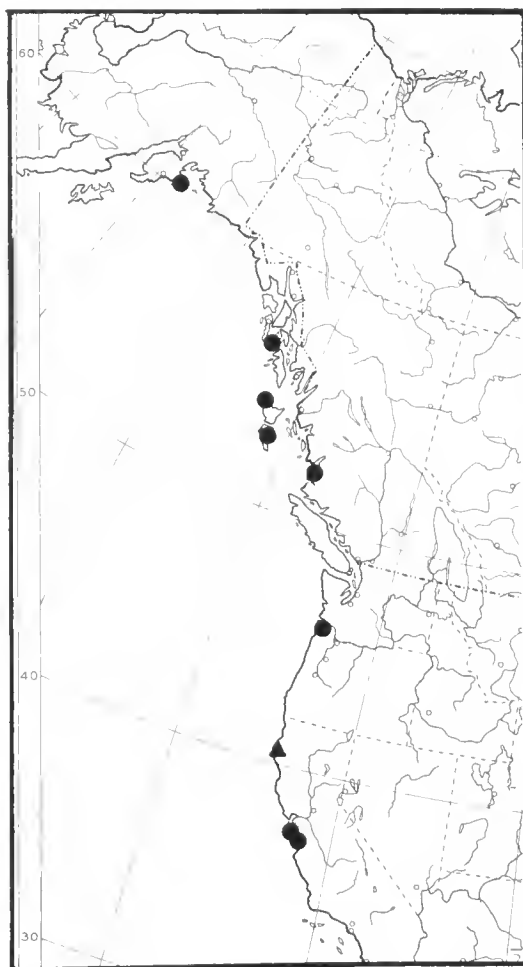


Fig. 39. ● *Bryoria subcana*. N. American distribution. ▲ *Bryoria spiralifera*. Known distribution.

regions, has only tuberculate soralia, and is more regularly fertile. As this species is known in North America only from a few specimens several of which are poorly developed, it would be premature to comment on its variability on this continent.

Atranorin s. lat. occurs together with fumarprotocetraric acid in small amounts in at least some European material of this species.

B. subcana has generally been a poorly understood species in Europe although it has been accepted in the British Isles for over a century. It has most frequently been subsumed

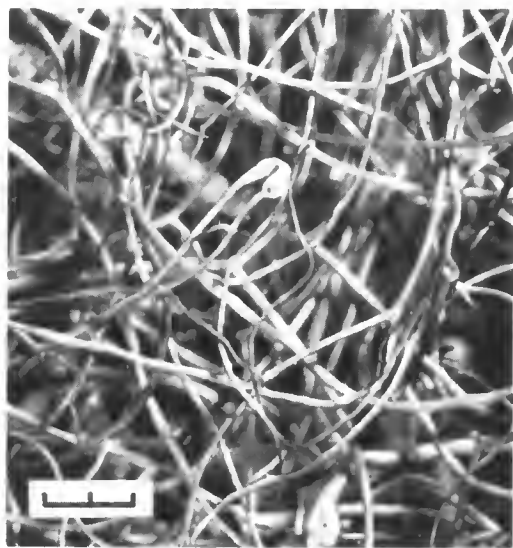


Fig. 40. Irregular soralia found on the sorediate morphotype of *Bryoria trichodes* showing the characteristically reflexed filaments. Quebec, Gaspé, Brodo 18694 (CANL). Scale 0.5 mm.

into *B. capillaris* by Scandinavian lichenologists. More recently Motyka and Bystrek have been applying this name to *B. implexa*. See the comments in Hawksworth (1972 p. 250).

Several specimens of a very odd morphotype (virtually caespitose, with large, empty soralium-like fissures; somewhat spinulose) were seen from the San Francisco area of California and Oregon. They are only provisionally referred to *B. subcana* based on their very pale colour and strong PD+ red outer cortex (see Discussion under *B. furcellata*). More typical *B. subcana* is known from the same area.

Reports of *B. subcana* from British Columbia (Motyka 1964), Ontario (Ahti 1964) and Alaska (Krog 1968, sub *Alectoria haynaldii*) based on specimens determined by Motyka have proved, on reexamination, to be errors for other species, most commonly *B. capillaris*.

Specimens

Canada, British Columbia. Coastal District: Namu Harbor at the west end of Burke Channel, Ohlsson 2082 (MSC) – Islands North District: Langara Island, Persson 34, 38A (S) – Lyell Island, Brodo 11800 (CANL).

U.S.A. Alaska. Central Pacific Coast District: Knight Island, Prince William Sound, Eyerdam (244)A (FH) – Eastern Pacific Coast District: Washington Bay, Kuiu Island, Eyerdam 856 (WIS) – *California.* San Mateo County: San Francisco Watershed, Cahill Ridge, Jordan WJ956B (WIS, SFS) – Santa Clara County: Santa Cruz Mountains above Saratoga, Herre 491 (FH) – Santa Cruz, Anderson 530 (FH) – Near Ben Lomond, Thiers et al. 9139 (WIS) – *Oregon.* Clatsop County: Saddle Mtn. State Park, summit, Pike 3818 (OSC).

6 a. *Bryoria trichodes* (Michx.) Brodo & D. Hawksw., comb. nov. subsp. *trichodes*

Setaria trichodes Michx., Fl. Bor.-Am. 2: 331 (1803); type: Canada, ad ramulos putridos (PC holotype!); basionym. – *Alectoria trichodes* (Michx.) D. Hawksw., Lichenologist 5: 252 (1972).

Alectoria jubata f. *minuscule* Merr., Bryologist 14: 36 (1911); type: Nova Scotia, near Digby, on spruces, J. Macoun, 20 May 1910 (FH lectotype!).

Alectoria canadensis Mot., Bryologist 67: 35 (1964); type: Ontario, Thunder Bay District, Slate Islands on north shore of Lake Superior, small island on south-east side of Edmonds Island, 48°40' N, 87°01' W, on *Abies balsamea* in rich forest, abundant. T. Ahti 4369, 10 July 1958 (H lectotype!); nom. inval. (Art. 37). – *Bryopogon canadensis* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 271 (1971); nom. inval. (Arts. 33, 37).

Alectoria delicata Mot., Bryologist 67: 34 (1964); type: Alaska, Sitka, Sitka National Monument, H. Krog 6254, 1 September 1957 (O lectotype!); nom. inval. (Arts. 36, 37). – *Bryopogon delicatus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 274 (1971); nom. inval. (Arts. 33, 36, 37).

Alectoria cervinula var. *eciliata* Mot., in Krog, Norsk Polarinst. Skr. 144: 135 (1968); type: Alaska, Central Pacific Coast District, Richardson Highway, mile 9, H. Krog 2176, 18 August 1957 (O lectotype!); nom. inval. (Arts. 32, 36, 37).

Thallus pendent, subpendent, or prostrate, usually 7–15(–20) cm long; branching anisotomic dichotomous (to isotomic dichotomous in subsp. *americana*), frequent from the base, angles between the dichotomies mainly acute (to obtuse and rounded in subsp. *americana*), occasionally with short perpendicular lateral spinulose branches; branches terete, uneven (to even in subsp. *americana*), 0.2–0.3 mm diam. at the base, main branches 0.1–0.2(–0.45) mm diam.; translucent to pale cervine brown or dark brown, often with blackened stems and fragmentation regions, consistently shiny.

True lateral spinules absent. Soralia rare, modified fissural, in which the filaments are strongly split, opening flat and recurving the branch, exposing an irregular mass of white

farinose soredia (Fig. 40). Pseudocyphellae abundant in subsp. *trichodes*, where they are white, oval and raised; sparser in subsp. *americana* where they are fusiform to elongate-fusiform, brownish, depressed and 0.5–1 mm long.

Apothecia occasional, sometimes abundant, lateral; excipulum thallinum concolorous with the thallus, thin, becoming excluded; disc becoming convex, reddish brown, 0.5–1(–2) mm diam. Spores 8 per ascus, ellipsoid, hyaline, simple, $5.5\text{--}6(-7) \times 4\text{--}5 \mu\text{m}$. Pycnidia unknown.

Outer cortex K–, C–, KC–, PD–; inner cortex and sometimes medulla K–, C–, KC–, PD+ red at least in parts (very rarely PD– in subsp. *americana*). Contains fumarprotocetraric acid and usually chloroatranorin (the latter absent in subsp. *americana*).

Ecology. Mainly on coniferous trees, especially spruce and fir, usually in open, wet habitats such as bogs, swamps, lake and river edges; sometimes in spruce-fir or beech-maple forests. One specimen (Michigan, Isle Royale, Wetmore 2135A [MSC]) was collected on rock. The sorediate morphotype is not associated with bogs but rather appears to be found in open or closed woodlands.

Distribution. Subsp. *trichodes* occurs in the Great Lake–St. Lawrence forest region in the east, extending southward in the coniferous forests of the Appalachians and northwards into the southern boreal zone where it can be locally abundant (Fig. 41A). In the west it occurs in the coastal forest region from the Olympic Peninsula to the Central Pacific Coast district of Alaska.

B. trichodes subsp. *trichodes* is not uncommon in Japan (Kurokawa in litt., Hawksworth 1972, Yoshimura 1974 sub *Alectoria americana*).

Discussion

Bryoria trichodes is readily separated from other brownish pseudocyphellate members of the genus by its chemical reactions. Most specimens of subsp. *trichodes* can be easily separated from those of subsp. *americana* on the basis of the former's uneven stems, raised pseudocyphellae, generally paler thallus, and the regular occurrence of chloroatranorin. Some intergradation does occur (see below).

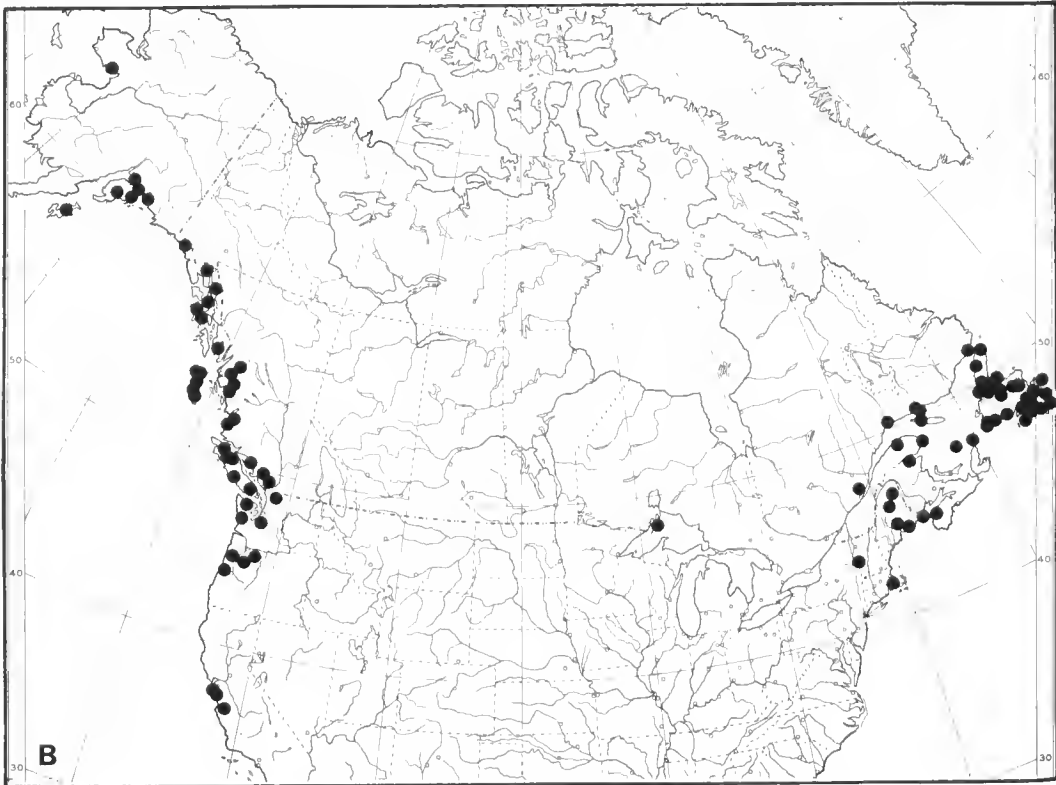
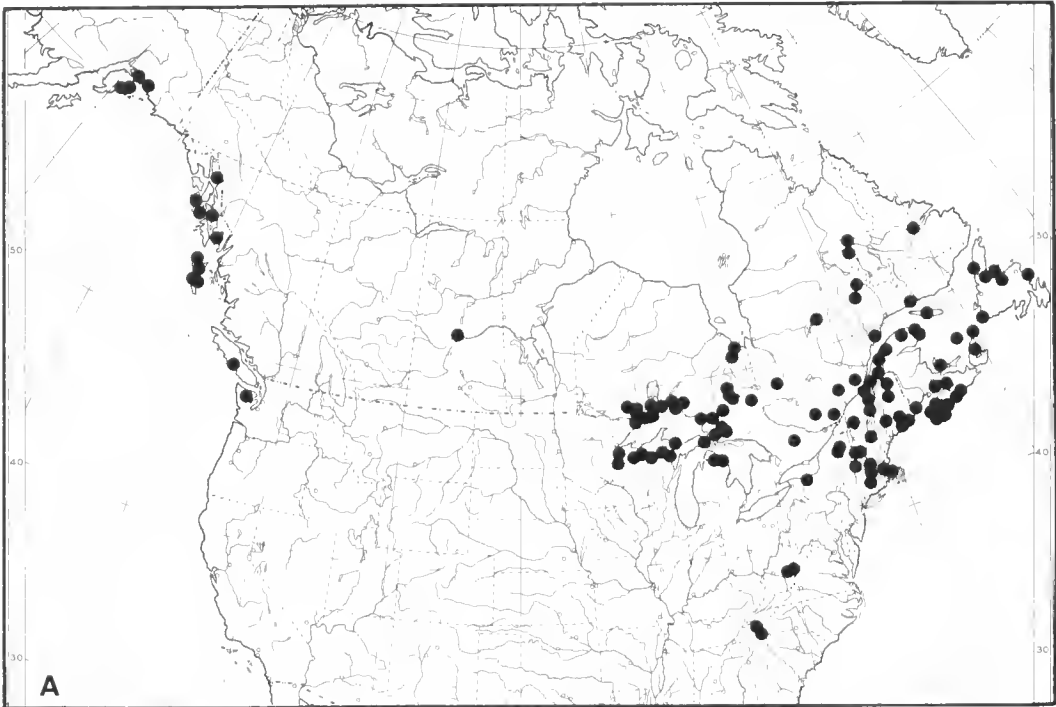
Fumarprotocetraric acid is almost invariably

present in subsp. *trichodes* and occurs in much larger amounts than is generally true for subsp. *americana* in which this compound can be difficult to detect. The presence of chloroatranorin in this subspecies but not in subsp. *americana* is difficult to explain, although it must be stressed that it is not always detectable in subsp. *trichodes* and it is also at low concentrations. West coast specimens of subsp. *trichodes* are often extremely pale and may be nearly translucent due to the almost complete absence of any cortical pigments. This morphotype, which is represented by the type specimen of "*Alectoria delicata* Mot.", may perhaps represent an infraspecific taxon, but its status is in need of further investigation.

Were it not for the large numbers of intermediate specimens encountered in areas where the two subspecies are sympatric (e.g., Newfoundland; Ahti & Hawksworth 1974), we would have been inclined to recognize two species in view of the several differentiating characters and different distributions in North America. Because of the intergradation, the rank of subspecies, as interpreted by Hawksworth (1974), appears to be particularly appropriate. Because it is frequently fertile and is widely distributed, subsp. *trichodes* is perhaps of greater antiquity than subsp. *americana*.

Over the major part of its range, subsp. *trichodes* is a rather uniform taxon. However, one interesting ecological modification is characterized by being quite small, often with somewhat contorted branches, and an abundance of spinulose side branches. This morphotype is generally found growing on coniferous trees in *Picea mariana* bogs and peatlands. (We have seen specimens from Connecticut, Michigan, Quebec, and other areas.) A complete intergradation of the spinulose morphotype and typical specimens of the subspecies has been examined by both of us in the field, in La Verendrye Park (Quebec). In this area, the spinulose morphotype occurred in exposed habitats on isolated trees and those at forest margins, whilst normally developed plants were encountered as one moved into more protected (sheltered) parts of the adjoining forest. The spinulose morphotype thus appears to be merely an ecad.

The epithet *trichodes* has long been overlooked by North American lichenologists. Fol-



lowing the rediscovery of the holotype specimen in PC by Dr. H. A. Imshaug in 1971, this was sent on loan to us. After we examined the specimen, the epithet *trichodes* was taken up as the correct name for the species previously called *Alectoria pseudofuscescens* Gyeln. (Hawksworth 1972) and treated as *Bryoria pseudofuscescens* here. The holotype was re-examined since Michaux (1803) reported apothecia in his species and since our studies showed these to be absent in North American material of *B. pseudofuscescens*. Also, it became clear that Michaux's specimen was undoubtedly gathered from eastern America (probably Quebec; see below), quite outside the range of *B. pseudofuscescens*. The holotype actually consists of two *Bryoria* species on a spruce twig: small, typical, fertile plants of *B. furcellata*, together with abundant material of a very dark, pendent, esorediate, sparsely pseudocyphellate *Bryoria* with uneven branches which is also fertile. TLC had earlier revealed a substance which appeared to represent norstictic acid in the blackish pendent specimen and it was for this reason that the epithet was employed for *B. pseudofuscescens* by Hawksworth (1972). *B. furcellata* and *B. pseudofuscescens* are not, however, sympatric in North America (compare Figs. 48 and 60A). In re-examining the material we also discovered that neither *B. furcellata* nor fragments of *Hypogymnia plysodes* (L.) Nyl. present in the packet appeared to contain any PD+ compounds although these taxa normally react readily with this reagent. It therefore seems likely that the whole collection may have been treated in some way, perhaps by immersion in alcohol, which removed the original substances. The PD+ compound originally determined by TLC as norstictic acid might have been some unrelated compound, possibly resulting from a reaction of a thallus substance with the preservative.

These data forced us to make some reluctant decisions with respect to the epithet *trichodes*. At first we considered the possibility of rejecting the name as one based on discordant elements (Art. 70). Since the original description, "*S. tenuissime capilliformis, proluxa, fuliginos- atra, laevigata; scutellis concoloribus, peltatis, convexis*" (Michaux 1803 pp. 331-332), could

be interpreted as referring to the blackish pendent thallus alone, this procedure could not be justified. In fact, the diagnosis supports the treatment of this element as the holotype, and this is the conclusion reluctantly reached here. Furthermore, this interpretation of the name is in agreement with the early usage of it by at least one early author: Bachelot de la Pylaie (see *Alectoria trichodes* under Excluded taxa). Apart from the dark colour and the lack of demonstrable fumarprotocetraric acid, the holotype conforms to the present subspecies which we termed *canadensis*, following Motyka, earlier in our investigations. We are thus forced to take up Michaux's name for this taxon and reject our first interpretation of it.

Field work in the spruce and fir forests north of Quebec City by one of us (I.M.B.) in the autumn of 1974 and spring of 1975 uncovered the fact that a fine, very dark, frequently fertile morphotype of this taxon is extremely common in that region and almost invariably grows with *B. furcellata*. The holotype of *Setaria trichodes* almost certainly came from this area, since Michaux's travels took him from the Lake Champlain area through the Richelieu Valley and then northward through the southern and middle boreal forests near Lac Saint-Jean and Lac Mistassini (Marie-Victorin 1964).

Acharius (1810) was uncertain of the identity of Michaux's *Setaria trichodes* but doesn't appear to have examined it. Müller Argoviensis (1878), however, did examine the holotype and stated that it was identical to "*A. jubata* var. *lanestris* Ach.", also evidently regarding the darkish pendent plant as the portion to be treated as the holotype for Michaux's name.

Selected specimens

Exsiccatae. Howe: Lich. Novae Angl. 70 (mixed): Maine, Hancock County: Bar Harbor, Hopkins (FH, NYBG) - Thomson: Lich. Wisc. Exs. 25: *Wisconsin*, Ashland County: Glidden, J. W. Thomson (CANL, COLO, DUKE, LAM, US, WIS) - Tuckerman: Lich. Amer. Septen. 2: *New Hampshire*, County unknown: White Mountains, Tuckerman (BM).

Canada. *British Columbia*. Islands North Region: Graham Island, Juskatla, Brodo 11675 (CANL) - Islands South Region: Vancouver Island: Long Beach Campground, Tibell 5132 (UPS) - *Saskatchewan*. Waskesiu, Prince Albert Provincial Park, Jesberger 1240 (SASK) - *Ontario*. Algoma District: N Aubina-

Fig. 41. N. American distribution. - A: *Bryoria trichodes* subsp. *trichodes*. - B: *B. trichodes* subsp. *americana*.

dong R., Cain 26009 (US, CANL, TRTC) – Cochrane District: Moosonee area, Wetmore 5967A (MSC) – Quebec. Territoire d'Abitibi: Guyenne, Gaudreau 8213 (CANL) – Cté Frontenac: N-D des Bois, Masson 6046B (WIS) – Territoire du Nouveau Québec: Schefferville, Brodo 9125D (p.p.) (CANL) – New Brunswick, Albert County: Fundy National Park, Ireland 11370 (CANL) – Prince Edward Island. Queens District: West Barkley Beach, Charlottetown, Fabiszewski s.n., 21 July 1970 (CANL) – Nova Scotia. Annapolis County: Kejimikujik National Park, Ireland 12448 (CANL) – Victoria County: Ingonish, Brodo 19069 (CANL) – Newfoundland. Humber East District: NE of Deer Lake, Taylor 1736B (MSC) – Labrador North District: North West River Twp., Coleman 28 (CANL) – Labrador West District: Faden, Brodo 8837-5B (CANL).

U.S.A. Alaska. Eastern Pacific Coast Region: Ketchikan, Krog 6225 (O) – Central Pacific Coast Region: Kenai Peninsula, Marathon Mt., Krog 2180 (O) – Connecticut. Hartford County: Suffield, Evans s.n., 19 Aug. 1923 (FH) – Maine. Hancock County: Mt. Desert I., Davis 32 (US) – Massachusetts. Plymouth County: Plymouth, Faxon s.n., 1 Mar. 1884 (FH) – Michigan. Chippewa County: Lower Tahquamenon Falls, Imshaug 19944 (MSC) – Minnesota. Cook County: Horseshoe I., Lake Saganaga, Hale 33526 (US) – New Hampshire. Cheshire County: Jaffrey, Riddle 1714 (FH-Riddle) – New Jersey. Morris County: Austin, Herb. of P.V. Le Roy s.n., Oct 1871 (NYBG) – New York. Hamilton County: Adirondack Mts., Hermann 13851 (p.p.) (CANL) – North Carolina. Macon County: Fodderstack Mt., Moore 1954 (DUKE) – Tennessee. Sevier County: Great Smoky Mts. Nat. Park, Mt. Leconte, Dey 3357A (DUKE) – Vermont. Addison County: Goshen (Corners), Dutton 1850 (FH) – Washington. Clallam County: Olympic National Park, Brodo 14396 (CANL) – West Virginia. Pocahontas County: Cranberry Glades, Gray 211 (FH) – Wisconsin. Douglas County: Brule River Valley, J. W. Thomson 2014 (WIS).

6b. *Bryoria trichodes* subsp. *americana* (Mot.) Brodo & D. Hawksw., comb. nov.

Alectoria americana Mot., Fragm. Florist. Geobot. 6: 449 (1960); type: America borealis, New Brunswick, Grand Manon, H. Willey, 1879 (US holotype!); basionym. – *Bryopogon americanus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C. 26: 274 (1971); nom. inval. (Art. 33).

Alectoria ambigua Mot., Bryologist 67: 17 (1964); type: Newfoundland, Ferryland, 6 miles north-west of Cape Broyle, east side of Mt. Carmel Pond, boulder in upland heath, abundant, T. Ahti 582, 26 May 1956 (H holotype!). – *Bryopogon ambiguus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C. 26: 270 (1971); nom. inval. (Art. 33).

Alectoria septacea Mot., in Krog, Norsk Polarinst. Skr. 144: 139 (1968); type: Alaska, Central Pacific Coast Distr., Kenai Peninsula, Marathon Mt., lower part, H. Krog 2197, 1 June 1957 (O lectotype!); nom. inval. (Arts. 32, 36, 37).

Plants differing from subsp. *trichodes* in the generally darker brown colour of the thallus, consistently isotomic dichotomous branching pattern, with branches which are even in diameter and often have blackened fragmentation regions. The pseudocypheallae are often sparse, fusiform, depressed, brownish and longer than those of subsp. *trichodes* measuring 0.5–1 mm in length. Contains fumarprotocetraric acid, but in this subspecies, it is often in low concentrations, and a PD+ red reaction is often difficult to demonstrate; some plants may lack this acid. Chloroatranorin appears to be absent in subsp. *americana*.

Ecology. On trees, especially conifers; most abundant in bogs or swamps or along rivers or lake edges; sometimes on trees in meadows. In the west it is found equally on *Picea sitchensis*, *Pinus contorta*, *Thuja plicata* and *Tsuga heterophylla*; in the east it is usually found on *Picea glauca*. The "ambigua"-morphotype (see below) usually occurs on rocks and dry soil, often in heathland areas, but is also rarely present on trees.

Distribution. Restricted to lowland coastal forests along both the east and west coasts corresponding closely with areas having a high annual rainfall (Fig. 41 B). The Mt. Washington and Isle Royale outlying localities are well known for their "oceanic" character with frequent mists. The disjunct Californian population is difficult to explain. This subspecies appears to be endemic to North America to judge from material we have examined, although it should be pointed out that Motyka (1960) also reported it from eastern Asia (Saghalien). Records of "*Alectoria americana*" in Japan refer to subsp. *trichodes*.

Discussion

This subspecies is rather variable with respect to the thickness of the main stems, the frequency of blackened regions on the thallus, and the abundance of pseudocypheallae. This subspecies, like subsp. *trichodes*, has a tendency to produce short, pointed, lateral branches recalling spinules but differing from them in being broad at the base. Soralia are very rarely found in subsp. *americana* and occur mainly in the west. The extent of fumarprotocetraric

acid production is also somewhat variable, and in some cases (particularly terricolous populations in the east) this acid may be entirely absent; PD+ reactions are thus sometimes difficult to demonstrate.

In his accounts of this taxon Motyka (1960, 1964) indicated that the holotype was PD- and made no reference to the occurrence of pseudocyphellae. In fact the holotype reacts readily with PD and has pseudocyphellae, although these are of the slightly depressed, dark and easily overlooked type characteristic of this subspecies.

Specimens from the oceanic heaths of Newfoundland were treated as a distinct species, *Alectoria ambigua* Mot., by Motyka (1964). This morphotype commonly has apothecia, is often PD-, and frequently has short, perpendicular lateral, spinulose branches, but otherwise appears identical to many of the corticolous specimens examined. On the basis of extensive field observations in Newfoundland, Dr. T. Ahti (in litt.) considers this morphotype to belong to subspp. *americana* and we concur with this view.

Selected specimens

Exsiccatae. Howe: Lich. Novae Angl. 70 (mixed): Maine, Hancock County: Bar Harbor, Hopkins (FH-Riddle); Merrill: Lich. Exs., Ser. II, 129 (mixed): Alaska, Fairbanks, Palmer (COLO).

Canada. British Columbia. Islands North District: Graham Island, head of Awun Lake, Brodo 18485 (CANL) - Islands South District: Mt. Cain, N of Schoen Lake, Ohlsson 1199B (MSC) - Coast District: 19 miles E of Bella Coola, Ohlsson 2273 (CANL) - Skeena River District: 21 miles E of Terrace, Ohlsson 2835 (CANL) - Quebec. Cte Gaspé-Est: Ile Bonaventure, Beaudoin 86 (CANL) - Cte Montmorency: Laurentide Park, junction Hwy 54A and 54B, Scotter 6880 (H) - New Brunswick. Charlotte County: Grand Manon (sic) (Manan) Island, Willey s.n., 1879 (US) - Restigouche County: Dalhousie, Reijonen s.n., 16 Nov. 1930 (H) - Nova Scotia. Victoria County?: St. Paul Island, Erskine 53C2403 (NSPM) - Newfoundland. Bonavista S. District: Charlottetown, Taylor 2110 (MSC) - Isle Miquelon: Delamare s.n., Sept. 1886 (COLO).

U.S.A. Alaska. Central Pacific Coast District: 1 mile from Sterling Hwy. on Mt. Aleyska Rd., J. W. Thomson 17817 (CANL, WIS) - East Pacific Coast District: Juneau, Krog 5529 (O) - Bering Strait of Lower Yukon River District: Darby Mountains, Pegau 44 (WIS, ALA) - California. San Benito County: Cook's Bear Valley, Hannibal s.n., 16 Feb. 1907 (LAM) - San Mateo County: Pilarcitos Creek Canyon, Herre & Doty 3348 (p.p.) (NYBG) - Maine. Aroostook County: Portage, Riddle s.n., Aug. 1907 (LAM) -

Massachusetts. Bristol County: New Bedford, Willey s.n., 1862-1898 (US) - Michigan. Keweenaw County: Isle Royale National Park, Lowe 937J (FH) - Forbes Lake, Wetmore 4116A (MSC) - Oregon. Lane County: Florence, Pike L-414 (PIKE) - Vermont. Rutland County: Sherburne, Dutton 2410 (FH) - Washington. Clallam County: Olympic Peninsula, Hurricane Ridge, Brown and Muenscher 129 (FH).

7. *Bryoria vrangiana* (Gyeln.) Brodo & D. Hawksw., comb. nov.

Alectoria vrangiana Gyeln., Magy. Bot. Lapok 31: 46 (1932): type: Sweden, Prov. Dalecarlia, par. Loksund, Låknäs, E. P. Vrang 236, 18 July 1931 (BP 33.967 holotype!); basionym.

For further synonyms see Hawksworth (1972 pp. 253-254).

Thallus pendent, to 10(-12) cm long; branching isotomic dichotomous towards the base but becoming anisotomic dichotomous towards the apices so as to appear submonopodial, angles between the branches mainly acute; branches even to uneven in diameter, becoming spirally twisted and contorted to foveolate, main branches (0.3-)0.5-1.0 mm diam.; thallus often bearing irregular contorted spinules not constricted at the bases and which usually arise at acute angles; thallus usually concolorous, matt, dark olive brown to blackish.

True lateral spinules and pseudocyphellae absent. Soralia absent to sparse or more rarely abundant, mainly tuberculate on the main branches, some fissural soralia often also present, white to brownish, to 1.0 mm long.

Apothecia and pycnidia unknown.

Cortex and medulla K-, C-, KC-, PD-; soralia K-, C-, KC-, PD+ red. Contains fumarprotocetraric acid.

Ecology. On conifers in the subalpine *Abies lasiocarpa*, *Larix lyalii*-*Pinus albicaulis* forests (1650-2250 m elevation in the Canadian Rockies; 2950-3250 m in the southern Rockies). We saw one collection on lignum from the arctic coastal strip of Ontario.

Distribution. Because we are still not sure about the taxonomic limits of this species, it is difficult to be certain of its distribution. It would appear that *B. vrangiana* is a montane forest species in North America (Fig. 42), as it is in Europe (Hawksworth 1972).

This species appears to have been first reported from North America by Räsänen (1933), but

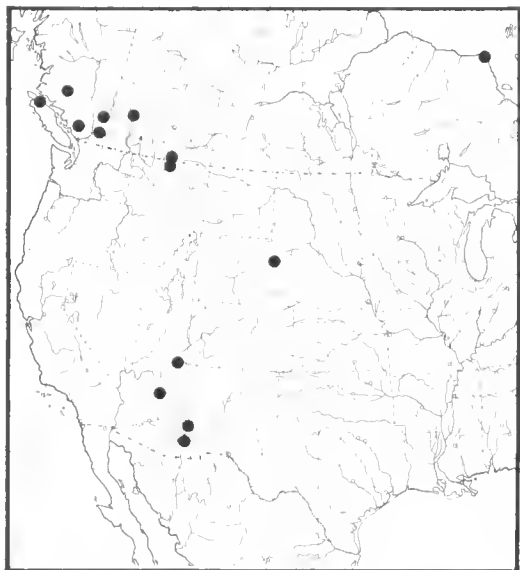


Fig. 42. *Bryoria vrangiana*. N. American distribution.

the specimen from Hazelton, British Columbia, upon which this report was based (H!) was found to be a mixture of *B. fuscescens* and *B. pseudo-fuscescens*.

Discussion

Circumscription of *B. vrangiana* has proved difficult and is discussed together with *B. fuscescens*. Rather few collections of the species have been seen, and its limits are likely to remain somewhat uncertain until more collections of it are available and it has been studied carefully in the field.

A specimen superficially extremely similar to *B. vrangiana* but containing norstictic acid is referred to *B. pseudofuscescens* (see the discussion under the latter species).

Specimens

Canada. *British Columbia*. Coastal District: Garibaldi Park, ridge to Little Diamond Head, Otto 8041 (p.p.) (CANL, H) – Garibaldi Mountains, Whistler Mountain, Brodo 13939 (CANL) – Lake Tatleh (sic) (Tatla Lake), Rothrock s.n., 21 Aug. 1863 (1865?) (US) – *Columbia River Basin*: Revelstoke National Park, ridge between Millar and Upper Jade Lake, Otto 3131B (UBC) – 22 miles N of Rossland, Brodo 15125B (CANL) – *Fraser River Basin*: 28.9 miles S of Merritt, Brodo 8500 (CANL) – *Kootenay District*: Rogers Pass, Brodo 7661B (CANL) – *Alberta*. Banff, Sanson S-27 (FH) –

Waterton Lakes National Park, Bird & Lakusta 16836, 16841 (CANL) – *Ontario*. Kenora District: Cape Henrietta Maria, Courtin 28 (CANL).

U.S.A. Arizona. Apache County: Trail to Mt. Baldy, Nash 7838 (p.p.) (CANL) – *Graham County*: Pinaleno Mountains, top of Mt. Graham, Nash 4223, 4236 (NASH) – *Montana*. Glacier County: Glacier National Park, Ptarmigan Creek, Imshaug 6036 (CANL) – *South Dakota*. Custer County: Cicero Peak, Custer, Weismore 6993 (MSC) – *Utah*. San Juan County: Navaho Mountain, Nash 5185 (CANL).

Bryoria sect. *Divaricatae* (DR.) Brodo & D.

Hawksw., comb. nov.

Alectoria subgen. *Bryopogon* sect. *Divaricatae* DR., Ark. Bot. 20A (11): 10 (1926); basionym. – *Alectoria* sect. *Bryopogon* subsect. *Divaricatae* (DR.) Keissl., Rabenh. Krypt.-Fl. 9, 5(4): 138 (1958).

Alectoria subgen. *Bryopogon* sect. *Divaricatae* subsect. *Subfibrillosae* DR., Ark. Bot. 20A (11): 10 (1926); type: *A. bicolor* (Ehrh.) Nyl. [= *B. bicolor* (Ehrh.) Brodo & D. Hawksw.], lectotype; nom. illegit. (Art. 63). – *Bryopogon* sect. *Eujubatae* subsect. *Subfibrillosae* (DR.) Gyeln., Feddes Repert. 38: 223 (1935). – *Alectoria* subgen. *Bryopogon* sect. *Subfibrillosae* (DR.) Mot., Fl. Polska, Porosty 5(2): 58 (1962). – *Bryopogon* sect. *Subfibrillosae* (DR.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 270 (1971).

Bryopogon sect. *Fuscidulae* subsect. *Divaricatae* Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 272 (1971), "(DR.)"; type: *B. altaicus* Gyeln. [= *Bryoria nadvornikiana* (Gyeln.) Brodo & D. Hawksw.], holotype; nom. illegit. (Arts. 48, 64).

Bryopogon sect. *Perspinosae* Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 273 (1971); type: *B. perspinosus* (Bystr.) Bystr. [= *Bryoria perspinosa* (Bystr.) Brodo & D. Hawksw.], holotype; nom. inval. (Art. 36).

Type species: *Bryoria bicolor* (Ehrh.) Brodo & D. Hawksw. (syn. *Lichen bicolor* Ehrh., *Alectoria bicolor* (Ehrh.) Nyl.; lectotype).

Thallus erect, decumbent, caespitose or sub-pendent to pendent; olivaceous-grey, brownish or black, frequently with extensive blackened areas, particularly towards the base, which are devoid of algal cells. Lateral spinules generally with somewhat constricted bases frequent to numerous, arising either perpendicularly or at slightly acute angles to the main stems, usually rather short, straight or arcuate. Soralia present in only a few species, fissural, white or brownish, bearing tufts of isidiiform spinules in some species. Pseudocyphellae present or absent, inconspicuous, fusiform, depressed, often very sparse. Cortex tending to become fasciculate. Apothecia frequent in some species, very rare or unknown in most; margins not ciliate, becoming sorediate in one species; discs reddish brown.

Atranorin and chloroatranorin usually absent; fumarprotocetraric acid present in most species; other β -orcinol depsidones and pulvinic acid derivatives absent.

Discussion

Bryoria sect. *Divaricatae* is the largest section of the genus recognized here comprising about 20 species of which only 7 are known from North America. This section shows its maximum diversity in the mountains of south-east Asia.

The chemical components of the species in this section are extremely uniform. Of those species in which lichen products have been demonstrated almost all have fumarprotocetraric acid (sometimes in very low concentrations) alone. *B. nadvornikiana*, although it contains fumarprotocetraric acid, also has compounds otherwise confined in *Bryoria* to sect. *Implexae* (i.e., alectorialic and barbatolic acids) and is placed in that section here. It is tempting to speculate that this aberrant chemistry may have been derived from an ancient hybridization between members of these two different sections (see also Discussion under *Alectoria sarmentosa* subsp. *sarmentosa*).

Many species in this section tend to have erect to caespitose habits and to occur predominately on the ground or on moss-covered boulders while others are strictly corticolous.

The species of the sect. *Divaricatae* are generally very sharply delimited from one another and present few difficulties in determination. This suggests that the group is particularly ancient and not undergoing active speciation at the present time.

8. *Bryoria bicolor* (Ehrh.) Brodo & D. Hawksw., comb. nov.

Lichen bicolor Ehrh., Beitr. Naturk. 3: 82 (1788); type: Hercynia, Ehrhart Crypt. Exs. no. 40 (LINN-Sm. 1712.2(3) lectotype!); basionym. – *Alectoria bicolor* (Ehrh.) Nyl., Actes Soc. Linn. Bordeaux 21: 291 (1856).

For further synonyms see Hawksworth (1972 p. 204–206).

Thallus erect or caespitose, rigid, usually 2–3.5(–4) cm tall; branching isotomic dichotomous, angles between the dichotomies variable; secondary and tertiary branches usually at right angles present, often obtuse at the base;

branches terete, even in diameter, sometimes becoming slightly compressed towards the base, usually 0.2–0.3(–0.5) mm diam.; basal parts black, apices olivaceous grey to cervine brown, shiny.

Numerous perpendicular lateral spinules with somewhat constricted bases present. Soralia absent. Pseudocyphellae usually sparse, inconspicuous, fusiform, dark to pale brown, plane or slightly raised, to 0.2–3.5 mm long.

Apothecia and pycnidia not seen.

Inner cortex and medulla K–, C–, KC–, PD+ red at least in parts (never PD–). Contains fumarprotocetraric acid.

Ecology. Mainly on rock and heath, but often on trees, in subalpine or coastal habitats. Degelius (1941), describing the ecology of the southern Appalachian population, said the species is found above 1540 m, mainly in the *Abies fraseri* forest. Some of Degelius' plants, however, have been identified here as *B. tenuis*, and so his comments may apply in part to both species.

Distribution. In oceanic and suboceanic areas along the west coast from Vancouver Island to south-east Alaska, in the Great Smoky Mountains, the White Mountains, and a few other mountain or heath areas (Fig. 43). Reports of this species in Mexico (see Imshaug 1956 p. 366) appear to be erroneous and probably refer to *Oropogon* spp.

The tendency of this species to occupy "oceanic" habitats in the northern Alps (Schauer 1965), Scandinavia (Degelius 1935) and in the British Isles (Hawksworth 1972) has been well documented. Hawksworth (1972) mapped the world distribution of *B. bicolor* noting its occurrence in montane subalpine and subarctic areas of Europe, Himalaya, Japan, and Malaysia. Krog & Swinscow (1975) consider the montane East African species *Bryoria ruwenzoriensis* to be conspecific with *B. bicolor*, but in view of its very robust habit and characteristic habitat we accept it as a species as did Jørgensen (1972).

Discussion

Bryoria bicolor is a clearly circumscribed species in North America and is only likely to be confused with *B. nitidula* (from which it is easily distinguished by the black main stems and

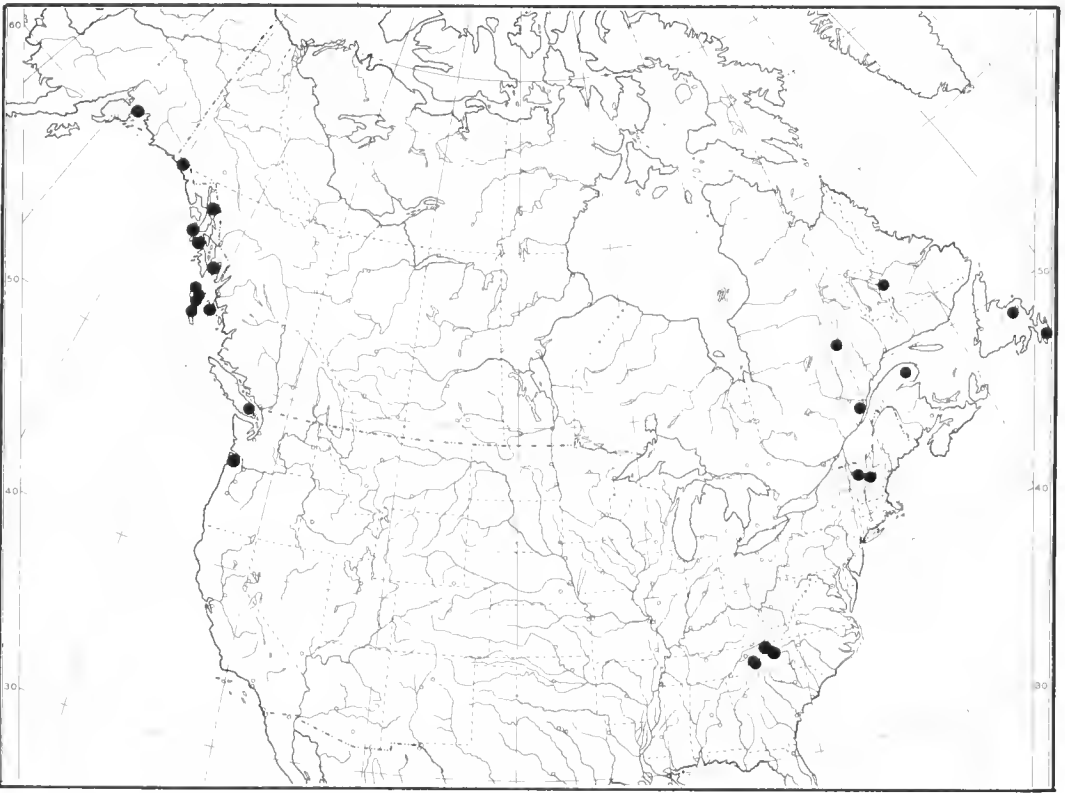


Fig. 43. *Bryoria bicolor*. N. American distribution.

pale perpendicular lateral spinules), and *B. tenuis* (from which it can be distinguished in that *B. bicolor* forms dense tufts with abundant third-order branches arising at right angles). The separation of *B. bicolor* from *B. tenuis* has been discussed in some detail by Jørgensen & Ryvarden (1970).

Motyka (1964) reported that the "f. *melaneira* (Ach.) Nyl." (see Hawksworth 1972 pp. 205–206 for the nomenclature of this taxon) occurred in North America. This morphotype, characterized by concolourous apices (and lateral spinules as well, on occasion), does not appear to be well-marked in North America.

Apothecia have been described for this species by a number of workers but it seems that these reports have been based on examinations of incorrectly determined (mainly Asian) material: the reports of them in Wade (1959), for example, are known to have been based on nineteenth century sources (A. E. Wade in litt.).

As far as we are aware, Motyka's (1964) statement that apothecia are unknown in this species is correct.

Selected specimens

Canada. British Columbia. Islands North District: Graham Island: Juskatla, Brodo 11676 (CANL) – Coast District: Banks Isles, Menzies s.n., 1785 (BM) – Island South District: Vancouver I., summit of Mt. Benson, Macoun 202 (CANL) – *Quebec.* Côté Charlevoix Ouest: Laurentide Park, Scotter 6693 (H) – Gaspé-Nord: Mt. Albert, Gauthier 2638 (CANL) – Territoire de Mistassini: Otish Mts., Shchepanek 71-L-13 (CANL) – *Newfoundland.* Labrador West District: Churchill Falls, Brassard 5326 (CANL) – Ferryland District: Biscay Bay, Tuomikoski 393 (H) – Gander District: Mt. Peyton, Ahti 8961 (H).

U.S.A. Alaska. Central Pacific Coast District: Prince William Sound, Pigot Bay, Krog 2203 (O) – Eastern Pacific Coast District: Sitka, Krog 6241 (O) – *New Hampshire.* County unknown: White Mts., Tuckerman s.n., 1840 (US) – *North Carolina.* Swain County: Great Smoky Mts., Clingman's Dome, Degelius s.n., 12 Sept. 1939 (DEGELIUS) – County unknown: Great



Fig. 44. *Bryoria carlottae*. Holotype. Scale 0.5–1.0 mm.

Smoky Mts., Forney Ridge, Degelius s.n., 12 Sept. 1939 (DEGELIUS) – Yancey County: Mt. Mitchell, Black Mts., Sierk 784 (DUKE) – Oregon. Clatsop County: Saddle Mountain State Park, Pike 3812A (OSC) – Tennessee. Carter County: Roan Mountain, Dey 2125 (DUKE) – Sevier County: Mt. LeConte, Great Smoky Mts., Degelius s.n., 13–14 Sept. 1939 (DEGELIUS) – Vermont. Lamoille County: Mt. Mansfield, Cain 26002 (TRTC).

9. *Bryoria carlottae* Brodo & D. Hawksw., sp. nov.

Thallus pendulus vel subpendulus, 7–8 cm longus; rami praecipue aniso-dichotomiter vel fere submonopodialiter sed basi iso-dichotomiter fastigiati et in angulos obtusos divergentes; rami principales basi 0.2–0.25 mm diam., ramulis numerosis brevibus praecipue 2–4 mm longis perpendiculariter instructi; tota planta olivacea sed interdum basi brunneo-olivacea.

Rami laterales spiniformes veri, isidia et soralia desunt. Pseudocyphellae copiosae, albae, fusiformes, aliquando elongatae, planiusculae vel interdum leviter elevatae.

Apothecia et pycnidia ignota.

Cortex K–, C–, KC–, PD–; medulla K–, C–, KC–, PD+ rubescens. Thallus acidum fumarprotocetraricum continens.

Holotypus: America septentrionalis, Canada, British Columbia, Insulae Queen Charlotte, Insula Graham, 2 mls austro-orientalem versus a Port Clements, australem versus a Tlell–Port Clements Road, 53°40'N, 132°09'W, in aperto turbario *Pinus contortae* et proxima sylvae *Tsugae–Thujae*, corticola, I. M. Brodo 18096, 11 July 1971 (CANL 38266). Isotypus: BM. Fig. 44.

Thallus pendent to subpendent, 7–8 cm long; branching mostly anisotomic dichotomous to

almost submonopodial except at the base where the dichotomies are isotomic and the angles between the branches obtuse; main branches 0.2–0.25 mm diam. at the base, with numerous short perpendicular side branches 2–4 mm long; uniformly olivaceous but sometimes brownish-olivaceous at the base.

True lateral spinules, isidia and soralia absent. Pseudocyphellae abundant, white, fusiform, sometimes elongated, plane or sometimes slightly raised.

Apothecia and pycnidia unknown.

Outer cortex K–, C–, KC–, PD–; inner cortex and medulla K–, C–, KC–, PD+ red. Contains fumarprotocetraric acid.

Ecology. On trees at the edge of bogs, or on exposed bluffs.

Distribution. Endemic to Queen Charlotte Islands (Fig. 45). Plants which are restricted to the Queen Charlotte Islands or which have their centres of distribution there are not uncommon (see general section Distribution, category 9).

Discussion

The broadly divergent habit and frequently perpendicular side branches together with the distinctive olive colour of *B. carlottae* readily distinguish it from *B. trichodes* subsp. *americana*, the only other uniformly coloured non-sorediate species containing fumarprotocetraric

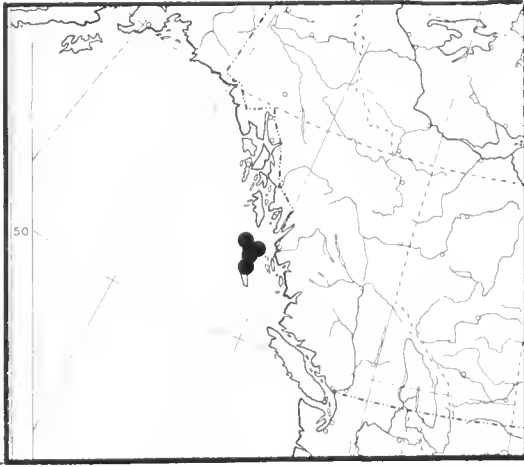


Fig. 45. *Bryoria carlottae*. Known distribution.

acid in the medulla and found in the same region. Its relationships to other species are unclear from the relatively few specimens examined so far but its affinities appear to lie with the section *Divaricatae* which has its centre in Asia.

Specimens

Canada. British Columbia. Islands North District: Graham Island: Tow Hill, Brodo 9900 (CANL) – Port Clements, Brodo 18093, 18096 (CANL) – Langara Island: McPherson Point, Brodo 10657B (CANL) – Moresby Island: Between Sandspit and Copper Bay, Brodo 12879 (CANL) – Skidegate Lake, Brodo 18499, 18503B (CANL).

10. *Bryoria cervinula* Mot. ex Brodo & D. Hawksw., sp. nov.

Alectoria cervinula Mot., Bryologist 67: 19 (1964); type: Alaska, East Pacific Coast District, Sitka, Harbour Mt., lower part, H. Krog 6222, 31 August 1957 (O lectotype!); nom. inval. (Arts. 36, 37). – *Bryopogon cervinulus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 271 (1971); nom. inval. (Arts. 33, 36, 37).

Thallus decumbens vel suberectus, 6–10 cm longus; rami praecipue monopodialiter fastigiati, ramulis numerosis brevibus et crassis perpendiculariter vel arcuate instructi, quare thallus spinosus videtur, ramis diametro aequalibus, basi 0.25–0.5 mm diam.; planta pallide brunnea vel atrobrunnea, non concolor, aspectu variegato, opaca vel bombycina, plerumque non nitida.

Rami laterales spiniformes veri, isidia et soralia

desunt. Pseudocyphellae praesentes sed plerumque rarissimae, albae vel brunneae, fusiformes, depressae. Apothecia et pycnidia ignota.

Cortex K–, C–, KC–, PD–; medulla K– vel + brunnea, C–, KC–, PD+ rubescens. Thallus acidum fumarprotocetraricum continens.

Holotypus: America septentrionalis, U.S.A., Alaska, East Pacific Coast District, Sitka, ad pedes montis Harbour Mountain, H. Krog 6222, 31 August 1957 (O).

Thallus decumbent to somewhat erect, 6–10 cm long; branching mostly monopodial, with numerous short stout perpendicular to arcuate side branches giving the thallus a very spiny appearance; branches even in diameter, 0.25–0.5 mm diam. at the base; pale brown to dark brown, not concolourous, appearing variegated, matt to satiny, not generally shiny. Fig. 46.

Truc lateral spinules, isidia and soralia absent. Pseudocyphellae present but often very sparse, white or brown, fusiform, depressed.

Apothecia and pycnidia unknown.

Outer cortex K–, C–, KC–, PD–; inner cortex and medulla K– or + brown, C–, KC–, PD+ red. Contains fumarprotocetraric acid.

Ecology. On soil and vegetation between rocks, on subalpine slopes, and on coniferous tree limbs in subalpine or subarctic localities.

Distribution. Southeastern Alaska and the Queen Charlotte Islands, with a single locality in the Bering Sea region (Fig. 47). This North American endemic should be sought on the Aleutian Islands.

Discussion

Bryoria cervinula is a very distinctive species characterized by extremely stout, often somewhat arcuate, lateral, secondary branches. It appears to show affinities with a number of species in the “*A. asiatica* group” known only from Asia (Bystrek 1969, Jørgensen 1972, Nuno 1971) but to differ from all those described in many features. (The types of all pertinent taxa have been examined by us.)

Specimens

Canada. British Columbia. Islands North District: Moresby Island: Laing Point, Brodo 10786 (CANL) – SW of Skaat Harbour, Brodo 17769 (CANL).

U.S.A. Alaska. Central Pacific Coast District: Cor-



Fig. 46. *Bryoria cervinula*. B. C., Queen Charlotte Islands, Brodo 17769 (CANL). Scale 0.5–1.0 mm.

dova, Auliot 1550 (DUKE) – Eastern Pacific Coast District: Baranoff I., Trelease s.n., 15 June 1899 (US) – Juneau, Krog 5511 (O) – Sitka, Harbour Mt., Krog 6222, 6223 (O) – Sitka, Indian River, Cooley s.n., 12 Aug. 1891 (NYBG) – Kuiu I., Washington Bay, Eyerdam 1117 (COLO) – Lower Yukon River District: 60 miles NW of Golovin, Pegau 43 (WIS).

11. *Bryoria furcellata* (Fr.) Brodo & D. Hawksw., comb. nov.

Cetraria furcellata Fr., Syst. Orb. Veg. 1: 283 (1825); type: *America borealis* (UPS-Fr. holotype!); basionym. – *Evernia furcellata* (Fr.) Fr., Lich. Eur.: 468 (1831).

Non *Alectoria furcellata* R. Sant., Svensk Bot. Tidskr. 62: 489 (1968).

Alectoria nidulifera Norrl., in Nylander, Flora 58: 8 (1875); type: Fennia, Tavastia australis, Korpilähti, super corticem *Pini*, E. Lang, 1873 (H-Nyl. 35979 holotype!). – *Bryopogon niduliferus* (Norrl.) Elenk., Lich. Fl. Ross. 1: 84 (1906). – *Alectoria chalybeiformis* f. *nidulifera* (Norrl.) Merr., Bryologist 14: 37 (1911).

? *Alectoria simplicior* v. *alba* Gyeln., Nyt Mag.

Naturvid. 70: 62 (1932); type: Fennia, Karelia ladogensis, Sortavala, Kotiluoto, ad scopulos, Linkola (holotype; not traced). – *Bryopogon niduliferus* f. *albus* (Gyeln.) Gyeln., Acta Geobot. Hung. 2: 166 (1937).

Bryopogon niduliferus f. *compactus* Gyeln., Acta Geobot. Hung. 2: 166 (1937); type: U.S.A., New York, Essex Co., Minerva, on twigs, H. D. House, 11 August 1927 (US lectotype! "portion of specimen sent to Gyelnik").

Bryopogon niduliferus f. *isidialius* Gyeln., Acta Geobot. Hung. 2: 166 (1937); type: U.S.A., New Jersey, Point Pleasant, C. C. Plitt (holotype not traced; ?isotypes! "Plitt 405, 29 Aug. 1909" FH, US).

Alectoria curta Ostm., in Hasselr., Ark. Bot. 30A (13): 3 (1943); nom. inval. (Arts. 32, 34, 36, 37).

Thallus caespitose, usually 3–5(–12) cm long; branching regularly isotomic dichotomous, angles between the basal dichotomies usually broad, those between the apical dichotomies usually acute; branches even in diameter, sometimes becoming slightly compressed towards the base, 0.3–0.4(–0.5) mm diam.; very pale brown to cervine brown or rarely dark brown

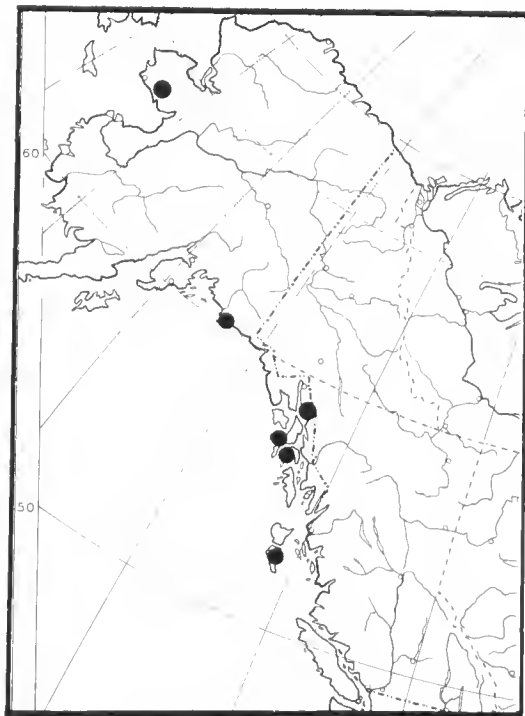


Fig. 47. *Bryoria cervinula*. Known distribution.

to black, often darker towards the base; base persistent.

Short perpendicular lateral spinulose branches sometimes present, occasionally abundant. Pseudocyphellae absent. Soralia usually abundant, fissural, sometimes slightly raised, narrower than the branches on which they occur, white, 0.3–1.0 mm long, becoming covered with tufts of isidiiform spinules 0.5–2.5 mm long.

Apothecia very rare, lateral; excipulum thallinum concolourous with the thallus, thick, usually becoming soroidate; disc concave at first but becoming convex and excluding the margin with age, light brown to reddish brown, 0.8–2.0(–4.0) mm diam. Spores 8 per ascus, subglobose, hyaline, simple, $6-7 \times 3-4 \mu\text{m}$.

Outermost portion of cortex K–, C–, KC–, PD–; inner cortex and medulla K–, C–, KC–, PD+ red or very rarely PD–; soralia K–, C–, KC–, PD+ red. Contains fumarprotocetraric acid.

Ecology. Mainly on coniferous trees, especially *Pinus* spp. and *Picea mariana*, but also found

on rock faces, boulders, coastal heaths (especially in Newfoundland; Ahti & Hawksworth 1974), lignum (especially fence rails), and, rarely, soil. In the north, it is a characteristic species of the more open conifer forests such as those dominated by jack pine and black spruce. In northeastern United States, it is frequently associated with bogs and pine stands (see Brodo 1968). In the southeastern United States, it seems to be largely restricted to pine forests at high elevations.

Distribution. *Bryoria furcellata* is the most widespread species treated in this paper. It is basically found in the Appalachian–Great Lakes region, ranging northward into the middle boreal and even the northern boreal zones (Fig. 48), but its "front of abundance" ends in the southern half of the latter zone (Ahti 1964 p. 193). Its restriction to the mountains and its absence in the Piedmont in southeastern United States has been well documented by W. Culberson (1958). The occurrence of disjunct populations in the southern Rocky Mountains and in the Mexican highlands is not unusual for this kind of distribution, and many examples can be cited (see Brodo 1968 pp. 82, 73). The disjunct west coast localities are more noteworthy, probably demonstrating the great age of the North American population. In Europe, where it appears to have a continental distribution (Ahlner 1948), the species is found mainly in the boreal forest region (Poelt 1969), especially associated with pine forests (Ahlner 1948), but it also occurs in Madeira (Jorgensen 1972) and has recently been discovered in Scotland (Hawksworth & Coppins 1976). *B. furcellata* (sub *Alectoria nidulifera*) has been reported from Himalaya by Bystrek (1969), and from Japan by Kurokawa (1959) who indicated that it was not rare in inland forests in central and northern Japan; this can therefore be considered a circumboreal species. *B. furcellata* also occurs as a disjunct in Central America in the Costa Rican highlands (Cartago Prov., S slope of Volcan Irazu, c. 3000 m, R. W. Holm & H. H. Iltis 1415 [herb. Dodge]), but is so far unknown from South America.

Discussion

The identification of this very clearly delimited species rarely presents much difficulty. Very

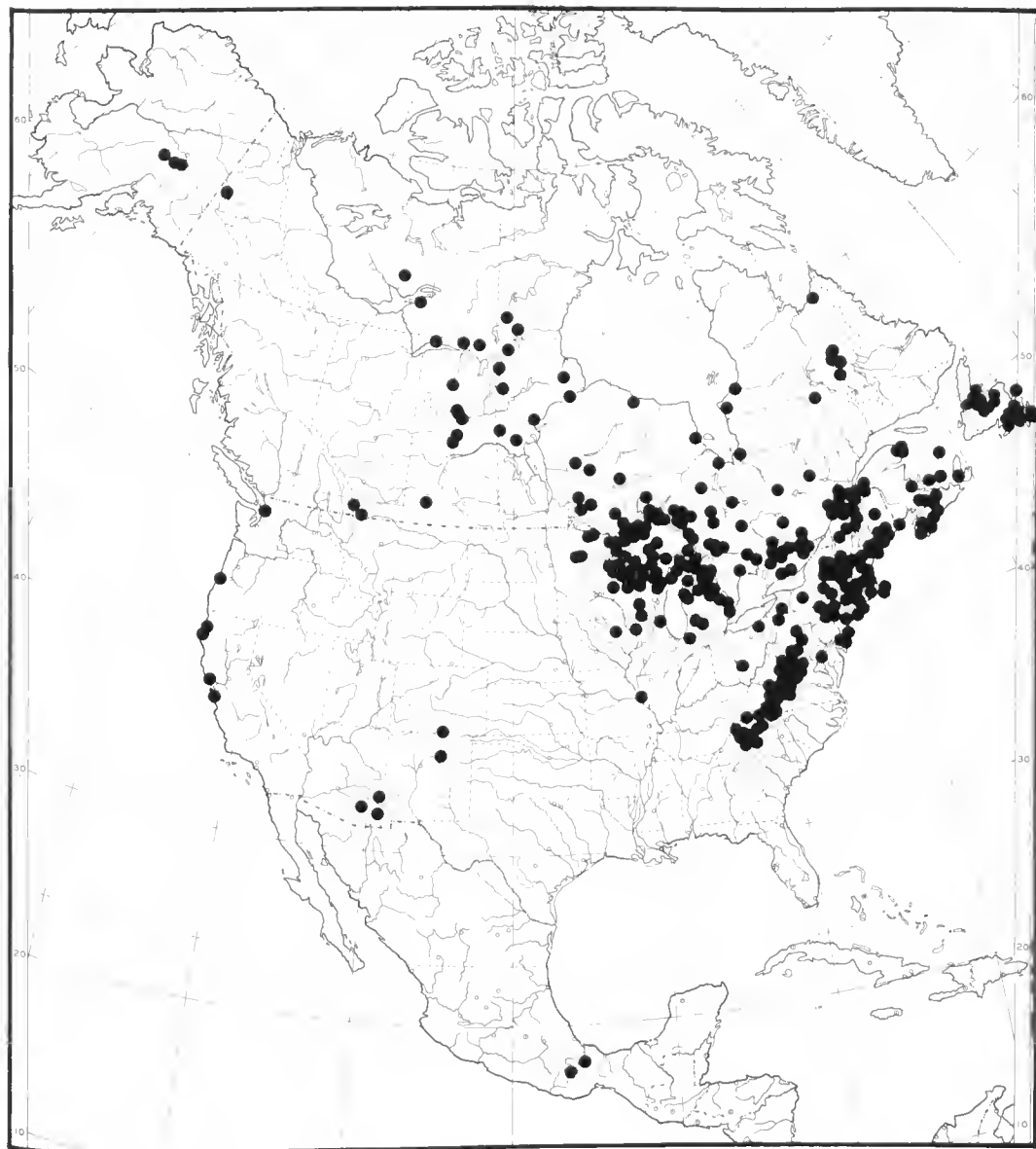


Fig. 48. *Bryoria furcellata*. N. American distribution.

rare specimens lacking sprouts of spinules in the soralia might possibly be confused with *B. simplicior* but these two species can be easily distinguished in that *B. simplicior* has greenish-black soralia broader than the branches on which they occur (a most useful character

apparently first noted by Degelius (1934) and is always PD -.

Motyka (1964 p. 15) considered that the North American material of this species tended to differ from that in Europe in having soralia located in minute tubercles rather than in deeply

incised fissures. However, we have found that many North American specimens have deeply incised soralia, and European material can have somewhat raised soralia. Furthermore, these types intergrade, frequently on the same thallus.

An extremely pale, grey-brown specimen with many spinulose branches and adventitious spinules was seen from Oregon (Pike 3818 [OSU]). Although resembling *B. furcellata* in branching type, it lacks true soralia and is probably conspecific with the material tentatively called *B. cfr. subcana* (see Discussion under that species) from California. A decision on its true affinities will have to await further studies.

The name *Alectoria chalybeiformis* has been incorrectly applied to this species by a number of early North American authors (e.g., Howe 1911).

Hawksworth (1969 p. 397) pointed out that the earliest name for this taxon at the rank of species was *Cetraria furcellata* Fr., something Ahlner had been aware of in 1941. In view of the existence of the name *Alectoria furcellata* R. Sant., which was treated as a synonym of *A. nigricans* by Hawksworth (1970, 1972), the epithet was preoccupied in *Alectoria* and so could not be taken up for this species then. When *A. nidulifera* is considered to belong to a genus other than *Alectoria*, however, Fries' name cannot be rejected and must be taken up in accordance with Art. 11. It is with some reluctance that we introduce this change here since the epithet *nidulifera* is so well-known on both sides of the Atlantic. Two methods of saving this epithet were considered, (a) to transfer Santesson's epithet into *Bryoria* and (b) to describe one of our new species of *Bryoria* under this epithet. The first alternative is untenable as Santesson's "species" does not belong to *Bryoria* but to *Alectoria* s. str. as understood here. To implement the second would establish three "*furcellata*" epithets in this group of genera all based on different types – something contrary to Rec. 23B(h).

Selected specimens

Exsiccatae. Brodo: Lich. Can. Exs. 82: Ontario, Cochrane District: Moosonee, Brodo 14779 (CANL) – Cummings, Seymour & Williams: Dec. N. Amer. Lich. 53: Virginia, Norton, Seymour (BM, CANL,

DUKE, MSC, NYBG, US, WIS) – Cummings, Williams & Seymour: Lich. Bor. Amer. 16: Maine, Washington County: Lubec, Cummings & Teller (NYBG, US) – Hale: Lich. Amer. Exs. 74: West Virginia, Randolph County: Spruce Knob Lake, Hale (BM, CANL, COLO, DUKE, LAM, MSC) – Merrill: Lich. Exs., Ser. 1, 211: Maine, Knox County: Warren, G. K. Merrill (BM, CANL, FH, NYBG, US) – Rel. Tuck. 3: Massachusetts, Hampshire County: Amherst, Tuckerman (BM, CANL, COLO, DUKE, FH, LAM, MSC, NYBG, US, WIS).

Canada. Alberta, Waterton Lakes National Park, Redrock Canyon, Imshaug 6112 (MSC) – Saskatchewan, Lake Athabasca, Uranium City, Scotter 3785 (WIS) – La Ronge, Jesberger 1281 (SASK) – Manitoba, Lac Brochet, Scotter 2800 (WIS) – Ontario, Algoma District: Mississagi R., Twp. 196, Cain 26011 (CANL, UBC, TRTC) – Haliburton County: W of Algonquin Park Gate, Cain 27295 (US) – Quebec, Cte Dorchester: Morisset, Masson 5632 (WIS) – Cte Gaspé-Est: Cap-des-Rosiers-Est, Brodo 18674 (CANL) – Territoire de Mistassini: Otish Mts., Mont du Lagopède, Shchepanek 71-L-59 (p.p.) (CANL) – Territoire de la Baie de James: Rupert House, Kucyniak & Tuomikoski 51A (p.p.) (CANL) – Territoire du Nouveau Québec: George River, Hustich s.n. (H) – New Brunswick, Albert County: Fundy National Park, Ireland 11332 (p.p.) (CANL) – Nova Scotia, Halifax County: Lake Charlotte, Taschereau B-8 (NSPM) – Prince Edward Island: Kings County: Montague, Ireland 10208A (p.p.) (CANL) – Newfoundland, Labrador West District: Menihek Lake, Brodo 8853-5B (CANL) (See Ahti & Hawksworth 1974.) – Yukon, Hunker Creek, Mascoun s.n., 26 July 1902 (FH) – Northwest Territories, Mackenzie District: Middle Ross Lake, Ahti 10271 (H) – Keewatin District: Ennadai Lake, Brown 1330 (CANL).

U.S.A. Alaska, Alaska Range District: McKinley Park, Hanson 461 (COLO) – Arizona, Cochise County: Chiricahua Mts., Weber & Shushan s.n., 18 April 1957 (COLO) – Greenlee County: Hannaga Meadows campground, Nash 7710 (CANL, NASH) – Pima County: Mt. Lemmon, Darrow 774 (COLO) – California, Humboldt County: Arcata, North Spit, Becking 6104017 (US) – Marin County: Inverness, Tavares 561 (COLO) – Santa Clara County: Santa Cruz Mountains, Herre 798 (F) – Colorado, Costilla County: Purgatory, Faxon s.n., 6 April 1882 (FH) – Connecticut, New London County: Old Lyme, Evans 754 (FH) – Illinois, County unknown: Calkins (107) 491 (NYBG) – Indiana, St. Joseph County: South Bend, Bosch s.n., no date (FH-Tuck.) – Iowa, Fayette County: Locality unknown, Fink s.n., 1895 (WIS, MIN, US, NYBG). Fink s.n., 1899 (H) – Maine, Oxford County: Buckfield, Parlin 7438 (FH) – Maryland, Alleghany County: Oldtown, Hale 14483 (US) – Massachusetts, Barnstable County: Cape Cod, Nicholson State Park, Brodo 4209 (CANL, MSC) – Michigan, Alger County: NE of Kingston Lake, Harris 6039 (MSC) – Minnesota, St. Louis County: Near Bear Lake State Park, Hale 23220 (US) – Missouri, St. Louis, Engelmann s.n., 18 Aug. 1878 (US) – New Hampshire, Grafton County: Hanover, Croasdale 14 (US) – New Jersey, Sussex County: Highview Mt. State Park, Hale 17302 (US) – New Mexico, San Miguel County: Las Vegas,

Arsène 20086 (FH) – *New York*. Franklin County: Adirondack Mts., Hermann 15643 (US) – *North Carolina*. Macon County: Bearpen Mt., Moore 1418 (DUKE) – *Ohio*. Ashtabula County: Orwell, Bogue 864 (NYBG) – *Oregon*. Lane County: Florence, Pike 1-564 (CANL) – *Pennsylvania*. Luzerne County: Red Rock, Hale 16168 (US) – *Rhode Island*. County unknown: Gillman s.n., no date (NYBG) – *Tennessee*. Knox County: House Mt., Cain 132 (FH) – *Vermont*. Rockbridge County: Goshen, Dutton 2292 (FH) – *Virginia*. Floyd County: Near Rocky Knob, Blue Ridge Parkway, Hale 12833 (US) – *Washington*. Snohomish County: Near Big Four Inn, Schallert 3210 (US) – *West Virginia*. Nicholas County: Birch River, Hale 11562 (US) – *Wisconsin*. Ashland County: Apostle Islands, Outer Island, Tans 4 (WIS).

Mexico. Oaxaca. Sierra de San Felipe, Pringle 195 (p.p.) (DUKE) – 53 km NW of Oaxaca, Hale 20805 (p.p.) (US).

12. *Bryoria nitidula* (Th. Fr.) Brodo & D. Hawksw., comb. nov.

Bryopogon jubatum var. *nitidulum* Th. Fr., Nova Acta Reg. Soc. Sci. Upsal., ser. 3, 3: 25 (1860) [Reprint]; type: Norway, Finnmark, Varanger, Klubben, T. M. Fries, 15 August 1857 (UPS lecto-type!); basionym. – *Alectoria nitidula* (Th. Fr.) Vain., Medd. Soc. Fauna Fl. Fenn. 6: 116 (1881).

Alectoria irvingii Llano, J. Wash. Acad. Sci. 41: 198 (1951); type: Alaska, Anatumuk Pass, alt. 100 m, 151°32'W, 69°20'N, on ground talus slopes, west wall, G. A. Llano 307b, 15 July 1949 (US holotype!). – *Bryopogon irvingii* (Llano) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 275 (1971); nom. inval. (Art. 33).

For further synonyms see Hawksworth (1972 p. 228).

Thallus erect to decumbent, 5–8 cm tall; branching isotomic dichotomous at the base, becoming anisotomic dichotomous towards the apices, angles between the dichotomies mainly acute; branches even in diameter, straight, 0.5–0.6(–0.8) mm diam.; cervine brown to dark brown or black, usually concolourous; dying from the base.

Lateral spinules usually frequent, slightly constricted basally, arising over the whole thallus. Pseudocyphellae usually present, sparse, inconspicuous to conspicuous, elongate fusiform, plane to slightly raised, c. 0.5 mm long, brownish to dark brown or black. Soralia absent.

Apothecia and pycnidia unknown.

Inner cortex and medulla K–, C–, KC–, PD+ red at least in parts. Contains fumarprotocetraric acid.

Ecology. On dry or wet tundra, or occasionally, in pine stands in the northern hemiarctic region; generally associated with rocks, especially non-calcareous rocks, although we have seen some specimens from calcareous tundra. There is one specimen from the low branches of a white spruce (Ontario, Fort Severn, Ahti s.n., 2 Aug. 1958 [O]).

Recent research by K. A. Kershaw and D. W. Larson (Kershaw & Larson 1974, Larson & Kershaw 1975, Kershaw 1975) has helped to explain the physiological bases for the ecological and geographic distribution of *B. nitidula*. They have shown that this species is an extreme xerophile at cold temperatures, explaining its tendency to be found on ridge tops where air flow and drainage are at a maximum and where both moisture levels and temperatures are low (Kershaw & Larson 1974). Further work provided evidence for the adaptive value of dark colour for lichens such as *B. nitidula* which are found in habitats largely swept clean of snow during the winter (Larson & Kershaw 1975, Kershaw 1975). Whereas *B. nitidula* would seem to have a net carbon deficit during the summer months due to high respiration rates at high temperatures, in early spring its dark cortical pigmentation enables the thallus temperature to rise significantly above the air temperature and greatly increase its available growth period. In small "melt-pockets" caused by tufts of these dark plants, assimilation may even occur underneath thin layers of snow (Larson & Kershaw 1975).

Distribution. Arctic to hemiarctic; entirely absent from the western mountains with the exception of one collection from the Garibaldi Mountains north of Vancouver (Fig. 49). There are other populations in the Otish and Shickshock Mountains of Quebec. These peaks are all well known for their arctic disjuncts. The absence of *B. nitidula* in the forested interior of Newfoundland is striking but not unexpected. Its occurrence over granite on the wind-swept coastal heaths near Halifax is also not entirely surprising. These coastal localities have numerous northern relicts (Roland & Smith 1969 p. 296). *B. nitidula* is circumpolar, but is of very scattered occurrence in northern Europe and Asia (Hawksworth 1972).

It has recently been recognized in Japan as

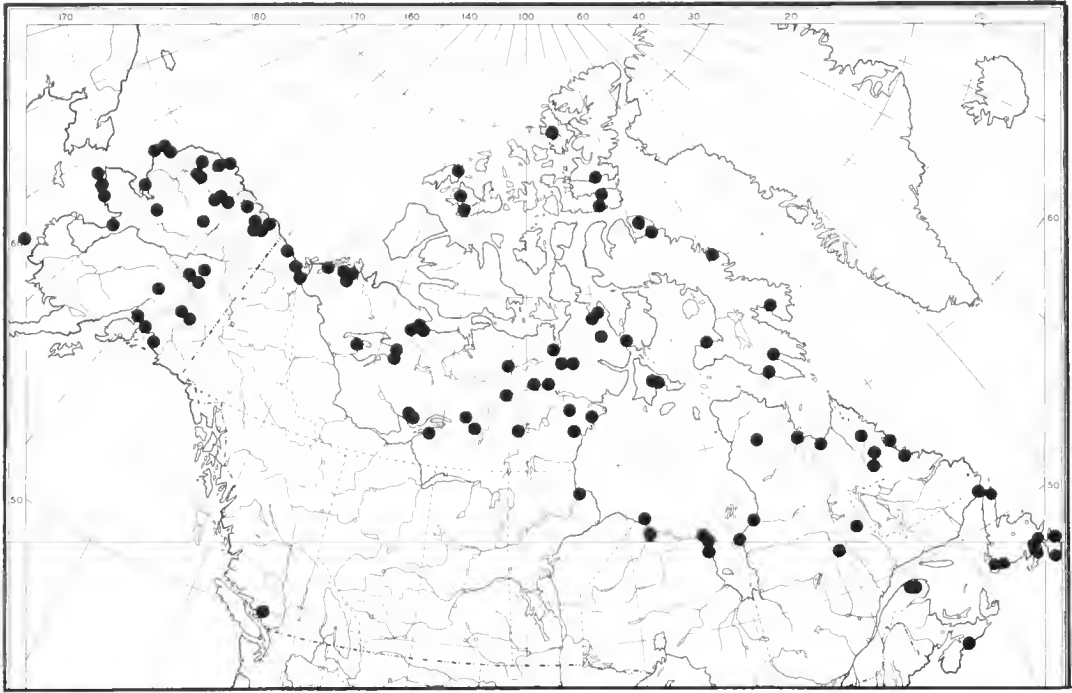


Fig. 49. *Bryoria nitidula*. N. American distribution.

part of the orohemiarctic zone flora (Jørgensen 1975).

Discussion

Bryoria nitidula has often been confused with *B. bicolor*, a species from which it is readily separated by its coarser habit, branching pattern, and concolourous darker thallus. In addition *B. nitidula* is essentially a species of the tundra in North America whilst *B. bicolor* is a coastal species restricted to more temperate parts of the continent. A more frequent cause of misidentification arises from the superficial similarities of *B. nitidula* and *Cornicularia divergens*, species which are often associated with one another. *C. divergens* is, however, easily distinguished by its white and more discrete oval pseudocyphellae which react C+ rose-red (olivetric acid), and its shiny, distinctly red-brown colour.

Ahti (1964) noted that Ontario material of *B. nitidula* tended to be coarser than the

Scandinavian specimens available to him. This species does indeed tend to be more luxuriantly developed in North America than either Europe or Japan, but as specimens similar to those in Europe occur in North America and intergrade with the coarser plants, the degree of luxuriance appears to be of little taxonomic importance.

This species varies considerably in colour from dark, dull red-brown to almost black, and the habit and branching vary from erect and almost strictly monopodial to decumbent and very irregularly branched (Fig. 50). While extreme morphotypes are often very distinctive, a complete series of intergradations occurs, indicating that these types of variations are of little taxonomic significance.

Motyka (1964) considered *Alectoria irvingii* Llano as a good species closely allied to "*A.*" *subdivergens* Dahl, and possibly belonging in *Oropogon* Th. Fr. We agree with Krog (1968) that this taxon comes within the range of variation of *B. nitidula* although the thalli of the type specimen are rather coarse.

A

B

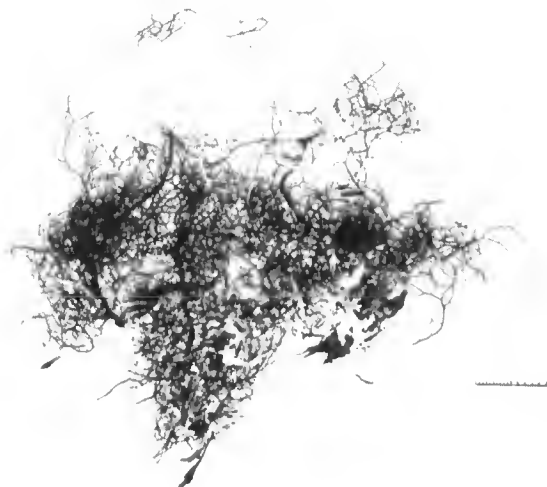


Fig. 50. *Bryoria nitidula*. – A: The common erect, robust morphotype. Ontario, Cape Henrietta Maria, Neal 019 (CANL). Scale 0.5–1.0 mm. – B: The small, prostrate morphotype. Quebec, Gaspé, Mt. Albert, Brodo 18538A (CANL). Scale 0.5–1.0 mm.

Selected specimens

Exsiccatae. Thomson: Lich. Arct. 84: N.W.T., District of Keewatin: Rossby Lake, J. W. Thomson & Larsen (CANL, COLO, DUKE, US).

Canada. British Columbia. Coast Area: Garibaldi Mountains (other data unknown) – *Manitoba*. Fort Churchill, Gillett 1608 (CANL) – *Ontario*. Kenora District: Cape Henrietta Maria, Cowell 1286A (CANL) – *Quebec*. Cté Gaspé-Nord: Mont Albert-Nord, Gauthier 2061 (CANL) – Territoire du Nouveau Québec: Great Whale River, L. Thomson 21 (US) – *Nova Scotia*. Halifax County: Duncan's Cove, Taschereau B-4 (NSPM) – *Newfoundland*, Labrador North District: Hopedale, Perrott 1-L (FH) (See also Ahti & Hawksworth 1974.) – *Yukon*. British Mountains, Trout Lake, J. W. Thomson & Larsen 14756 (p.p.) (WIS) – *Northwest Territories*. Franklin District: Baffin Island, Frohisher Bay, Hale 344 (CANL, WIS). – Keewatin District: Parsons Lake, J. W. Thomson & Larsen 5878 (WIS) – Mackenzie District: Crossley Lakes, Scotter 8058 (H).

U.S.A. Alaska. Aleutian Islands: Attu Island, Van Schaack 292 (US) – Amchitka Island, Reich & McCann 77 (F, WIS) – Arctic Coast District: Franklin Bluffs, J. W. Thomson 6474 (WIS).

13. *Bryoria simplicior* (Vain.) Brodo & D. Hawksw., comb. nov.

Alectoria nidulifera f. *simplicior* Vain., Medd. Soc. Fauna Fl. Fenn. 6: 115 (1881); type: Finlandia, Lapponia, Paatsjoki, E. A. Vainio, 1878, herb. Vainio no. 01067 (TUR 001403 lectotype!); basionym. – *Alectoria simplicior* (Vain.) Lynge, Norske Vid.-Akad. Oslo, Mat.-Nat. Kl. 1921 (7): 212 (1921). – *Bryopogon simplicior* (Vain.) Gyeln., Feddes Repert. 38: 233 (1935). – *Alectoria simplicior* f. *typica* Vain., Ann. Univ. Turku., ser. A, 7(1): 8 (1940); nom. illegit. (Art. 63).

Bryopogon nitidulum f. *caespitosa* Savicz, Trudy Student. Nauch. Fis. Mat. Fak. Univ. Jurjew 3: 40 (1911); type: U.S.S.R., Prov. Archangel, R. Pohle W538, 1904 (LE lectotype!). – *Alectoria nitidula* f. *caespitosa* (Savicz) Zahlbr., Cat. Lich. Univ. 6: 396 (1930). – *Alectoria lanca* f. *caespitosa* (Savicz) Gyeln., Nyt Mag. Naturvid. 70: 60 (1932). – *Bryopogon bicolor* var. *nitidulum* f. *caespitosus* (Savicz) Gyeln., Feddes Repert. 38: 237 (1935).

Alectoria simplicior f. *subintricans* Vain., Ann. Univ. Turku., Ser. A, 7(1): 8 (1940); type: Finlandia ladogensis, Sortavala, Kotiluoto, E. Vainio, 14 July 1926, herb. Vainio no. 01073-5 (TUR 001250 lectotype!).



Fig. 51. *Bryoria simplicior*. Quebec, Upper Seal Lake, Campbell s.n. (CANL 49618). Scale 0.5–1.0 mm.

Bryopogon simplicior f. *albidosorediosus* Gyeln., Acta Geobot. Hung. 2: 166 (1937); type: U.S.S.R., Sibirien, Jakutskaja A.S.S.R., Uralgebirge, Elbyn-torsee, W. Safrasknikow, 9 September 1919 (BP 33.975 holotype!).

Alectoria simplicior var. *lapponica* Gyeln., Nyt Mag. Naturvid. 70: 62 (1932); type: Suecia, Lapponia tomeensis, par. Jukkasjärvi, prope lacum Aptasjärvi, ad ramulos Pini desiccatos, G. Lång, Krypt. Exs. Vindob. no. 1977 (BP 33.962 holotype!). – *Bryopogon simplicior* f. *lapponicus* (Gyeln.) Gyeln., Feddes Rept. 38: 234 (1935).

Alectoria nana Mot., Bryologist 67: 16 (1964); type: Alaska, Alaska Range District, Mt. McKinley National Park, Wonder Lake, H. Krog 4779, 14 August 1957 (O lectotype!); nom. inval. (Arts. 36, 37). – *Bryopogon nanus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 371 (1971); nom. inval. (Arts. 33, 36, 37).

Thallus caespitose, sometimes becoming decumbent, 2–4(–5) cm long; branching mainly isotomic dichotomous from the base, angles between the dichotomies usually acute; branches even in diameter, usually straight, rarely becoming slightly foveolate, 0.2–0.4 mm diam.; cervine brown to dark brown or almost black, concolourous; base persistent. Fig. 51.

Lateral spinules with slightly constricted bases, sparse to frequent, becoming abundant in some forms. Pseudocyphellae absent. Soralia abundant, fissural, usually broader than the branches on which they occur, white to brownish black or more usually greenish black, normally without any spinules but sometimes bearing irregular, often contorted, non-isidiiform spinules.

Apothecia and pycnidia unknown.

Cortex, medulla and soralia K–, C–, KC–, PD–. Contains no lichen products.

Ecology. Characteristically on well-lighted twigs and small branches of *Picea mariana* and *Larix laricina* in the open black spruce muskeg of the northern boreal forest, but occasionally on other trees in that community (e.g., *Picea glauca*, *Betula* spp., *Populus balsamifera*). We have seen no specimens from *Abies balsamea*, a tree very common in the southern boreal forest. In the west, *Bryoria simplicior* is often found on *Pinus contorta*. Rarely, the species is collected from the ground or rock (on several occasions, associated with *B. chalybeiformis*), but it is often found on lignum. Krusenstjerna & Santesson (1950) have remarked that, in the subalpine birch forests of Jämtland (Sweden), this species and "*A. jubata*" are clearly restricted to the portions of the birch trees above the highest level of winter snow.

This species almost invariably grows mixed with *B. lanestris* and frequently with *B. furcellata* as well.

Distribution. Northern boreal to hemiarctic zone from Newfoundland to Alaska, with scattered occurrences in the western mountains south to Colorado, and in the Shickshock Mountains of Quebec (Fig. 52). The other Quebec localities (e.g., in Parc des Laurentides) undoubtedly represent edaphically northern boreal outliers. The species can occur in arctic localities on rock, as it does in southwest Greenland (Dahl 1950), but its main distribution even in Europe is clearly in the northern boreal forests (Ahlner 1948, Poelt 1969). Ahlner (1948) cites published reports from Siberia, Kamchatka and Japan, and we have also seen collections from Mongolia (Golubkova [LE]); the species can thus be regarded as circum-boreal, apparently with continental rather than oceanic tendencies (Ahlner 1948, Ahti & Hawksworth 1974).

Discussion

Bryoria simplicior is a clearly defined species which is only likely to be confused with unusually dark specimens of *B. furcellata* lacking their characteristic tufts of spinules in the soralia, or with young plants of *B. lanestris*, a species with which *B. simplicior* is frequently entangled. *B. simplicior* is always PD– throughout. (*B. furcellata* is PD+ red throughout.

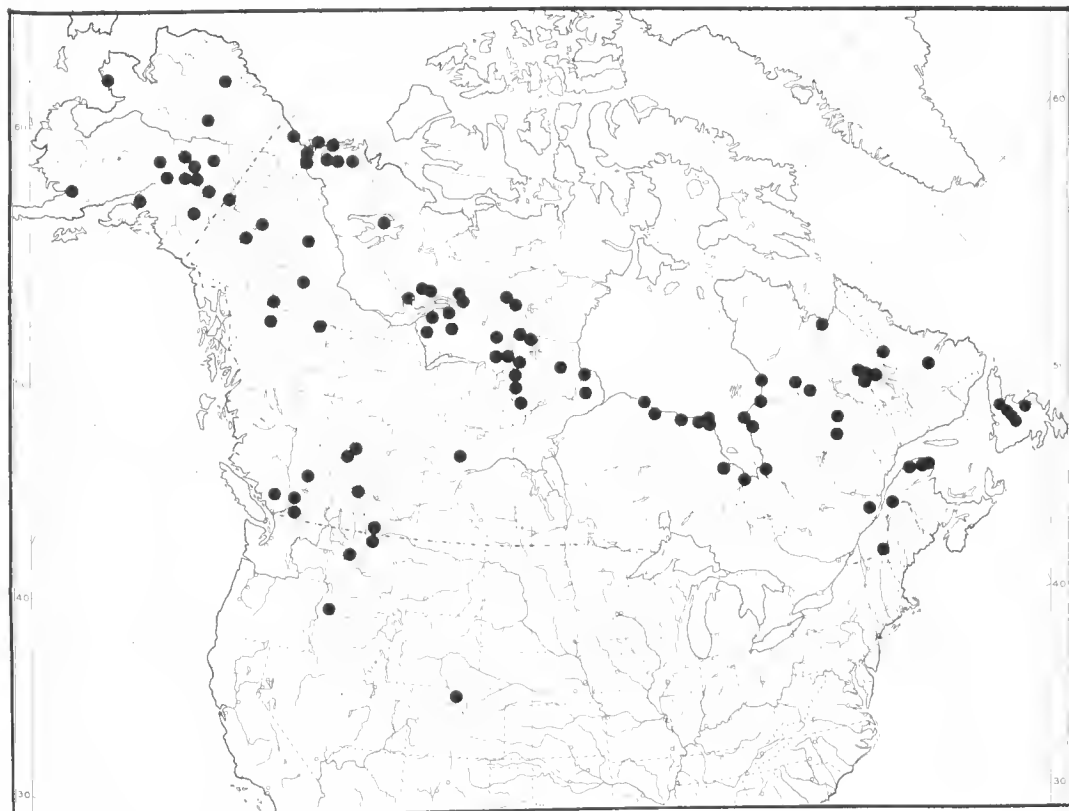


Fig. 52. *Bryoria simplicior*. N. American distribution.

and the soralia of *B. lanestris* are PD+ red whilst its thallus is PD-.) The greenish black soralia so characteristic of *B. simplicior* are unknown in any other North American species. (Soralia in both *B. furcellata* and *B. lanestris* are white or flecked with black.)

Attention is drawn to Ahlner's (1948) detailed discussion of this species.

Motyka (1964) indicated that the soralia of "*A. nana*", treated as a synonym of *B. simplicior* here, were PD+ red but this was due to some of the material he annotated as this being mixed with *B. lanestris*.

Selected specimens

Exsiccatae. Brodo: Lich. Can. Exs. 2: Ontario, Cochrane District: Moosonee, Fabiszewski M26/127 (CANL).

Canada, British Columbia, Coastal District:

Garibaldi Mountains, Whistler Mountain, Brodo 13939 (CANL) - Fraser River Basin: W of Marquart Lake, Scotter 9848 (WIS) - Liard River Basin: Cassiar, Szczawinski 684-8 (US. O) - Okanagan District: Princeton, Brodo 7815 (p.p.) (CANL) - Alberta, Banff National Park, canyon of Johnson Creek, Weber S23.592 (CANL, COLO) - 125 miles W of Edmonton, Turner s.n., 1 Aug. 1959 (LAM) - Waterton Lakes National Park, Redrock Canyon, Imshaug 6103 (WIS) - Saskatchewan, Hasbala Lake Region, Argus 953-62 (COLO) - Prince Albert National Park, Waskesiu, Jesberger 1171 (SASK) - Manitoba, Brochet, Scotter 3031 (WIS) - Fort Churchill, Crum & Schofield 6889 (CANL) - Ontario, Cochrane District: Mouth of the Moose River, Brodo 14748 (CANL) - Kenora District: SE of Fort Severn, Ahti 3726 (H) - Quebec, Cte Frontenac: Woburn, Masson 6030B (QUE) - Cte Gaspé-Est: Penouille Point, Gaspé, Brodo 18706 (p.p.) (CANL) - Parc des Laurentides: 70°47'W, 47°39'N, Scotter 6515 (H) - Cte Témiscouata: St-Juste-du-Lac, near Lac Témiscouata, Masson 11403B, (WIS) - Territoire de Mistassini: Otish Mountains, Mont du Lagopède, Shchepanek 71-L-58 (p.p.)



Fig. 53. *Bryoria tenuis*. A specimen from the tundra showing some pale tips. N. W. T., Spence Bay, McGrath 18 (CANL). Scale 0.5–1.0 mm.

(CANL) – Territoire du Nouveau Québec: Chimo Air Base, Marr 5 (COLO) – *Newfoundland*. Central Labrador: Goose Bay, Haufe 25098 (US) – Knob Lake, J. W. Thomson 13730 (WIS). (See also Ahti & Hawksworth 1974). – *Yukon*. 40 miles W of Watson Lake, Ahti 23492 (H) – British Mountains, Trout Lake, J. W. Thomson & Larsen 14758 (WIS) – Mountains N of the McQuesten River, Christie s.n. (CANL, LAM) – *Northwest Territories*. Mackenzie District: 3 miles SE of Indian Mountain Lake, Cody 16024 (CANL, WIS) – Keewatin District: Ennadai Lake, J. W. Thomson 11803 (CANL, US, WIS).

U.S.A. Alaska. Alaska Range District: Dry Creek, 63°53'–59'N, 147°20'–35'W, Viereck 6000 (ALA, COLO, CANL, WIS) – Arctic Coast District: Umiat, Llano 511x (US) – Bering Sea District: Safety Lagoon, Krog s.n., 22 June 1969 (O) – Central Yukon River District: Tanana River at mouth of Delta Creek, Viereck 7567F (ALA, WIS) – Western Pacific Coast: Nanwhyenuk Lake, Muller 855 (p.p.) (US) – *Colorado*. Larimer or Middle Grand County: Rocky Mountain Park, Summit Simpson Pass, Sanson 18 (FH) – *Idaho*. Payette County: Payette Lakes, A. H. Smith 16076C (WIS) – *Montana*. Sanders County: Fishtrap Creek, Taylor 7071 (p.p.) (WIS).

14. *Bryoria tenuis* (Dahl) Brodo & D. Hawksw., comb. nov.

Alectoria tenuis Dahl, Meddl. Grönl. 150(2): 144 (1950); type: Greenland, Julianehaab District, Igalik-

fjord, Egeluit, E. Dahl, 9 August 1937 (O holotype!); basionym. – *Bryopogon tenuis* (Dahl) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 271 (1971); nom. inval. (Art. 33).

Alectoria bicolor var. *subbicolor* Mot., Bryologist 67: 9 (1964); type: Alaska, Eastern Pacific Coast District, Ketchikan, Deer Mt., lower part, H. Krog 6252, 3 September 1957 (O lectotype!); nom. inval. (Arts. 36, 37).

Thallus erect to decumbent, or rarely subpendent, 4–6(–12) cm long; branching isotomic dichotomous towards the base but often tending to become anisotomic dichotomous towards the apices, angles between the basal dichotomies usually obtuse, angles between the apical dichotomies usually acute, third order branches usually absent; branches terete, even in diameter, sometimes becoming slightly compressed towards the base, 0.3–0.4(–0.5) mm diam.; basal branches becoming black, apical branches pale brown to brown (always paler than the basal parts); base often dying. Fig. 53.

Perpendicular lateral spinules with slightly constricted bases present, sometimes poorly developed. Soralia absent.

Pseudocypheallae abundant to scanty, fissural, plane to slightly raised, usually dark and inconspicuous.

Apothecia very rare (known from one collection from Alaska, Krog 6252), lateral, appearing geniculate; excipulum thallinum concolourous with the thallus, thin, becoming excluded as the ascocarps mature; disc concave at first, becoming convex when mature, yellowish brown to reddish brown, to 1.5 mm diam. Thecium c. 70 μ m high, tall, asci c. 45 \times 15 μ m, epithecium IKI + acruiginose. Spores 8 per ascus, subglobose to ellipsoid, hyaline, simple, with a rather thick (1 μ m) wall, (6–) 7–9.5 \times 5–7 μ m. Pycnidia not seen.

Inner cortex and medulla K–, C–, KC–, PD + red at least in parts (perhaps rarely PD–). Contains fumarprotocetraric acid.

Ecology. Characteristically on mossy trees and rocks in moist conifer forests, but also found in rock crevices and on mossy rock surfaces in more exposed subalpine sites. In the southern Appalachian mountains, it is apparently restricted to the fir forests above 1800 m. All the specimens we have seen from that area are from *Abies* (presumably *A. fraseri*). The arctic collections (e.g., McGrath, Spence Bay,

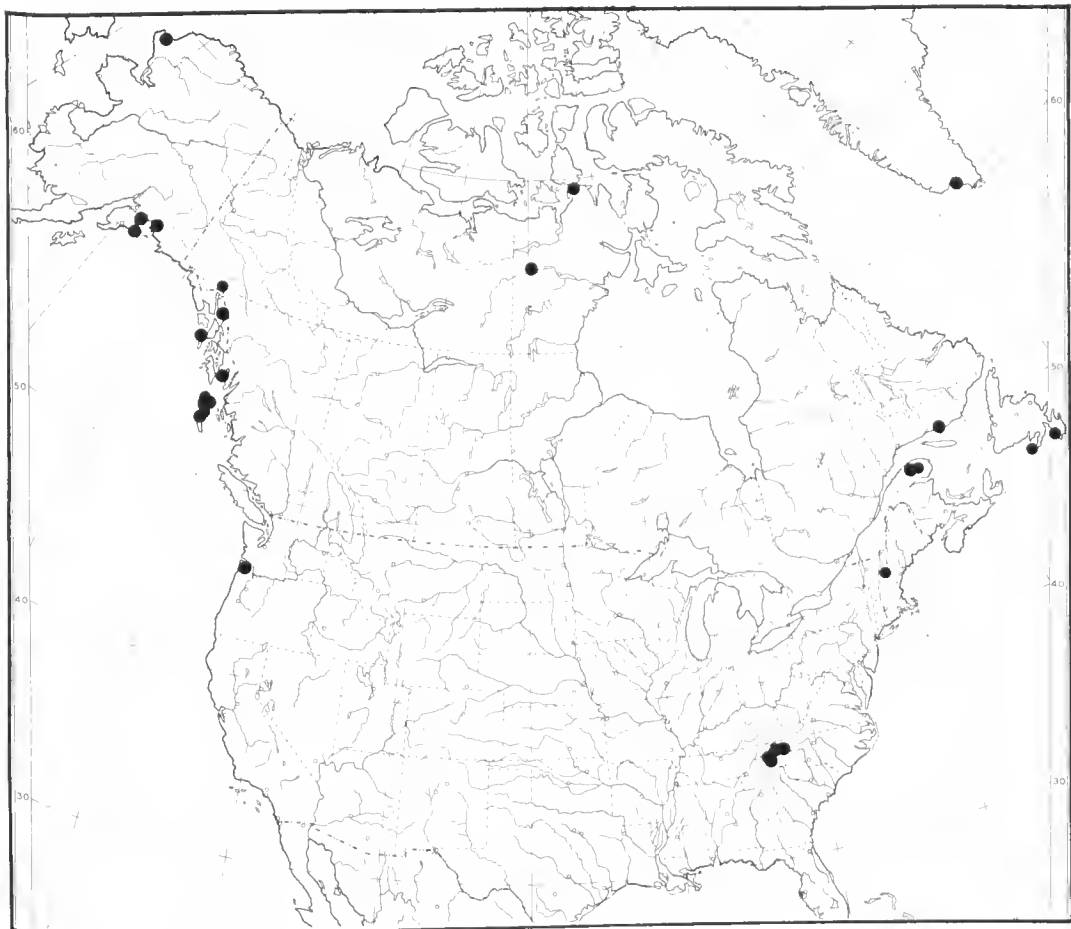


Fig. 54. *Bryoria tenuis*. N. American distribution.

N.W.T.) were generally growing between rock fragments much as *Alectoria ochroleuca*. They are fairly typical in morphology, although sometimes lacking in the long, curled tips described by Dahl (1950) in the original Greenland material. In the alpine areas of the Tyrolian Alps, the species grows on boulder surfaces mixed with other saxicolous foliose and fruticose lichens.

Distribution. Oceanic localities along the Appalachian Mountains, and along the coasts of British Columbia and Alaska, with scattered arctic populations in northern Alaska, Keewatin (N.W.T.) and southwestern Greenland (Fig. 54). In Europe, *B. tenuis* does not seem to be

as clearly oceanic as it does in North America. Although it is known from western Norway, Jørgensen & Ryvarden (1970) point out that the localities are in the mountains. The species is also known from a few localities in Sweden (Jørgensen 1972). One of us (I.M.B.) has seen and collected it on rocks near tree-line in the Austrian Alps. Its occurrence in the American arctic is not entirely surprising since the species was described from the tundra of southwest Greenland (Dahl 1950). A very similar distribution is shown by the clearly oceanic crustose lichen, *Placopsis gelida* (L.) Linds. (Thomson 1972). We have not seen the specimen from the Aleutian Islands (Adiak Island) reported by Jørgensen (1972) but presume it is correct.

Discussion

Bryoria tenuis is most closely allied to *B. bicolor*. The decumbent habit and the third-order perpendicular branches in *B. bicolor* serve to distinguish the two species. The branching pattern of *B. tenuis* is not unlike that of *B. nadvornikiana* which is easily distinguished by its chemical reactions (K + bright yellow, KC + red, PD + orange-yellow) and much paler apical parts. More detailed information on the differences among these three species may be found in Dahl (1950) and Jørgensen & Ryvarden (1970).

Although some specimens of *B. tenuis* appear to be PD- on the basis of routine testing, a careful re-examination using the methods described under Chemistry (Figs. 17, 18) shows them all to be PD + red at least in some of their pale, apical branches. This is also true of the type specimen of *B. tenuis* which, contrary to the findings of earlier authors, proves to be PD + red in part. Consequently, we do not believe there to be a truly "inactive strain" of this species as was suggested by Krog (1968), but would stress that the amount of fumarprotocetraric acid in this species may sometimes be so small as to be barely detectable in routine testing.

Motyka (1964) treated only specimens he found to be PD- as "*Alectoria tenuis*", referring PD+ plants to "*A. bicolor* var. *subbicolor*". As pointed out by Krog (1968) and Jørgensen (1972), such a view is in any event entirely unacceptable as it ignores the morphological differences which readily serve to distinguish these two species.

Apothecia have not previously been reported in this species and were seen by us only in the single collection cited above.

One specimen of *B. tenuis*, collected in the White Mountains of New Hampshire by Tuckerman (FH-Tuck.), was superficially much like *B. smithii* but lacked soralia and the typical clusters of isidioid spinules. Per M. Jørgensen (in litt.) examined the material at our request and concluded that it did not seem to be *B. smithii*, but was more likely a rather coarse *B. tenuis*. The thallus is completely PD- and revealed nothing in TLC; it is therefore the only specimen of *B. tenuis* we have seen totally lacking in fumarprotocetraric acid.

Selected specimens

Exsiccatae. Brodo: Lich. Can. Exs. 83; *British Columbia*, Moresby Island, Brodo 18507 (CANL).

Canada. *British Columbia*. Chilkat River Basin: Near Chilcoat Pass, Williams 69 (NYBG) - Islands North District: Graham Island: Awun Lake, Brodo 18478 (CANL) - Moresby Island: Between Sandspit and Copper Bay, Brodo 12880 (CANL) - *Quebec*. Cte Gaspé-Nord: Mont Albert Nord, Gauthier 2637 (CANL) - Cte Matane: Between Mount Mattaouisse and Mount Collins, Collins 2155 (FH) - Cte Saguenay: Archipel de Mingan, Marie-Victorin & Rolland-Germain 18,298 (p.p.) (US) - *Newfoundland*. Placentia East District: St. Bride's, Ahti 8867 (H) - *Ile Miquelon*. Delamar S211 (S) - *Northwest Territories*. Keewatin District: Spence Bay, McGrath 18 (CANL) - Thelon River, Aberdeen Lake, Scotter 4233 (WIS).

U.S.A. *Alaska*. Arctic Coast District: Pitmegea River, Cape Sabine, J. W. Thomson 5530 (WIS) - Central Pacific Coast District: Prince William Sound. Pigot Bay, Krog 2206 (O) - Eastern Pacific Coast District: Sitka, Sitka National Monument, Krog 6245 (O) - *New Hampshire*. County unknown: White Mountains, Herb. E. Tuckerman 676 (FH) - *North Carolina*. Yancey County: Black Mountains, Mt. Mitchell State Park, Dey 1197 (DUKE) - *Oregon*. Clatsop County: Saddle Mountain State Park, Pike 3763 (OSC) - *Tennessee*. Sevier & Cocke Counties: Old Black in the Great Smoky Mountains National Park, Dey 6628 (DUKE).

***Bryoria* sect. *Implexae* (Gyeln.) Brodo & D. Hawksw., comb. nov.**

Bryopogon sect. *Implexae* Gyeln., Feddes Repert. 38: 223 (1935); basionym. - *Bryopogon* sect. *Bryopogon* subsect. *Implexae* (Gyeln.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 274 (1971).

Bryopogon sect. *Fuscidulae* Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 271 (1971); type: *B. fuscidulus* (Arnold) Bystr. nom. inval. [= *Bryoria capillarlis* (Ach.) Brodo & D. Hawksw.], holotype.

Bryopogon sect. *Flexuosae* Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 272 (1971); type: *B. flexuosus* (Mot.) Bystr. nom. inval. [= *Bryoria pseudofuscescens* (Gyeln.) Brodo & D. Hawksw. aggr., see Hawksworth 1972], holotype.

? *Alectoria* subgen. *Bryopogon* sect. *Pellucidae* Mot., Fl. Polska, Porosty 5(2): 39 (1962); type: *A. pellucida* Mot. [= *Bryoria* sp., see p. 59], holotype. - *Bryopogon* sect. *Pellucidae* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 275 (1971), as "Mot."

Type species: *Bryoria implexa* (Hoffm.) Brodo & D. Hawksw. (syn. *Usnea* tax. vag. *implexa* Hoffm., *Alectoria implexa* (Hoffm.) Nyl.; lectotype designated by Bystrek 1971 p. 274).

Thallus decumbent to subpendent or pendent; greyish green, fuscous or brown to dark brown, generally not becoming blackened except in

fragmentation regions. True lateral spinules and isidia absent. Soralia absent in most species, frequent in others, mainly tuberculate, white. Pseudocyphellae always present, very variable in size, fusiform and inconspicuous to spiralled and readily visible, depressed or very slightly elevated, usually whitish. Cortex composed of broad hyphae with very little matrix. Apothecia rare, unknown in many species; margins not ciliate; discs orange-brown to reddish brown or rarely white. β -orcinol depsidones other than fumarprotocetraric acid frequent; atranorin and/or chloroatranorin, and fumarprotocetraric acid sometimes present in traces; pulvinic acid derivatives absent.

Discussion

This section comprises about 12 species characterized principally by the occurrence of β -orcinol depsidones other than fumarprotocetraric acid, small pseudocyphellae, and a characteristic cortical structure which tends to make the branches more friable than usual in the genus. Two species with conspicuous spiral pseudocyphellae (*B. pseudocapillaris* and *B. spiralifera*) are being included here with some hesitation.

As a result of our studies it has become clear that this group is much more varied than previously supposed. While most of the taxa accepted here are readily recognizable, taxonomic problems exist with several of them as will be evident from the discussions following individual species.

This section is alone amongst *Alectoria* and its allied genera in including species able to produce a tridepside (gyrophoric acid): *B. friabilis* (consistently), and *B. pikei* (some specimens).

15. *Bryoria capillaris* (Ach.) Brodo & D. Hawksw., comb. nov.

Parmelia jubata β . *capillaris* Ach., Meth. Lich.: 273 (1803); type: Suecia (H-Ach., upper specimen, lectotype!); basionym. – *Alectoria capillaris* (Ach.) Cromb., J. Bot., Lond. 9: 177 (1871).

For further synonyms see Hawksworth (1969 pp. 393–394, 1972 pp. 209–211).

Thallus pendent, commonly 10–15(–30) cm long; branching irregular, isotomic dichotomous to

anisotomic dichotomous, angles between the main branches usually acute; branches even to uneven in diameter, sometimes becoming slightly twisted or compressed especially towards the base, capillaceous, 0.1–0.3(–0.5) mm diam.; greenish grey to grey, sometimes becoming brown to dark brown, matt to slightly shiny.

True lateral spinules absent. Soralia absent in North American material. Pseudocyphellae usually present, inconspicuous on pale morphotypes, fusiform, white, 0.1–0.25 mm long.

Apothecia rare in North American material, seen in a single collection (Montana, Glacier National Park, H. & V. Bailey 17 p.p. [H]), lateral, up to 1.5 mm in diameter; discs becoming strongly convex, light brown, epruinose; excipulum thallinum concolourous with thallus, soon becoming reflexed and disappearing. Spores 8 per ascus, hyaline, ellipsoid to subglobose, simple, 5.3–6.8 \times 4.0–4.5 μ m. Pycnidia not seen.

Cortex, medulla and soralia K + bright yellow, C + pink or –, KC + red, PD + yellow. Contains barbatolic acid, \pm alectorialic acid.

Ecology. On trees of all kinds, especially *Picea*, *Pseudotsuga*, *Abies* and *Tsuga* species, mainly in well-lighted portions of mature coniferous forests. Collected once from rock (Michigan, Isle Royale, Wetmore 1597 [MSC]). In oceanic or suboceanic forests, such as those on the Queen Charlotte Islands (British Columbia) the species grows in great abundance forming large, grey clumps hanging from low branches.

Distribution. Southern boreal to north temperate (hemiboreal) distribution in the east; Rocky Mountains of Alberta, British Columbia, Idaho and Montana; and coastal forests from California to southern Alaska (Fig. 55). The North American distribution shows distinct clumping in the more humid forest zones: coastal and interior *Tsuga-Thuja* forests; Lake Superior region corresponding to the “strongly humid southern boreal zone” (Ahti 1964); the St. Lawrence region; and the Atlantic coastal region. Scattered middle and northern boreal forest localities are also known. Hawksworth (1972) comments on the world distribution of *B. capillaris*, citing it from northern and southern Europe, the Canary Islands, and Japan.

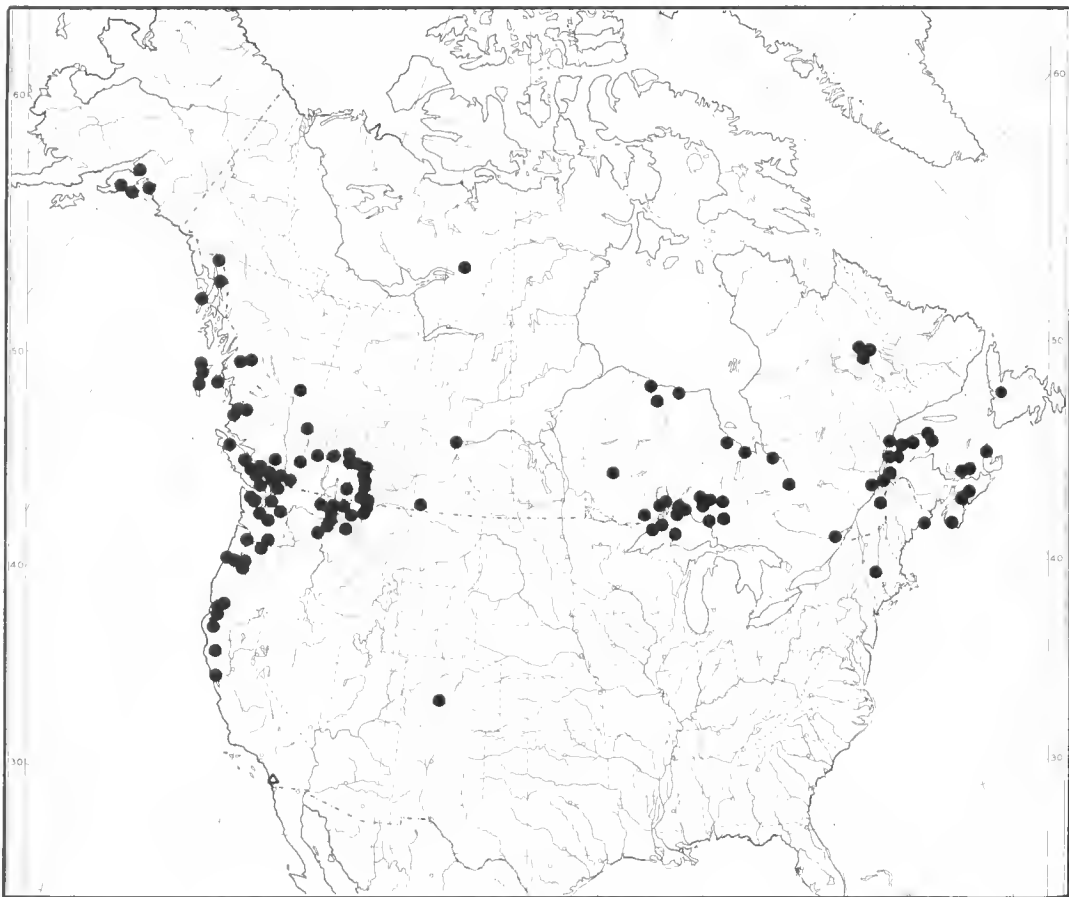


Fig. 55. *Bryoria capillaris*: N. American distribution. Δ determination uncertain.

The species is probably circumboreal in the Northern Hemisphere.

Discussion

Our study has revealed a number of problems in the systematics of this species arising from both morphological and chemical variability. Firstly, while *B. capillaris* is frequently (but by no means always) sorediate in Europe, no sorediate North American specimens have been found by us; this character is therefore regionally useful for the separation of *B. capillaris* from exceptionally pendent specimens of *B. nadvornikiana* which is almost invariably sorediate in North America. Secondly, there are variations in the degree of shininess, the

thickness of the main stems, and colour. Thirdly, these latter variations may perhaps be related to differences in the ratio of alectorialic to barbatolic acid and thus to differences in the intensity of the K^+ reaction. (In the presence of alectorialic acid without barbatolic acid, a K^+ very pale yellow or K^- reaction is obtained.) The species is clearly very closely allied to *B. pikei* (see Discussion under that species). It also appears to be related to *B. pseudofuscescens*, to judge from the discovery of a collection with both barbatolic and norstictic acids (Washington, near Dungeness, A. S. Forster 2552a [FH!]; mixed with typical *B. capillaris* and *Sulcaria badia*) which might even be considered a hybrid (see pp. 33, 71).

When the chemistry of some European

collections was examined by TLC, further difficulties came to light. It now appears that many European specimens (those with soredia) contain chloroatranorin or atranorin, or both, and often traces of fumarprotocetraric acid in addition to the usual American components. We have not found any atranorin or chloroatranorin in any North American material of this species. The lectotype specimen of *B. capillaris* is mainly esorediate but has a few basal sorediate branches. Through the courtesy of Mr. O. Vitikainen, we have been able to examine both sorediate and esorediate portions of it by TLC. These prove to have similar chemistries with chloroatranorin, possibly a trace of atranorin (a weak spot evident in PD but not under UV alone), alecatorialic acid, barbatolic acid, and a spot which may be fumarprotocetraric acid (very faint).

Material identical to the North American *B. capillaris* (i.e., esorediate, containing alecatorialic and barbatolic acids and lacking atranorin and chloroatranorin) does, however, occur in parts of Europe (e.g., Arnold, Lich. Exs. no. 914a, sub *A. cana* f. *fuscidula* [M!]). If this population later proves to be of taxonomic significance at the species level, type specimens of the numerous synonyms of *B. capillaris* will require examination by TLC before the appropriate name can be determined.

Specimens corresponding to Hawksworth's (1972) concept of *A. capillaris* f. *fuscidula* occur in North America. We have reinvestigated the status of this name, however, since Motyka has applied the epithet in herbaria to specimens more properly identified as *B. kuemmerleana* (Gyeln.) Brodo & D. Hawksw. or, more rarely, *B. capillaris* and *B. pseudofuscescens* as understood by us. This confusion appears to have arisen primarily from Motyka (1960) considering the epithet to have been published in 1884 (when it in fact was validated in 1882) and to his treating as the holotype a specimen in M which was collected in the type locality in 1896 (M!) (rather than in 1880 as stated by Motyka 1960). The lectotype designated by Hawksworth (1972) was at least an isotype and could have been considered the holotype apart from the fact that Arnold did not annotate any one collection "typus". This specimen, and duplicates of it, consist of mixture of *B. capillaris* and fragments of *B. kuemmerleana*,

in which *B. capillaris* clearly predominates. An examination of all available material in M which was collected by Arnold and was annotated by him as *fuscidula*, showed that he had not applied this name consistently. In view of this confusion, it is probably in the best interests of taxonomic stability to consider this epithet a *nomen ambiguum* to be rejected in accordance with the provisions of Art. 69.

It will be evident from the above comments that many critical studies considering both morphological and chemical characters on a world scale need to be carried out in order to ascertain the taxonomic importance of the findings reported here. We consequently feel that it would be premature for us to propose any changes in the nomenclature or circumscription of *B. capillaris* and its allied chemo- and morphotypes here.

Selected specimens

Exsiccatae. Brodo: Lich. Can. Exs. 78: *British Columbia*, Moresby Island, Brodo 12247A (CANL) – 79: *British Columbia*, Creston, Brodo 15110 (CANL) – ?80: *British Columbia*, Earl's Cove, Brodo 8330 (CANL) – Lich. California Exs. (no number): *California*, Marin County Sausalito, M. A. Howe 79 (COLO, DUKE, FH, NYBG).

Canada. British Columbia. Islands North District: Moresby Island: Harriet Harbour, Brodo 12551 (CANL) – Islands South District: Little Qualicum Falls Provincial Park, Ahti 6528 (H) – Coastal Area: Alice Lake, Ohlsson 436A (CANL) – Columbia River Basin: Valley of Illecillewaet R., Brodo 7668 (CANL) – Dean River Basin: Stuie, Tweedsmuir Lodge, Ohlsson 2165 (CANL) – Fraser River Basin: Near Malakwa, Bird 15275 (p.p.) (WIS) – Kootenay River Basin: Creston, Brodo 15123A (CANL) – Okanagan: 34.6 miles S of Princeton, Brodo 8503B (CANL) – Peace River Basin: Alaza (sic) (Aleza) Lake, Kujala s.n., 24 July 1931 (H) – Skagit River Basin: Manning Park, Ahti 15399 (H) – Skeena River Basin: Hazelton, Ohlsson 2962B (MSC) – *Alberta*, Bragg Creek, Bird 10966 (p.p.) (CANL) – *Saskatchewan*, Cypress Hills Park, Looman s.n., 7 April 1959 (LAM) – *Ontario*, Algoma District: Near Brule, Grassl 1674 (MSC) – Cochrane District: Near Moose Factory, Brodo 14694 (CANL) – Kenora District: Fort Severn, Ahti 3950 (H) – Thunder Bay District: Shebandowan, Brodo 13632 (CANL) – *Quebec*, Cte Abitibi Ouest: Guyenne, Brodo 16889 (CANL) – Cte Gaspé Est: Cap-des-Rosiers-Est, Brodo 18668 (CANL) – Cte Rimouski: Ile au Massacre, Masson 14162 (WIS) – *Prince Edward Island*, Kings County: Montague, Ireland 10207B (CANL) – *Queens County*: 14 miles NW of Charlottetown, Fabiszewski s.n., 22 July 1970 (CANL) – *Nova Scotia*, Colchester County: Macoun s.n., 12 June 1883 (CANL). Kings

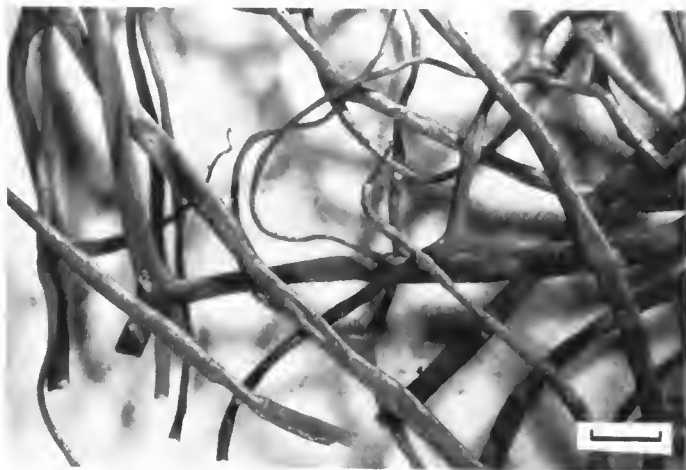


Fig. 56. *Bryoria friabilis*. Note the irregularly broken end of the filaments. B. C., Skeena River, Macoun s.n. (CANL 16156). Scale 0.5 mm.

County: Wolfville, Gillett 15683C (CANL) – *Newfoundland*. Labrador West District: Schefferville, Brodo 9343B (CANL) – Humber East District: Cormack, Ahti 5930 (H) – *Northwest Territories*. Mackenzie District: Artillery Lake, J. W. Thomson & Larsen 12623 (WIS).

U.S.A. Alaska. Central Pacific Coast District: Kenai Peninsula, Seward, Krog 2195 (O) – Eastern Pacific Coast District: Auke Lake, Imshaug 28490 (MSC) – *California*. Humboldt County: Horse Mountain, Brodo 20516 (CANL) – *Colorado*. Chaffee County: Near Buena Vista, Imshaug 11679 (MSC) – *Idaho*. Latah County: Bovill, Schroeder L367, 13 Sept. 1969 (SCHROEDER) – *Maine*. Hancock County: Salisbury Cove (sic) (Salisbury Cove), Plitt 167 (US) – *Michigan*. Keweenaw County: Isle Royale National Park, Capt. Kidd I., Wetmore 4674 (MSC) – *Minnesota*. Cook County: Grand Portage I., Fink 17 (H, US, FH) – *Montana*. Flathead County: Glacier National Park, Grinnell Creek, Imshaug 5547 (CANL, LAM, WIS, US) – *Oregon*. Lane County: Willamette Pass, Becking 6308194 (BECKING) – *Vermont*. Windham County: Stratton, Moore 1532 (US) – *Washington*. Kittitas County: Wenatchee National Forest, Hoffman OP-27 (US) – Whitman County: Kamiak Butte, Esslinger 1774C (WIS).

16. *Bryoria friabilis* Brodo & D. Hawksw., sp. nov.

Thallus pendulus, vel raro ubi saxicola decumbens, friabilis, ad tactum disrumpens, ad 15 cm longus; rami praecipue aniso-dichotomiter fastigiati et in angulos obtusos ad proxime 90° divergentes, plerumque diametro inaequales, valde contorti, rugosi et foveolati, ramis principalibus crassis plerumque ramis brevibus gracilibus perpendiculariter instructis (similibus iis *Bryoriae fremontii*); planta

pallidissime cervineo-brunnea, in herbario denigrans.

Rami laterales spiniformes veri, isidia et soralia desunt. Pseudocyphellae copiosae, brunneolae vel albae, late fusiformes, circa ramos tortuosae. Cortex tenuis, e hyphis distincte undulatis compositus, parietibus cellularum subtilibus.

Apothecia rarissima, lateralia, 0.35–0.5(–0.8) mm diametro, saepe aliquantum elongata; discus convexus et reflexus, albus vel dilute fuscus, epruinosis; excipulum proprium hyalinum vel brunneum. Ascosporae incolores, ellipsoideae, simplices, parvae, $4.2\text{--}5.0 \times 2.4\text{--}3.0 \mu\text{m}$. Pycnidia ignota.

Cortex K–, C+ rubescens vel roseus, KC+ roseus, PD–; medulla K–, C–, KC–, PD–; apothecia PD+ lutea, K–, C–, KC+ rosea. Cortex thalli acidum gyrophoricum continens; epithecium, hymenium et excipulum proprium apothecii acidum alectorialicum continentia.

Holotypus: America septentrionalis, U.S.A., Washington, Gate, in *Quercu*, rara, A. S. Foster s.n., 14 October 1911 (NYBG).

Thallus pendent, or rarely decumbent when on rocks, brittle, breaking when touched, to 15 cm long; branching mainly isotomic dichotomous, angles between the dichotomies obtuse to almost 90°, branches usually uneven, very contorted, wrinkled and foveolate, main branches often with short, slender, perpendicular side branches (similar to those of *B. fremontii*); very pale cervine brown, becoming darker in the herbarium. Fig. 56.

True lateral spinules, isidia, and soralia absent. Pseudocyphellae abundant, brownish to white, broadly fusiform, twisting around the branches. Cortex thin, composed of distinctly undulating thin-walled hyphae.

Apothecia rare (seen only in a single specimen: British Columbia, Vancouver Island, Nimpkish Valley, Stevenson 747a, 2 Nov. 1975 [UBC]), lateral, 0.35–0.5(–0.8) mm in diameter, often somewhat elongated along the filament; discs strongly convex and reflexed, white to very pale buff (or rarely brown in apothecia having a pigmented excipulum), epruinose; excipulum thallinum concolourous with disc and hardly distinguishable from it; excipulum proprium hyaline, or brown in some apothecia. Spores eight per ascus, hyaline, ellipsoid to subglobose, simple, very small, $4.2\text{--}5.0 \times 2.4\text{--}3.0\ \mu\text{m}$. Pycnidia not seen.

Cortex K–, C+ red or pink, KC+ pink, PD–; medulla K–, C–, KC–, PD–; apothecia PD+ deep yellow, K–, C–, KC+ pink. Contains gyrophoric acid in the thallus cortex and alecatorialic acid in the epithecium, hymenium and excipulum proprium of the apothecia.

Ecology. On trees in exposed habitats, from sea level to 1500 m elevation; very rarely on rocks or shrubs.

Distribution. West coast-east coast disjunct distribution, with a few isolated localities in the interior montane forests (Fig. 57 A). It is likely that this North American endemic was once widespread (see general section on Distribution, category 11).

Discussion

Bryoria friabilis is almost unique in the Alec-torioid genera in producing gyrophoric acid. Its relationships are obscure, but on the basis of external morphology it is not unlike *B. implexa* in many respects. Some difficulty may be encountered in distinguishing *B. friabilis* from some morphotypes of *B. fremontii* and *B. pikei* in the absence of chemical examinations; this latter species sometimes has trace amounts of gyrophoric acid in addition to its main component (alecatorialic acid).

In the single fertile specimen examined (cited above), gyrophoric acid was produced in the thallus filaments and alecatorialic acid was produced in certain tissues of the apothecia. The filaments were entirely devoid of the latter substance (verified by TLC). Assuming that this chemical distribution is characteristic of the

species as a whole, this would provide additional evidence for the close relationship between *B. friabilis* and *B. pikei*. The restriction of lichen substances to apothecial tissues is well known in many genera of lichens (*Lecanora*: Imshaug & Brodo 1966, *Letharia*: W. Culberson 1969a, *Ramalina*: Krog & Swinscow 1974, etc.) and should not be regarded as very unusual.

It should also be noted that *B. friabilis* is the only species of *Bryoria* with white apothecial discs; its spores are the smallest seen in the genus.

An extremely perplexing specimen from the Olympic Mountains in Washington (Thomson 16261 [WIS]), which we are referring to *B. friabilis* with some hesitation, gives the impression of being a hybrid between this species and *B. glabra*. Although this collection has the very fragile branches and gyrophoric acid of *B. friabilis*, at the same time it possesses the olivaceous and regularly dichotomous, smooth, even, and very shiny branches and white soralia of *B. glabra*. The soralia are, however, tuberculate rather than fissural (as is usual for *B. glabra*) and react C+ red and PD–. Gyrophoric acid could be detected by TLC examination only from branches bearing soralia; esorediate branches contained no lichen products. The colour and evenness argue against this being a “white-sorediate” *B. fremontii* (see Discussion under that species). *B. friabilis* is normally very uneven and twisted, only rarely shiny, with a quite different branching system, and it normally lacks soralia. Furthermore, the gyrophoric acid in *B. friabilis* occurs in the cortex of the whole thallus. The area from which this specimen was collected is remarkable for its abundance of *B. glabra* (it is also the type locality for that species) and is also within the distributional range of *B. friabilis*. *B. glabra* is very rarely fertile and *B. friabilis* has only once been found with ascocarps, but, on the basis of the above information, it is conceivable that this specimen represents some sort of hybridization between these two species. It may prove to represent a further undescribed gyrophoric acid-containing *Bryoria* but with only a single collection available, we consider it premature to describe this as a new taxon despite its high degree of distinctness.

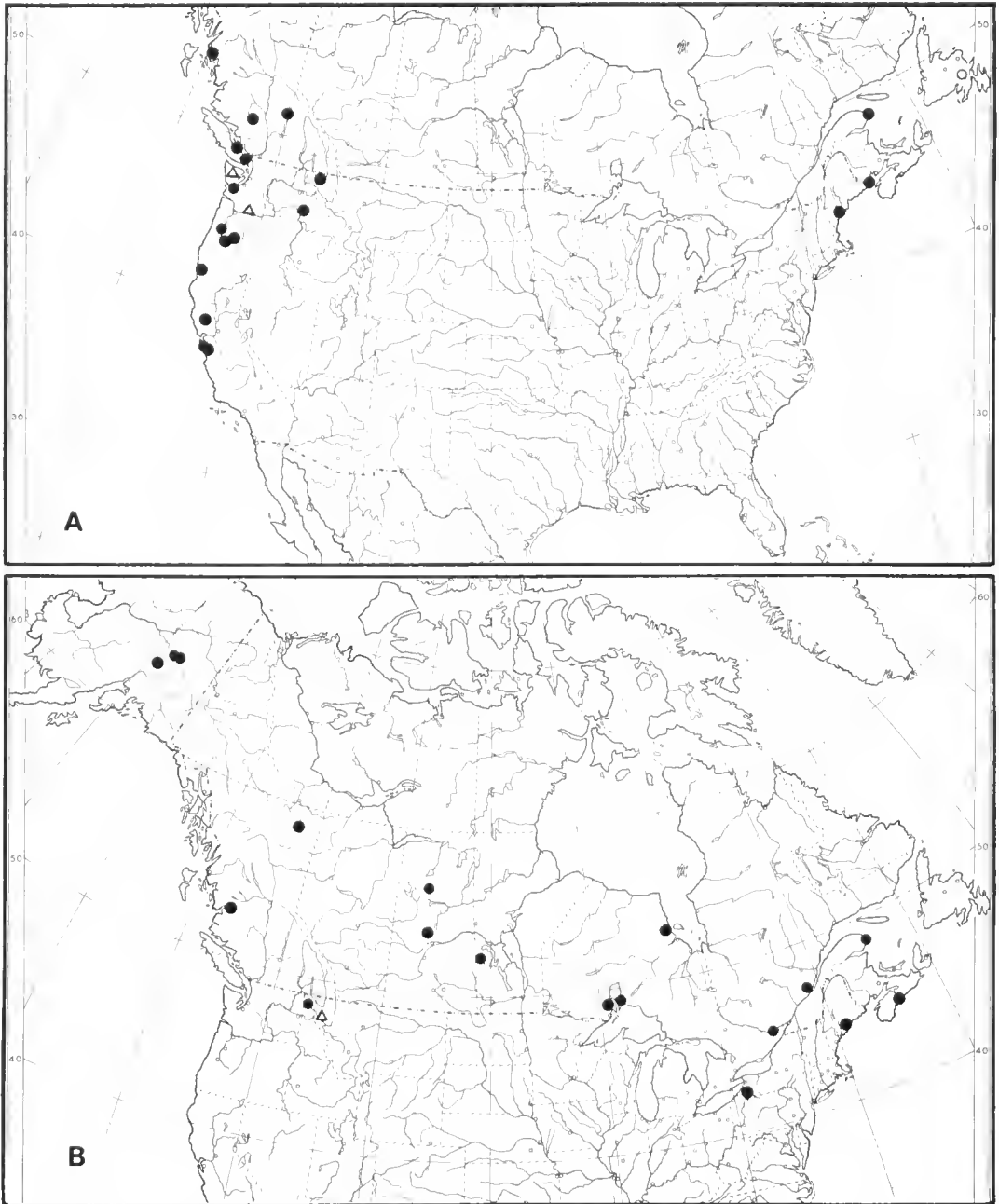


Fig. 57. A: *Bryoria friabilis*. Known distribution. Δ determination uncertain. \circ locality uncertain. — B: *B. implexa*. N. American distribution. Δ determination not confirmed chemically.

Specimens

Canada, British Columbia. Coastal Area: Garibaldi, Brodo 8179 (CANL) – Fraser River Basin: Wells Gray Provincial Park, Clearwater Lake, Ahti 7332 (H) – Islands South District: Vancouver Island, Little Qualicum Falls Campground, Tibell 5076 (UPS) – Sidney, Macoun 77 (CANL, FH) – Salt Spring Island, Bird 25604 (UAC) – Victoria, Macoun s.n., 6 June 1908 (NYBG) – Skeena River Basin: Skeena River, Macoun, 2 Oct. 1891 (CANL) – *Quebec*. Cte Gaspé-Est: Cap-des-Rosiers-Est, Brodo 18678 (CANL) – Bonaventure Island, Brodo 18691D (CANL) – *New Brunswick*. Charlotte County: Campobello, no collector, s.n., July 1902 (FH) – *Newfoundland*. District unknown: Middle Bay, A. Hodgkins s.n., 1897 (M).

U.S.A. California. Mendocino County: Ukiah, McClain 39 (US) – Del Norte County: Near Bear Basin, Tucker 6434 (p.p.) (US) – San Mateo County: Cahill Ridge, Jordan WJ956A (WIS) – Pilarcitos Creek Canyon, J. W. Thomson 4754 (WIS) – Santa Clara County: Devil's Canyon, J. W. Thomson 4700 (WIS) – Santa Cruz County: Santa Cruz Mountains, above Saratoga, Herre 491 (590) (p.p.) (FH) – Santa Cruz Mountains, Herre 491 (425) (NYBG, US) – *Idaho*. Bonner County: Priest River Experimental Forest, Esslinger 282 (WIS), 318 (H) – Latah County: Dry Creek, Cooke 23060 (WIS) – *Maine*. Sagadahoc County: Reid State Park, Taylor 487 (MSC) – *Montana*. Lincoln County: Yaak River campsite, J. W. Thomson 16308 (p.p.) (WIS) – *Oregon*. Benton County: Corvallis, Hawkins s.n., Aug. 1921 (CANL, WIS) – 13 miles W of Corvallis, Brodo 20923 (CANL) – Lane County: Willamette National Forest, Pike L-494 (PIKE) – Willamette Pass, Becking 6308194 (BECKING) – Andrews Exp. Forest, 44°N, 122°W, Pike s.n. (OSC 31,421) – *Washington*. Clallam County: Olympic Peninsula, Hurricane Ridge, J. W. Thomson 16261 (WIS) – Klickitat County: Goldendale, Foster 1154 (FH) – County unknown: Gate, Foster 1977 (NYBG).

17. *Bryoria implexa* (Hoffm.) Brodo & D. Hawksw., comb. nov.

Usnea [tax. vag.] *implexa* Hoffm., Deutsch. Fl. 2: 134 (1796); type: sine loc. (MW-Hoffm. 8569 neotype!); basionym. – *Usnea implexa* (Hoffm.) Hoffm., Herb. Viv. 2: 453 (1825). – *Alectoria implexa* (Hoffm.) Nyl., Lich. Scand.: 72 (1861).

For further synonyms see Hawksworth (1969 pp. 395–396).

Thallus pendent, 6–15 cm long; branching irregularly isotomic dichotomous, angles between the dichotomies acute or obtuse, tending to be acute towards the apices; branches even to uneven in diameter, often becoming twisted, compressed and slightly foveolate especially towards the base, 0.1–0.3 mm diam.;

pale brown to greenish brown or dark brown, concolourous or slightly paler towards the base.

True lateral spinules and soralia absent in North American material. Pseudocypheae sparse to abundant, conspicuous, elongate fusiform, usually depressed, often becoming twisted around the branches, white, to 1.5 mm long.

Apothecia and pycnidia unknown.

Outer cortex K–, C–, KC–, PD+ yellow; medulla K–, C–, KC–, PD+ yellow or –. Contains psoromic acid.

Ecology. On conifers and lignum in the boreal spruce-fir forest.

Distribution. Widely scattered in the middle boreal to southern boreal zones, and in the western mountains (Fig. 57 B). We have seen specimens from central, northern, and eastern Europe (Hawksworth 1969), but as the taxonomy of this species is still not entirely settled (see below), it would be premature to comment further on its extra-American distribution.

It should be noted that most literature reports of this species refer to *B. capillaris* but that the name has also been applied to *B. trichodes* by some early North American authors.

Discussion

This species is clearly closely allied to *B. pseudofuscescens* from which it is distinguishable by its chemical components and to some extent by its colour. The North American collections of *B. implexa* tend to be somewhat more delicate and paler than those from Europe and always lack soralia (as is often the case in Europe as well). Extremely pale almost pigment-deficient plants corresponding to the European *B. osteola* (see Hawksworth 1972 p. 253 for probable synonyms of this name) have not been noted amongst the North American material examined. Heavily sorediate, rather pale and coarse specimens from central Europe may be specifically distinct, but their nomenclature is obscure at the present time.

Specimens

Exsiccatae. Merrill: Lich. Exs., Ser. II, 129 (mixed); *Alaska*, Fairbanks, Palmer (NYBG).

Canada. British Columbia. Dean River Basin: Along Mosher Creek, Tweedsmuir Provincial Park, Ohlsson 1932 (MSC) – Liard River Basin: Fort Newson, Gillett 2995 (CANL) – *Saskatchewan.* Prince Albert Nat. Park, Waskesiu, Jesberger 1224, 733 (WIS), 737 (SASK) – *Manitoba.* Porcupine Mountains, Macoun 463? (CANL) – *Ontario.* Thunder Bay District: Nipigon River, Macoun s.n., 2 July 1884 (CANL) – Edmondson Lake, N of Port Arthur, Garton 10027 (CANL) – Kenora District: Attawapsikat, Ahti 3942 (H) – *Quebec.* Cte Gaspé-Est: Penouille Point, Brodo 18706 (p.p.) (CANL) – Cte de Québec/Montmorency: Montmorency River, Macoun s.n., 30 June 1905 (CANL) – *Nova Scotia.* Halifax County: Upper Brookside, East Mt., Prince 6240 (FH).

U.S.A. Alaska. Alaska Range District: Cantwell, Krog s.n., 10 June 1969 (O) – Central Yukon River District: Cheena Ridge near Fairbanks, J. W. Thomson 5078 (p.p.) (WIS) – *Idaho.* Bonner County: Minar's Bay, Priest Lake, MacDougal 267 (NYBG) – *Maine.* Knox County: Camden, Merrill s.n., Oct. 1904 (FH) – *Montana.* County unknown: John's Lake, Vreeland 1123 (NYBG) (Specimen not tested for psoromic acid). – *New York.* Cattaraugus County: Lime Lake (Machias?), Clinton s.n., no date (US).

18. *Bryoria nadvornikiana* (Gyeln.) Brodo & D. Hawksw., comb. nov.

Alectoria nadvornikiana Gyeln., Acta Fauna Fl. Univ., ser. 2, 1: 6 (1932); type: Rossia carp., Turkul, alt. 1850 m, G. Nádornik, 1930, herb. Servit 17.653 (BP 167267 holotype!); basionym. – *Bryopogon implexus* var. *nadvornikianus* (Gyeln.) Gyeln., Feddes Repert. 38: 242 (1935). – *Bryopogon nadvornikianus* (Gyeln.) Gyeln., Ann. Mus. Nat. Hung., Bot. 32: 154 (1939). – *Alectoria implexa* var. *nadvornikiana* (Gyeln.) Zahlbr., Cat. Lich. Univ. 10: 555 (1940).

Bryopogon altaicus Gyeln., Acta Geobot. Hung. 2: 166 (1937); type: U.S.S.R., Siberien, Altaigebirge, N. N. Lawrow, 1927, ex herb. Tomin 20 (H holotype!). – *Alectoria altaica* (Gyeln.) Räs., Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo 12(1): 34 (1939).

Alectoria altaica var. *spinulosa* Räs., Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo 12(1): 34 (1939), as "(Ahlén.) Räs."; type: Suecia, Helsingia, in par. Alfia, Grannäs, Jägtjärn, ad ramum *Piceae*, S. Ahlner, 3 July 1936 (S holotype; not seen). – *Alectoria nadvornikiana* var. *spinulosa* (Räs.) Mot., Fragm. Florist. Geobot. 4: 235 (1958); nom. inval. (Art. 33).

Alectoria karelica Räs., Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo 12(1): 34 (1939); type: U.S.S.R., Karelian A.S.S.R., Karelia ladogensis, Kurkijoki, Lapinlahti, Ristissaari, ad rupicariam, V. Räsänen, 21 May 1937 (H holotype!); nom. inval. (Art. 34).

Alectoria curta f. *pallidior* Östm., in Hasselr., Ark. Bot. 30A (13): 3 (1943); nom. inval. (Arts. 32, 34, 36).

Alectoria nadvornikiana var. *extensa* Mot., Fragm. Florist. Geobot. 4: 236 (1958); type: In Tartorum

monte dicta Lysanki, alt. 1300 m, in silva *Picearum* fere primitiva Augusto 1925 (holotype; not seen).

Alectoria nadvornikiana var. *eciliata* Mot., Fragm. Florist. Geobot. 4: 237 (1958); nom. inval. (Art. 37). – *Bryopogon eciliatus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 271 (1971); nom. inval. (Arts. 33, 37).

Thallus caespitose to subpendent (or rarely pendent in unusually long corticolous specimens) usually 4–7(–9) cm long; branching isotomic dichotomous towards the base but strictly anisotomic dichotomous towards the apices, angles between the basal dichotomies obtuse, angles between the apical dichotomies acute (Fig. 1 D, E); branches terete, even in diameter, straight, or more rarely flattened at the axils and somewhat twisted; (0.1–)0.2–0.3 (–0.4) mm diam.; basal branches becoming black, apical branches pale greyish green to pale brown or olivaceous brown, or rarely dark brown to almost black (always paler than the basal parts); base persistent.

Lateral, perpendicular, spinulose branches present, sparse to frequent (Fig. 3). Pseudocyphellae absent or sparse, to abundant, plane, 0.25–0.50 μ m long. Soralia abundant to sparse, or rarely absent, tuberculate or sometimes fissural, usually broader than the branches on which they occur, white or greenish white, to 1 mm long.

Apothecia and pycnidia not seen.

Cortex, medulla, and soralia K+ bright yellow, C– or + pink, KC+ red, PD+ deep orange to reddish. Contains barbatolic acid and small amounts of alectorialic acid, fumarprotocetraric acid, chloroatranorin, and traces of atranorin (in most specimens).

Ecology. On *Abies balsamea*, *Picea* spp., *Larix laricina*, *Betula papyrifera*, and occasionally other trees in the southern boreal spruce-fir forest; also frequently on vertical rock faces and cliffs, especially in ravines or along lake shores, and on rock in subarctic and subalpine sites; on *Alnus rubra* in British Columbia (Brodo 13881 [CANL]).

Bryoria nadvornikiana can be found in great abundance in fairly closed, almost pure stands of *Abies balsamea* in the southern boreal zone north of Quebec City, Quebec. Its tolerance of the shade and its absence in more open habitats are very striking.

Distribution. Mainly in the strongly humid

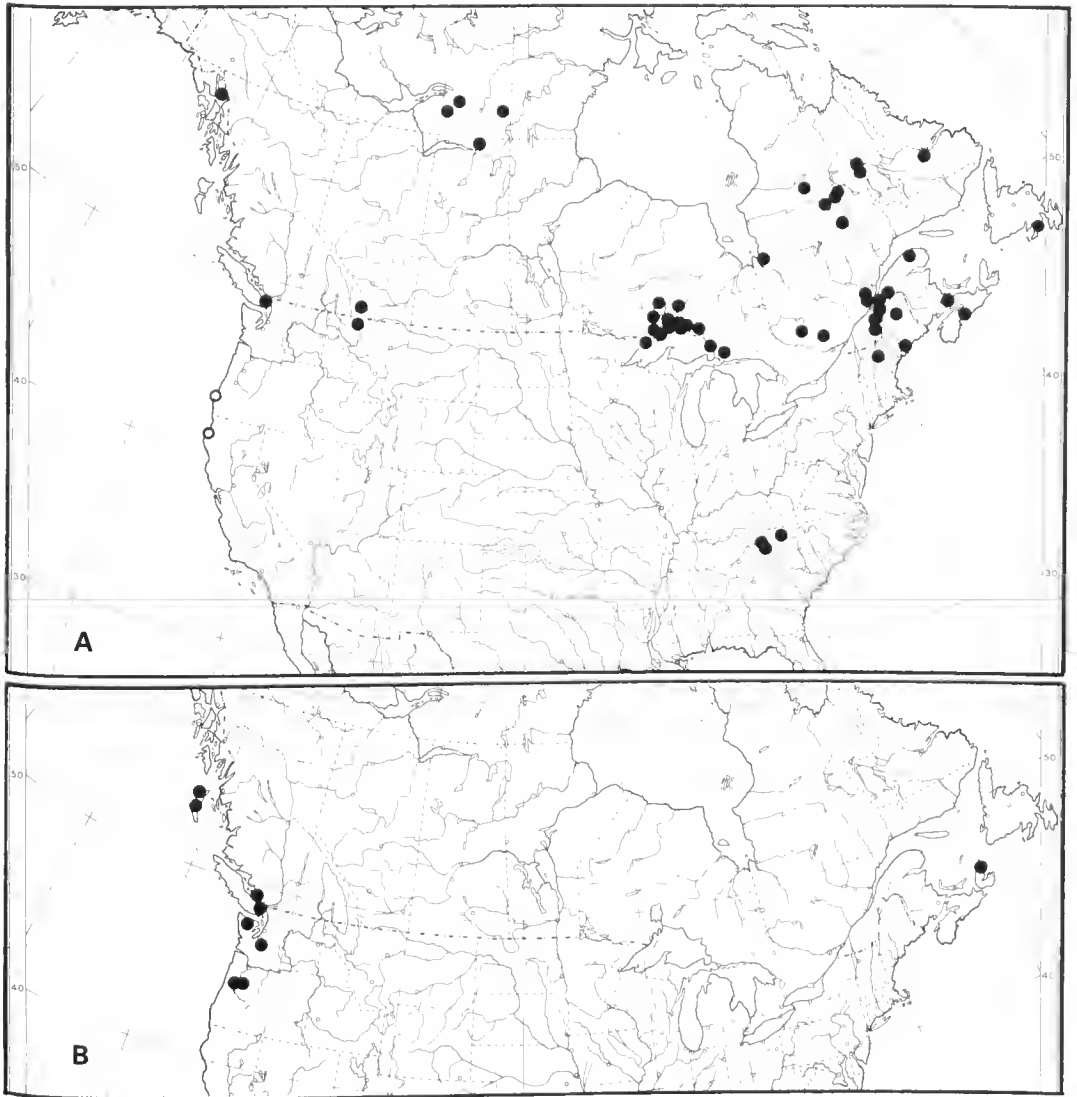


Fig. 58. N. American distribution. – A: ● *Bryoria nadvornikiana*, ○ *B. pseudocapillaris*. – B: *B. pikei*.

southern boreal forest zone, but with scattered occurrences in the northern boreal zones of Ungava (Quebec-Labrador) and Keewatin (N.W.T.), the southern Appalachians, the Rocky Mountains, the Gulf Islands near Vancouver (B.C.), and southeastern Alaska (Fig. 58 A). The same kind of clumping noted in the distribution pattern of *B. capillaris* is seen here, again, mainly corresponding to

areas of high precipitation. It is of scattered distribution in northern and middle Europe (Poelt 1969). Ahlner (1948), interpreting the Fennoscandian distribution of *B. nadvornikiana* (sub *Alectoria altaica*), suggested that the species survived the Pleistocene glaciation as a saxicolous plant, reinvading coniferous substrates with the reappearance of the forests. The tendency of this species in North America

to be saxicolous in cool ravines and exposed headlands in the southern boreal forest, and to appear on boulders and rock faces again in the most northern subarctic localities would support this hypothesis.

In addition to its European and North American localities, this species has also been reported from the Hawaiian Islands (Magnusson 1955), the East African mountains (Krog & Swinscow 1975), Himalaya (Bystrek 1969), and Japan (Yoshimura 1974).

Discussion

Bryoria nadvornikiana, although easy to identify by virtue of its chemistry and soralia, is nevertheless quite variable in appearance. Specimens which are basically caespitose can produce virtually pendent branches with occasional, spinulose laterals. Some specimens are almost entirely pendent except for the base, and can only be distinguished from *B. capillaris* by the short, pointed, lateral branches mentioned above, and the presence of soredia (in the North American material). *B. capillaris* also lacks atranorin, chloroatranorin, and fumarprotocetraric acid in North America and has a quite different branching pattern.

Chloroatranorin was present in all specimens of *B. nadvornikiana* tested by us (including some from Europe), and while fumarprotocetraric acid may also be a constant together with alectorialic and barbatolic acids, it sometimes occurs in such low concentrations as to be almost undetectable by TLC.

The soredial production is also variable. Some specimens are covered with abundant fissural or tuberculate soralia or occasionally both, but some are virtually esorediate, and a few are entirely without soralia. Colour varies from almost white to almost black, although most specimens are very pale fuscous to grey-brown except for the blackened basal region which may be extensive.

One group of specimens shares enough characters to warrant some sort of taxonomic recognition, but we are refraining from giving it a name here in the absence of a thorough study of the northern and eastern European material. These specimens are generally from the northern limits of the range and almost always are saxicolous. They are characterized by

being extremely dark in colour (dark brown to almost black), growing in dense, caespitose clumps, with abundant spinulose branches as in *B. furcellata* or *B. nitidula*, and having few soralia with those present being all fissural. Although a few of these specimens apparently lack fumarprotocetraric acid and/or atranorin (s. lat.), for the most part they are chemically indistinguishable from *B. nadvornikiana* s. str. In addition, one can find morphological intermediates with more typical *B. nadvornikiana*. Thus we are tentatively treating these morphotypes as conspecific.

Bryoria pseudocapillaris, found along the Oregon and California coasts, is also very similar in some respects to certain morphotypes of *B. nadvornikiana*.

There remains some question as to which section of the genus *Bryoria* is most appropriate for *B. nadvornikiana*. Bystrek (1971) placed the species in his subsection *Divaricatae* (of the section *Fuscidulae*), allied to other *Divaricatae* such as *B. asiatica*. Indeed, *B. nadvornikiana* often closely resembles members of the section *Divaricatae*, especially in the more northern morphotypes described above. However, its chemistry is clearly more closely allied to that of species in the *Implexae*, especially *B. capillaris*, in which the sorediate morphotypes are virtually identical chemically to *B. nadvornikiana*. Other characteristics such as colour, soralium type, and cortex are much more characteristic of species in the *Implexae* than the *Divaricatae*.

*Selected specimens (*dark, caespitose morphotype on rock)*

Exsiccatae. Brodo: Lich. Can. Exs. 81: *Quebec*, Montmorency County: Parc des Laurentides, Brodo 20595 (CANL).

Canada. British Columbia. Islands South District: Salt Spring Island, Brodo 13881 (CANL) – *Saskatchewan*. *W. Dodge Lake, Scotter 259 (WIS) – *Ontario*. Algoma District: 30 miles NW of Wawa, Brodo 6850 (CANL) – Thunder Bay District: St. Ignace I., Garton 6251 (US) – *Quebec*. Cte Charlevoix: Parc des Laurentides, Gauthier 2216B (CANL) – Cte Frontenac: Mont Mégantic, Masson 6067 (WIS) – Territoire de Mistassini: Otish Mts., Mont du Lagopède, Shchepanek 71-L-59 (p.p.) (CANL) – Territoire de la Baie de James: 54°00'N, 69°56'W, Gérardin QFB-E 4401 (CANL) – Territoire du Nouveau Québec: Fort-Rupert, (collector unknown) 12059 (CANL) – *Nova Scotia*. Halifax County:

Prospect Road, Brown s.n., 4 Aug. 1949 (NSPM) – *New Brunswick*. Albert County: Fundy National Park, Ireland 11332 (p.p.) (CANL) – *Newfoundland*. Placentia West District: Boat Harbor, Ahti 565 (H) – Labrador West District: Menihik Lake, Brodo 8837A-5B (CANL) – Central Labrador: Lake St. John, Lake Ducharme, Hustich s.n., 7 July 1948 (H) – *Northwest Territories*. District of Mackenzie: *North Talson R., Scotter 2333 (WIS) – Gordon Lake Area, Scotter 1552 (WIS) – *Thekulthili Lake, Scotter 2471 (WIS).

U.S.A. Alaska. Eastern Pacific Coast District: Juneau, Loop Road, Krog 5522 (O) – *Maine*. Knox County: Camden, Mt. Battie, Merrill s.n., Aug. 1904 (FH) – *Michigan*. Keweenaw County: W of Agate Harbour, Imshaug 4955 (MSC) – *Minnesota*. Cook County: Susie Islands, J. W. Thomson 3935 (COLO, DUKE, US, DEGELIUS) – *Montana*. Glacier County: Glacier National Park, Snyder Creek, Imshaug 7309 (S) – *New Hampshire*. Coos County: Mt. Washington, Burkholder 38A (p.p.) (US) – *North Carolina*. Avery County: Roane Mt., Hale 18043 (US) – Swain County: Mt. Kephart, Great Smoky Mts., Degelius s.n., 15 Sept. 1939 (US, DEGELIUS) – Yancey County: Mt. Mitchell, Becking 5907139 (BECKING) – *Tennessee*. Blount County: Mt. Le Conte, Great Smoky Mts., Degelius s.n., 14 Sept. 1939 (DEGELIUS).

19. *Bryoria pikei* Brodo & D. Hawksw.,
sp. nov.

Thallus pendulus, 10–15 cm longus; rami iso-dichotomiter ramosi, in angulos acutos et obtusos divergentes, aequales vel leviter inaequales diametro, non tortuosi, basi 0.2–0.35 mm diam.; planta olivacea vel parum olivaceo-brunnea sed basi pallidior.

Rami laterales spiniformes veri, isidia et soralia desunt. Pseudocypheellae copiosae, albae vel brunneae, fusiformes vel late fusiformes, saepe in spiram circa ramos contortae.

Apothecia et pycnidia ignota.

Cortex K– vel leviter flavescens, C+ roseus, PD+ flavescens; medulla K–, C–, KC–, PD–. Thallus acidum alectorialicum et interdum minime acidum gyrophoricum vel minime acidum barbatolicum continens.

Holotypus: America septentrionalis, U.S.A., Oregon, Marion County, Silver Creek Falls State Park, prope Winter Falls, orientem versus a Salem, 122°39'W, 44°53'N, alt. 1,450 ft, in *Pseudotsuga menziesii* juvenili, corticola, L. Pike 2475, 9 April 1972 (CANL 38271).

A duplicate (arithmotype) of Pike 2475 at OSC was found to be entirely *B. pseudoflavescens*. The holotype packet is a mixture of *B. pikei* and *B. pseudoflavescens*.

Thallus pendent, 10–15 cm long; branching isotomic dichotomous, angles between dichotomies acute and obtuse, branches even to slightly uneven in diameter, not twisted, 0.2–

0.35 mm diam. at the base; uniformly olivaceous or occasionally becoming olivaceous brown and somewhat paler at the base.

True lateral spinules, isidia, and soralia absent. Pseudocypheellae abundant, white to brown, fusiform to broadly fusiform, often spirally twisting around the branches.

Apothecia and pycnidia unknown.

Cortex K– or + weakly yellow, C+ pink, KC+ pink, PD+ yellow; medulla K–, C–, KC–, PD–. Contains alectorialic acid and sometimes also traces of gyrophoric acid or traces of barbatolic acid.

Ecology. On conifer branches and lignum, usually in humid forests close to the coast or a lake, at 0–1250 m elevation.

Distribution. West coast, from the Queen Charlotte Islands to Oregon, with a single disjunct locality on Cape Breton Island, Nova Scotia (Fig. 58 B). The comments for *B. friabilis* also apply to this North American endemic.

Discussion

Bryoria pikei seems to be most closely related to *B. capillaris* but can usually be distinguished from that species by its dark olivaceous colour; the shiny, smooth, and very even surface of its branches; the production of very distinct, long, white, fissural pseudocypheellae; and by its characteristic lack of barbatolic acid. We have seen specimens which are olivaceous only in part, with most of the thallus a variegated grey-brown. Some of these specimens also produce trace amounts of barbatolic acid. However, even dark specimens of *B. capillaris* (which are not rare) are usually quite dull and uneven, and tend to be smoky brown or brownish grey rather than olivaceous although the conspicuous white pseudocypheellae in these thalli are often quite similar of those of *B. pikei*. Despite the convergence of some of these characters, we believe that the two taxa are distinct. We have seen several mixed packets of *B. capillaris* and *B. pikei* in which it was easy to distinguish the two morphologically. *Bryoria pikei* also has a much more limited distribution.

This species is also closely related to *B. friabilis*, with some specimens being almost

intermediate in colour; *B. friabilis* is generally pale buff. The presence of trace amounts of gyrophoric acid in the holotype of *B. pikei* and the production of alectorialic acid in the apothecia of *B. friabilis* confirm their close relationship. *B. pikei*, however, is not nearly as friable, has a characteristic olive colour, and has alectorialic rather than gyrophoric acid as its principal constituent. Gyrophoric acid could not be detected at all in several specimens of *B. pikei*.

It should be noted that there is a distinct possibility that in our study some old and blached specimens of *B. pikei* have been misidentified as *B. capillaris*. Almost all the material of *B. pikei* traced has been collected recently, and we do not know how the characteristic olivaceous colour of the thallus stands up to ageing in herbarium packets. A number of specimens listed under *B. capillaris* here, which were examined early in our study, were rather shiny and therefore might conceivably represent *B. pikei*. If this proves to be the case *B. pikei* is a more common species than we have suggested.

Specimens

Canada, British Columbia. Islands North District: Graham Island: Ian Lake, Brodo 18435B (CANL) – Kumdis Bay, Port Clements, Brodo 18144A (p.p.) (CANL) – Moresby Island: Between Sandspit and Copper Bay, Brodo 12874A (CANL) – Skidegate Lake, Brodo 18513B (p.p.) (CANL) – Wathus Island: Masset Inlet, Brodo 18314A (CANL) – Islands South District: Saltspring Island, Brodo 13839 (CANL) – *Nova Scotia.* Victoria County: Cape Breton Highlands National Park, Speer 73-24 (CANL).

U.S.A. Oregon. Benton County: Corvallis, Mary's Peak, Brodo 20954 (CANL) – Linn County: Mount Jefferson National Wilderness, Hank Lake, Pike 1110 (CANL) – Marion County: Silver Creek Falls State Park E of Salem, Pike & Rossman 2475 (L.P.) (CANL, OSC) – *Washington.* Clallam County: Hurricane Hill, Pike 844 (CANL) – Pierce County: Mt. Rainier National Park near Paradise Valley, Brodo 15438B (p.p.) (CANL).

20. *Bryoria pseudocapillaris* Brodo & D. Hawksw., sp. nov.

Thallus subpendulus, 5–7 cm longus, parum rigidus; rami plerumque iso-dichotomiter fastigiati, sed ramulis copiosis brevibus acutis vel perpendicularibus instructi; rami principales plerumque omnino

teretes, non compressi vel tortuosi, diametro aequales, laeves, 0.25–0.33 mm diam.; planta pallidissime brunnea vel badia, opaca.

Rami laterales spiniformes veri, isidia et soralia desunt. Pseudocyphellae longae, lineares, albae, depressae, plerumque rectae sed interdum circa ramos leviter fortae, 1.2–3.0 mm longae.

Apothecia et pycnidia ignota.

Cortex K+ flavus, C+ roseus, KC+ roseus, PD+ aureus; medulla K–, C–, KC–, PD–. Thallus acidum alectorialicum, acidum barbatolicum et substantiam ignotum continens.

Holotypus: America septentrionalis, U.S.A., Oregon, Curry County, Cape Blanco, 8 mls boreo-orientem versus a Port Orford, in arboribus sejunctis summi ventosissimi, I. M. Brodo 20539, 28 June 1974 (CANL 50596). Isotypus: BM. Fig. 59.

Thallus subpendent, 5–7 cm long, rather stiff; branching mainly isotomic dichotomous but with frequent acute to perpendicular short side branches; main branches mostly terete throughout, not flattened or twisted, even, smooth, 0.25–0.33 mm diam.; very pale brown to badius, matt.

True lateral spinules, isidia and soralia absent. Pseudocyphellae long, linear, white, depressed, usually straight but sometimes slightly twisted around the branches, 1.2–3.0 mm long.

Apothecia and pycnidia unknown.

Cortex K+ yellow, C+ pink, KC+ pink, PD+ deep yellow; medulla K–, C–, KC–, PD–. Contains alectorialic and barbatolic acids together with an unidentified substance.

Ecology. Coastal trees and rocks in exposed situations.

Distribution. Rare, from coastal northern California to Oregon (Fig. 58 A).

Discussion

This species is being placed in the genus *Bryoria* due to its resemblance to certain forms of *B. capillaris* and *B. kuemmerleana*, although its pseudocyphellae are so striking that we cannot entirely exclude the possibility that it should be included in the genus *Sulcaria*. Its branching type and vaguely badius colour suggest a close relationship with *B. spirifer*, which shares the same habitat.

Chemically, it resembles *B. nadvornikiana* and *B. capillaris*, but differs from the former in lacking soralia and chloroatranorin, and from the latter in being stiff and having perpendicular



Fig. 59. *Bryoria pseudocapillaris*. Holotype. Scale 0.5–1.0 mm.

branches. It differs from both in the unusually long pseudocyphellae.

Specimens

U.S.A. California. Humboldt County: Manila, Brodo 20511B (CANL) – Oregon. Curry County: Cape Blanco, near Port Orford, Imshaug 17660 (MSC), Brodo 20539 (CANL).

21. *Bryoria pseudofuscescens* (Gyeln.) Brodo & D. Hawksw., comb. nov.

Alectoria pseudofuscescens Gyeln., Ann. Mus. Nat. Hung., Bot. 28: 283 (1934) et Revue Bryol. Lichén. 7: 51 (1934); type: "Oregon, Corvallis, on old apple trees, F. P. Sipe" (BP 33,958 holotype!); basionym.

Alectoria norstictica Mot., Bryologist 67: 33 (1964); type: Alaska, East Pacific Coast District, Juneau, Mindenhall Glacier Trail, H. Krog 5507, 27 August 1957 (O lectotype!); nom. inval. (Arts. 36, 37). – *Bryopogon norsticticus* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 274 (1971); nom. inval. (Arts. 33, 36, 37).

Alectoria subtilis Mot., Bryologist 67: 32 (1964); type: Alaska, Central Pacific Coast District, Kenai Peninsula, H. Krog 2164, 7 June 1957 (O lectotype!); nom. inval. (Arts. 36, 37). – *Bryopogon subtilis* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 274 (1971); nom. inval. (Arts. 33, 36, 37).

For further synonyms see Hawksworth (1972 p. 252).

Thallus pendent, usually 5–10(–15) cm long; branching isotomic dichotomous at least at the base but sometimes becoming submonopodial towards the apices, rarely with sparse, short, perpendicular, lateral branches, angles between the main dichotomies variable, branches even to uneven in diameter, straight or twisted, mainly 0.15–0.3(–0.35) mm diam., basal branches usually 0.20–0.35 mm diam.; pale brown to greyish in some specimens, darkening to dark brown or black, often olivaceous especially towards the base, dull or shiny.

Soralia and true lateral spinules absent. Pseudocyphellae usually abundant, white, short to elongate fusiform, depressed, often forming partial spirals around the filaments, often to 0.5–1.0 mm long.

Apothecia very rare, lateral, c. 0.4–0.5 mm diam., excipulum thallinum concolourous with the thallus, incurved, generally excluded at maturity; disc reddish brown, concave at first, sometimes becoming convex. Hymenium 36–40 μ m high. Ascospores 8 per ascus, hyaline, nonseptate, broadly ellipsoid to subspherical, 5.4–7.5 \times 4.0–4.5 μ m.

Pycnidia unknown.

Cortex and medulla K+ yellow changing

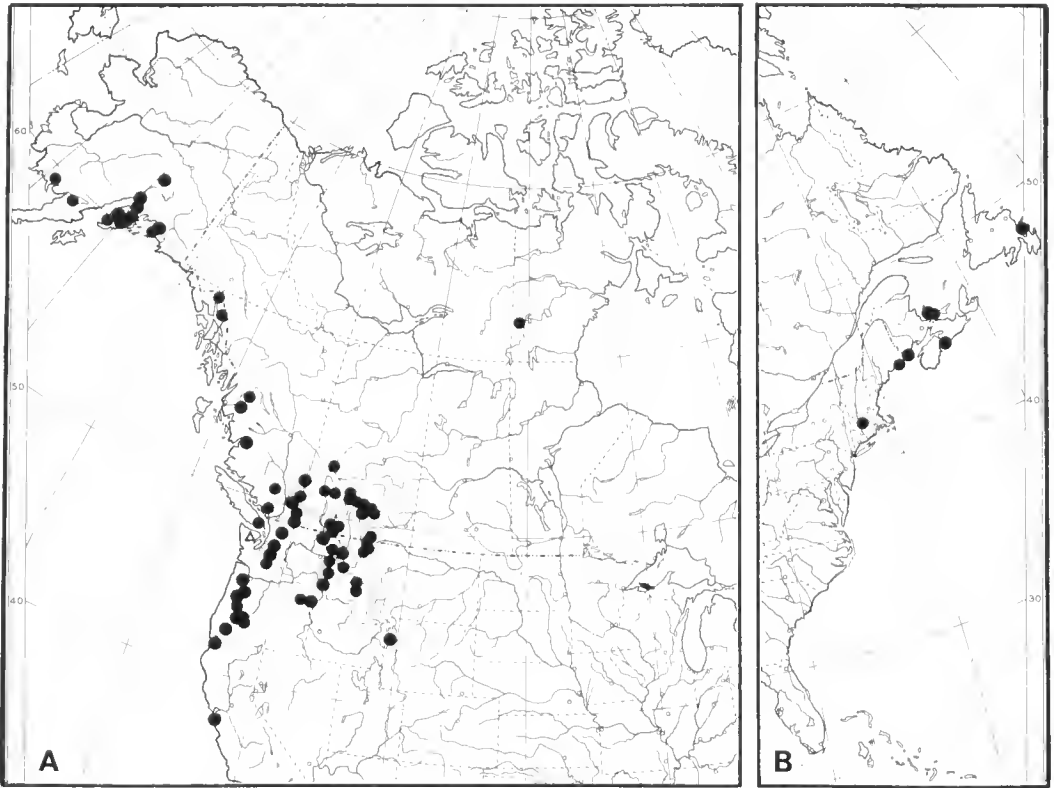


Fig. 60. A: *Bryoria pseudofuscescens*. N. American distribution. Δ determination uncertain. — B: *B. salazinicola*. Known distribution.

to red, or faintly yellow, C—, PD+ yellow. Contains norstictic acid, and rarely, traces of connorstictic acid.

Ecology. On coniferous trees, especially *Picea glauca*, *Abies lasiocarpa*, and *Pinus albicaulis* in montane conifer forests, mainly at 1100–2350 m. In some subalpine forests, *B. pseudofuscescens* drapes well-exposed fir trees from top to bottom. The holotype, however, is from apple trees close to sea level. One specimen was seen from rock (California, Santa Cruz Co., Becking 6607721 [BECKING]).

Distribution. West coast from southern Alaska to California, eastward into the northern Rocky Mountains and Douglas fir forests of northern Idaho and adjacent Washington and Montana, but avoiding the Columbia plateau (Fig. 60 A). Several of the Oregon localities, including that of the holotype, are in the more lowland oak

forest region which, however, also contains *Pseudotsuga* as a dominant tree species (Küchler 1964) (see below). The specimen from the Keewatin District west of Hudson Bay was reexamined and apparently is correct. Its occurrence there is extremely puzzling.

The taxonomy of this species with its many forms is still unsettled. It certainly occurs in the boreal forests of Europe and has been reported from a few localities in Scotland (Hawksworth 1972, sub "*Alectoria trichodes*").

Discussion

Bryoria pseudofuscescens appears to be most closely allied to *B. implexa* from which it differs primarily in having norstictic rather than psoromic acid. (See also the discussion under *B. implexa*.) The two species sometimes occur mixed together in Alaska (H. Krog pers.

comm.). *B. pseudofuscescens* is basically a slender, extremely dark plant with uneven filaments and scattered, dark or white pseudocyphellae. Like *B. implexa*, *B. pseudofuscescens* is esorediate in North America.

The morphology of *B. pseudofuscescens* is somewhat variable, and marked divergences from the above traits are sometimes seen. The type specimen of "*Alectoria subtilis*" is unusually pale in colour and has rather few pseudocyphellae, for example. A particularly distinct morphotype with extremely thick, twisted and foveolate main branches, superficially not unlike *B. vrangiana* except that it lacks soralia and has norstictic instead of fumarprotocetraric acid, has been encountered several times (Sansom, 1913 [FH]; Otto 3131b [UBC]). At first we were inclined to regard this morphotype as an infraspecific taxon of *B. vrangiana* but as the main branches of generally very slender specimens can become somewhat thickened and contorted, it seems that these specimens merely represent environmental modifications of *B. pseudofuscescens*.

Norstictic acid is only known otherwise amongst the North American *Bryoriae* in *B. spiralifera*, which is easily distinguished by its colour, elongate pseudocyphellae, and branching pattern. In addition, *B. spiralifera* always contains abundant connorstictic acid. A peculiar specimen of *B. pseudofuscescens* from Washington contains norstictic as well as barbatolic acid and is discussed under *B. capillaris*.

In Europe there may well be several norstictic acid-containing species in addition to *B. pseudofuscescens*, but they remain poorly known; for this reason Hawksworth (1972) treated them as a species aggregate (sub *Alectoria trichodes* (Michx.) D. Hawksw., a name which must now be used in a different sense; see Discussion under *Bryoria trichodes* subsp. *trichodes*). The pale, often variegated, grey-brown robust species of central and eastern Europe, *B. kuemmerleana* (Gyeln.) Brodo & D. Hawksw., is almost certainly worthy of this rank; we have found that at least some specimens (all which have been tested so far) of this species contain atranorin and connorstictic acid in addition to norstictic acid. No specimens referable to *B. kuemmerleana* have been seen by us from North America.

The amount of norstictic acid in this species

is rather variable, and for this reason, a positive K reaction is sometimes difficult to obtain (see p. 23). It may be that the apparent lack of connorstictic acid in all but two or three specimens is tied to the low concentrations of norstictic acid.

A certain amount of confusion surrounds the type material of *B. pseudofuscescens*. To begin with, an "isotype" in ORE (i.e., bearing the same number as that designated by Gyelnik as the holotype) is entirely different from the holotype in morphology and chemistry, and, in fact, represents a new species which we are calling *Sulcaria badia*. In addition, although the "isotype" packet is marked "No. 669, on old apple trees", it is labelled as being from "Philomath", while in the original description, "Corvallis" is given. This is not as serious as it might first appear since Philomath is a small village about seven miles west of Corvallis. It is understandable that Dr. Sipe would mark a specimen sent to a foreign colleague with the name of the closest city likely to be found on an ordinary map. Of course, it would have been easy to have collected a mixture of two species and sent only one of them away for determination.

More disturbing, however, is the fact that the Philomath-Corvallis area and most of the surrounding valley are quite unlike the "typical" habitat of *B. pseudofuscescens* as we have come to understand it, i.e., mountainous coniferous forests. The trees in the valley are mainly deciduous, occurring in open stands of *Quercus garryana* with occasional individuals or even small stands of *Pseudotsuga menziesii*. The area is dotted with old and recent apple orchards. One of us (I.M.B.) searched for both *B. pseudofuscescens* and *Sulcaria badia* on five separate occasions in old apple orchards, oak stands, *Pseudotsuga* forests, and pine stands, both in open valleys and on hills, without finding either of the lichens. There are some localities in the general area which may be sufficiently mountain-like to serve as a site for *B. pseudofuscescens*, for example Mary's Peak, several miles to the west of Philomath, but a short visit to that locality proved fruitless.

It seems impossible to definitely determine whether (a) the localities marked on the isotype and given in the original description were incorrect (i.e., mislabelled in some way), (b)

Gyelnik mislabelled the holotype, confusing it with a completely different collection, or (c) the two species in question are simply too rare in the Corvallis area to be found easily. In the latter connection, since we have seen several specimens conforming to our concept of *B. pseudofuscescens* collected in the oak-Douglas fir forest region of western Oregon, it would seem that even the unlikely locality can be accepted as probable.

As Gyelnik's descriptions are so brief and often unreliable, they help little in the elucidation of this problem. However, the epithet *pseudofuscescens* would have been an extremely inappropriate choice for *Sulcaria badia*. Even if the specimen in the "typus" packet in BP were not collected by Sipe at all but came from another locality, it is not nomenclaturally important since there can be no doubt that Gyelnik regarded that packet as the nomenclatural type. That Gyelnik intended his name to refer to the species treated here under this epithet is also supported by his application of the name to other collections (e.g., Lichenotheca no. 16 [BM]). If the holotype actually proved to be something other than Sipe's collection, the stated locality in the original description could simply be treated as a *lapsus*.

Selected specimens

Exsiccatae. Merrill: Lich. Exs., Ser. II, 129 (mixed); Alaska, Fairbanks, Palmer (MSC, NYBG, US, WIS).

Canada. *British Columbia*. Coastal District: E of Pemberton, near Lillooet Lake, Brodo 8313D (CANL) – Columbia River Basin: Big Bend District, Shaw 977 (NYBG, BM) – Dean River Basin: Mt. Walker, 40 miles E of Bella Coola, Ohlsson 2259 (CANL) – Islands South District: Vancouver Island: "on Lea's Farm", (Macoun?), Herb. G. K. Merrill, 17 June 1908 (FH) – Kootenay River Basin: Glacier National Park, Glacier Crest Trail, Ohlsson 395 (MSC, CANL) – Okanagan District: Princeton, Brodo 7811 (CANL) – Skagit River Basin: Manning Park, Blackwall Peak, Brodo 20565 (CANL) – Skeena River Basin: South Hazelton, Ohlsson 3020 (MSC, CANL) – *Alberta*. Banff National Park, trail from Lake Louise to Lake Agnes, Weber S23, 544 (CANL, NYBG) – *Northwest Territories*. Keewatin District: Dubawnt Lake, J. W. Thomson 14299 (p.p.) (WIS?).

U.S.A. *Alaska*. Alaska Range District: Cantwell, Krog s.n., 8 June 1969 (O) – Central Pacific Coast District: Anchorage Area, Krog 1420 (O) – Eastern Pacific Coast District: Juneau, Mindenhall Glacier Trail, Krog 5507 (O) – Western Pacific Coast District: Dillingham Quadrangle, Wood River Lakes,

Viereck 8964 (p.p.) (CANL, ALA) – *California*. Del Norte County: Near Bear Basin, Tucker 6434 (COLO) – S of Takilma, Oregon, Pike L-325A (CANL) – Santa Cruz County: Butano State Park, Becking 6607721 (BECKING) – *Idaho*. Bonner County: Priest River Experimental Forest, Esslinger 1580B (WIS) – Nez Perces County: Lake Waha, Heller 3364 (MSC) – *Montana*. Mineral County: Donna Morra campsite, J. W. Thomson 16300 (CANL) – Ravalli County: Bass Creek, Stevensville, Stiekney 1581 (WIS) – *Oregon*. Benton County: Corvallis, Sipe s.n., no date (BP) – Deschutes County: Doris Lake in the Deschutes National Forest, Pike L-392 (PIKE) – Klamath County: Crater Lake, Kraus s.n., Aug. 1921 (WIS) – Lane County: Eugene, Doty 3099 (p.p.) (NYBG) – Union County: Blue Mountain, Summit Pass (US 30), Imshaug 21 (MSC) – *Washington*. Pierce County: Mt. Rainier National Park, trail to Glacier Basin, Imshaug 315 (F, US) – *Wyoming*. Teton County: Cascade Canyon, Grand Teton National Park, Alexander s.n., 29 Aug. 1955 (COLO).

22. *Bryoria salazinica* Brodo & D. Hawksw., sp. nov.

Thallus pendulus vel subpendulus, plerumque crispatus et implexus, 5–9 cm longus; rami praeter basim praecipue aniso-dichotomiter fastigiati, in angulos obtusos vel perpendiculares valde divergentes, diametro aequales vel inaequales, recti vel leviter torti, in axillis saepe foveolati et complanati, 0.16–0.35 mm diam.; tota planta obscure olivaceo-brunnea vel pallide brunnea, opaca vel bombycina.

Rami laterales spiniformes veri, isidia et soralia desunt. Pseudocypheiae plerumque copiosae, impolite albae, fusiformes vel elongato-fusiformes, 0.08–0.4(–0.65) mm longae.

Apothecia et pycnidia ignota.

Cortex (et forsan medulla) K+ flavescens, C–, KC+ flavescens, PD+ aurantiaco-flavescens. Thallus acidum salazinicum continens.

Holotypus: America septentrionalis, U.S.A., Massachusetts, Springfield, W. G. Farlow, May 1878 (NYBG). Fig. 61.

Thallus pendent to subpendent, often curled and entangled, 5–9 cm long; branching mainly anisotomic dichotomous except at the base, branches broadly divergent at obtuse to perpendicular angles, even to uneven, straight to somewhat twisted, often foveolate and compressed at the axils, 0.16–0.35 mm diam.; dusky olivaceous brown to pale brown throughout, dull to satiny.

True lateral spinules, isidia, and soralia absent. Pseudocypheiae usually abundant, dull white, fusiform to elongate-fusiform, 0.08–0.4 (–0.65) mm long.

Apothecia and pycnidia unknown.

Cortex (and perhaps medulla) K+ yellow,

C–, KC+ yellow, PD+ orange-yellow. Contains salazinic acid.

Ecology. On coniferous trees along the coast or on the coastal plain.

Distribution. Northeastern coastal plain; North American endemic (Fig. 60 B).

Discussion

This species appears to be closely related to the *B. implexa* – *B. friabilis* – *B. pikei* group, all of which have long twisting pseudocyphellae, an olivaceous caste, and a similar uneven branching. *B. pseudofuscescens* is also very similar in many respects. We considered the possibility that *B. salazinic* might merely represent a chemical race of one of these four species but its remarkable chemistry and well-defined and restricted distribution prompted us to regard it as a species.

Alectoria angolensis Dodge, described from Africa, is reported as having salazinic acid, but that taxon is sorediate and, to judge from an authentic specimen examined by Hawksworth (1971 a), is almost certainly a species of *Ramalina* on the basis of its cortical structure. (Microtome sections are preserved in IML.) The only other previous report of salazinic acid in *Alectoria* s. lat. is Solberg's (1956) mention of it in European material named as "*A. cana* (Ach.) Leight." (a synonym of *B. capillaris*); this report should be verified since no other workers have found this compound in any European Alectorioid species.

Specimens

Canada, Nova Scotia. Halifax County: Ketch Harbour, Taschereau B-14 (NSPM) – *Prince Edward Island.* Prince County: Richmond, Ireland 10298 (CANL) – *Queens County:* West Barkley Beach, 14 miles NW of Charlottetown, Fabiszewski s.n., 20 July 1970 (CANL) – *Newfoundland.* Trinity North District: Bay Bull's Arm, Trinity Bay, collector unknown, April 1897 (M).

U.S.A. Maine. Washington County: Eastport, Herb. W. G. Farlow s.n., no date (FH) – Jonesport, Cheever 1314 (US) – *Massachusetts.* Hampden County: Springfield, Farlow s.n., May 1898 (NYBG).



Fig. 61. *Bryoria salazinic*. Holotype. Scale 0.5–1.0 mm.

23. *Bryoria spiralis* Brodo & D. Hawksw., sp. nov.

Thallus pendulus, 6–7 cm longus; rami basi isodichotomiter sed in ramis principalibus praecipue aniso-dichotomiter fastigiat; rami principales 0.2–0.25 mm diam., diametro inaequales, recti vel tortuosi, ramulis numerosis brevibus, gracilibus perpendiculariter instructi; planta atrobadia vel pallide badia, opaca, ramis lateralibus saepe dilutioribus.

Rami laterales spiniformes, isidia et soralia desunt. Pseudocyphellae copiosae, conspicuae, albae, lineatae, in spiras longas circa ramos contortae vel partim rectae, ad 4 mm longae.

Apothecia et pycnidia ignota.

Cortex K+ rubescens, C–, KC–, PD+ flavescens; medulla K–, C–, KC–, PD–. Thallus abundanter acidum norsticticum sed minime acidum connorsticticum et atranorinum (non chloroatranorinum) continens.

Holotypus: America septentrionalis, U.S.A., California, Humboldt County, in pineto prope Manila, in Pino contorta, S. Dowty 137, 22 January 1972 (CANL 38403). Fig. 62.

Thallus pendent, 6–7 cm long; branching isotomic dichotomous at the base but becoming mainly anisotomic dichotomous on the main branches; main branches 0.2–0.25 mm diam., uneven, straight to twisted, with numerous, short, slender, perpendicular branches; dark to pale badius, matt, lateral branches paler.

True lateral spinules, isidia, and soralia absent. Pseudocyphellae abundant, conspicuous, white, linear, twisted in long spirals around the branches or straight in parts, to 4 mm long (Fig. 5 E).



Fig. 62. *Bryoria spiralis*. Holotype. Scale 0.5–1.0 mm.

Apothecia and pycnidia unknown.

Cortex K+ red, C–, KC+ red, PD+ yellow; medulla K–, C–, KC–, PD–. Contains large amounts of norstictic acid together with smaller quantities of connorstictic acid and atranorin (not chloroatranorin).

Ecology. On *Pinus contorta*, *Picea sitchensis*, and shrubs in scrub forests near the coast; found in shaded or sunny habitats generally mixed with *Ramalina menziesii*.

Distribution. Known only from the Samoa peninsula in Humboldt County, California, where it is very scattered, but not uncommon (Fig. 39).

Discussion

The badious colour, and extremely long pseudocyphellae which sometimes become somewhat furrow-like, at first suggested that this species might belong to the genus *Sulcaria*. We now feel it more properly belongs in the genus *Bryoria*, closely allied to *B. pseudocapillaris* (see Discussion under this species). In some respects this species resembles the European *B. kuem-*

merleana (see Discussion under *B. pseudofuscescens*) but that species is generally much larger and has a different branching type.

Specimens

U.S.A. *California*. Humboldt County: Near Manila, Dowty 137 (HSC, CANL) – Manila (W of Arcata), Brodo 20501, 20509, 20511A (CANL) – Samoa Peninsula, Lindsay 782, 926 (WIS) – Locality unknown: J. Tallant s.n., 1856 (US).

Bryoria sect. *Subdivergentes* (Mot.) Brodo & D. Hawksw., comb. nov.

Alectoria subgen. *Bryopogon* sect. *Subdivergentes* Mot., Bryologist 67: 36 (1964); basionym. – *Bryopogon* sect. *Subdivergentes* (Mot.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 275 (1971), as "Mot."

Type species: *Bryoria subdivergens* (Dahl) Brodo & D. Hawksw. (syn. *Alectoria subdivergens* Dahl; holotype).

Thallus erect and caespitose to decumbent or pendent, reddish brown, matt, not becoming blackened. Lateral spinulose branches often present, rarely abundant, not constricted at the base. Isidia, soralia, and pseudocyphellae absent. Cortex distinctly cellular, knobby at the surface. Apothecia common in most species; margins ciliate; discs reddish brown, sometimes markedly convex. No lichen products known.

Discussion

This section comprises four species of which only two are recorded in North America with certainty; both of these are endemic here (*B. abbreviata* and *B. oregana*). The other two species of this section are *B. subdivergens* (only reliably recorded from southwest Greenland; see Excluded taxa) and *B. divergens* (a southeast Asian species). The section is well characterized by the colour of the thallus, the structure of the cortex, the ciliate apothecia, and the absence of lichen products. It appears to occupy a rather isolated position within *Bryoria*.

24. *Bryoria abbreviata* (Müll. Arg.) Brodo & D. Hawksw., comb. nov.

Alectoria divergens f. *abbreviata* Müll. Arg., Flora, Jena 72: 362 (1889); type: Oregon, Mt. Hood, Boell 111, 1889 (G holotype!); basionym. – *Alectoria abbreviata* (Müll. Arg.) R. Howe, Class. Fam. Usnea-

ceae: 22 (1912). – *Bryopogon abbreviatus* (Müll. Arg.) Gyeln., Feddes Repert. 38: 235 (1935).

Thallus caespitose, up to 2.5 cm in length; branching anisotomic dichotomous, broadly divergent at the base, angles between dichotomies acute or obtuse, branches uneven in diameter, 0.3–1.0 mm diam. at base, 0.2–0.4 mm diam. on main stem, foveolate and channeled; generally very angular or flattened; occasionally anastomosing, red-brown, matt. Fig. 63.

True lateral spinules, soralia, and pseudocyphellae absent; branches sometimes appearing spinulose due to short pointed lateral branches.

Apothecia common, subterminal or rarely lateral; excipulum thallinum concolourous with thallus, persistent and ciliate to disappearing, flat to recurved, red-brown darkening to almost black with age, 2.0–3.0(–3.5) mm diam. Spores 8 per ascus, broadly ellipsoid, c. $6.5 \times 4.5 \mu\text{m}$. Pycnidia not seen.

Cortical hyphae as in *B. oregana* (Fig. 12 A–E).

Cortex and medulla K–, KC–, C–, PD–; lichen substances absent.

Ecology. On coniferous trees, mainly *Pinus ponderosa* and *Pseudotsuga menziesii* in the rather dry Interior Douglas Fir forests, c. 700–1400 m in elevation.

Distribution. North American endemic of western Douglas fir forests from southern British Columbia and Alberta to Baja California (Fig. 64A). It has the most southerly continuous distribution among the North American *Alectoria* s. lat. and clearly avoids the more humid coasts of Oregon, Washington, and British Columbia, showing a preference for dry forest regions.

Discussion

This species has normally been included in *B. oregana* but appears to be distinct from it. The separation of these two species is discussed under *B. oregana*.

Bryoria abbreviata shows a strong superficial resemblance to *Cornicularia californica* (Tuck.) DR. and is often confused with it in herbaria. *C. californica* has an olive brown to greenish black thallus and a greenish to brown-black epithecium usually reacting K+ violet, whereas *B. abbreviata* is always dull red-brown

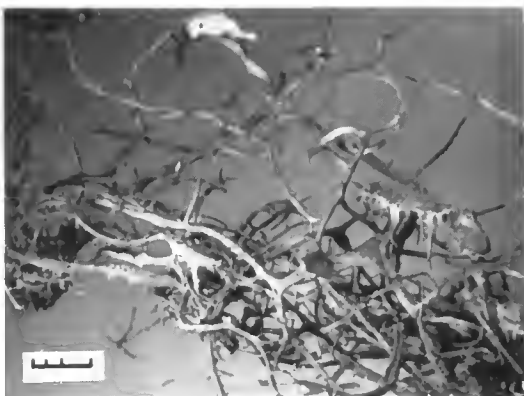


Fig. 63. *Bryoria abbreviata*. Note the "ciliate" apothecia. B. C., Creston, Brodo 15120 (CANL). Scale 0.5–1.0 mm.

and has a red-brown epithecium not reacting with K. The cortical structures in these two species also differ (see general section on Anatomy and morphology: Cortex).

Selected specimens

Exsiccatae. Cummings, Williams & Seymour: Lich. Bor. Amer. 18: *Montana*, Flathead County: Columbia Falls, Williams (FH, H, NYBG) – Cummings, Seymour & Williams: Dec. N. Amer. Lich. 96: *Montana*, Flathead County: Columbia Falls, Williams (CANL, DUKE, MSC, NYBG, US) – Krypt. Vind. 3711: *Washington*, Whitman County: Pullman, Herre (COLO, F, IAM, US) – Merrill: Lich. Exs., Ser. II, 36 (some mixed with *B. cfr. fuscescens*): *Washington*, Ferry County: Republic, Foster (F, MSC, NYBG, US, WIS).

Canada. *British Columbia*. Columbia River Basin: Kootanie Lake (sic), Macoun (440?) (CANL) – Fraser River Basin: Wells Gray Provincial Park, Ahti 14269 (H) – Kootenay River Basin: East of Creston, Brodo 15120 (CANL) – Okanagan River Basin: Mt. Anarchist near Osoyoos, Krajina 645-124 (CANL) – *Alberta*. Waterton Lakes National Park, Scotter 4901 (WIS).

U.S.A. *California*. Del Norte County: Near Fairview Peak in the Siskiyou National Forest, Pike L-329A (OSC) – Los Angeles County: San Gabriel Mts., Hasse 1485 (NYBG) – Tulare County: Sequoia National Park, Rundel 2569 (UCI) – *Idaho*: Bonner County: Priest R. Experimental Forest, on Gisborne Mt., Esslinger 392 (COLO) – *Montana*: Missoula County: S of Alberton, J. W. Thomson 16328 (WIS) – *Oregon*. Baker County: Unity, Shushan SL-3961 (BM, CANL, US, WIS) – Union County: Summit Pass, Blue Mt., Imshaug 19 (COLO) – *Washington*. Ferry County: Republic, Foster 36 (COLO) – Pierce County: Mt. Rainier National Park, Brodo 15475 (CANL) –

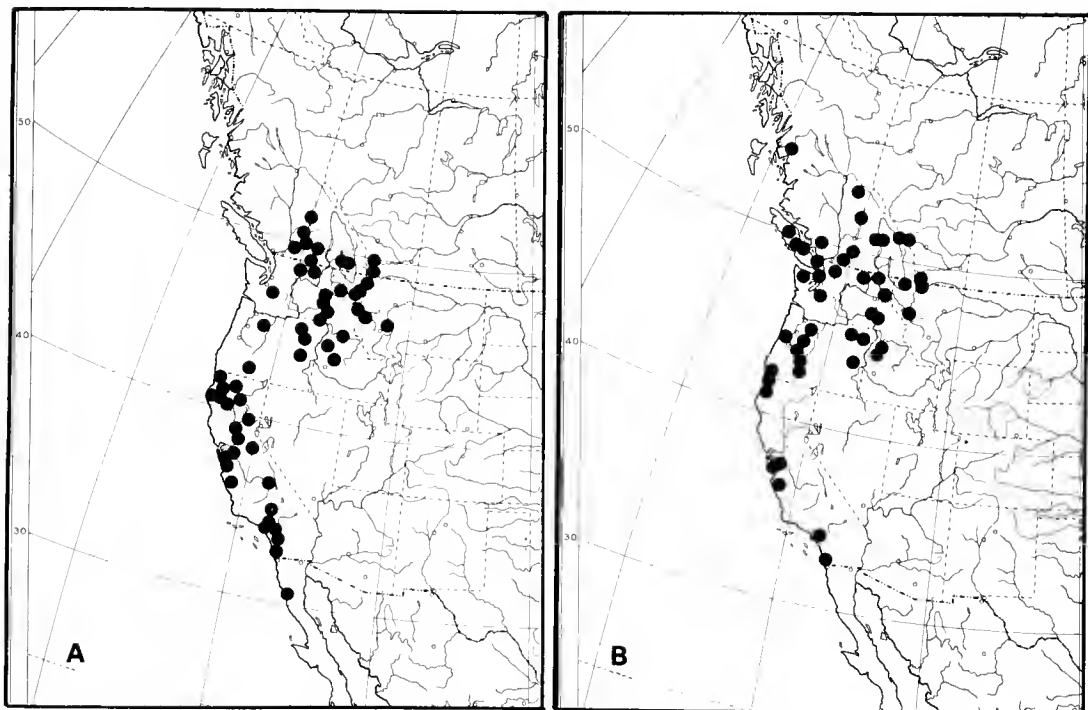


Fig. 64. Known distribution. – A: *Bryoria abbreviata*. – B: *B. oregana*.

Wyoming. County unknown: Belt Mts., Willey s.n., no date (US).

Mexico. *Baja California*. Cape San Quentin (sic) (San Quintin), Greene s.n., Feb. 1906 (FH), Greene 189? (NYBG).

25. ***Bryoria oregana*** (Tuck. ex Nyl.) Brodo & D. Hawksw., comb. nov.

Alectoria oregana Tuck. ex Nyl., Lich. Jap.: 104 (1890); type: Union, Oregon, W. C. Cusick (FH-Tuck. 472 holotype! H-Nyl. 35971 isotype!); basionym. – *Bryopogon oreganus* (Tuck. ex Nyl.) Schneid., Guide Stud. Lich.: 166 (1898). – *Coelocaulon oreganum* (Tuck. ex Nyl.) Choisy, Icon. Lich. Univ., ser. II, fasc. 2, sine pagin. (1931).

Thallus pendent, up to 17 cm in length; branching anisotomic dichotomous, angles between the branches acute or obtuse; branches very uneven in diameter, 0.25–0.40 mm diam. at the base, 0.10–0.20 mm on pendent branches; branches longitudinally foveolate and channeled, generally very angular; red-brown, matt (never shiny).

True lateral spinules, soredia, and pseudocyphellae absent; branches sometimes appearing

spinulose due to short, pointed, lateral branches. Apothecia infrequent, lateral; excipulum thallinum concolourous with thallus, smooth or sometimes ciliate, disappearing in age; to 2.0 mm diam.

Spores 8 per ascus, broadly ellipsoid, thin-walled, c. $6.5 \times 4.5 \mu\text{m}$. Pycnidia not seen.

Cortical hyphae in surface view short, knobbed, thin-walled, appearing like a jigsaw puzzle (Fig. 12A).

Cortex and medulla K–, C–, KC–, PD–; contains no lichen substances.

Ecology. On conifers, especially *Abies lasiocarpa*, *Picea*, and *Pinus* species, usually between 1500 and 2300 m in elevation, characteristically in subalpine *Abies lasiocarpa*–*Picea engelmannii* stands, but also in dry or exposed montane pine stands.

Distribution. Western montane, from southwestern Alberta and neighbouring Montana westward to the coast and southward through California (Fig. 64B). Apparently, *B. oregana*

requires, or is tolerant of, cooler, more humid habitats than is *B. abbreviata*, and is therefore more commonly found in the coastal mountains. *B. oregana*, like *B. abbreviata*, is a North American endemic.

Discussion

Bryoria abbreviata and *B. oregana* have generally been regarded as synonymous (Howe 1911, Motyka 1964). While the two taxa are clearly very closely allied, intergrades appear to be rare. The two species are able to grow side by side in nature and maintain their identities. *B. abbreviata* is invariably fertile and has large, ciliate, subterminal apothecia and a distinctly caespitose habit (although one or two of the marginal cilia may become elongate and develop into pendulose branches). In contrast, *B. oregana* only rarely forms apothecia. When they do occur they are almost eciliate and always clearly lateral. Furthermore, the thallus is pendent rather than caespitose.

These two species frequently occupy the same habitat in regions where they are sympatric and their thalli may be intricately entangled. It is undoubtedly this frequent admixture which has led to their being treated as conspecific in the past.

Sterile plants of *B. oregana* may be confused with some slender sterile and esorediate morphotypes of *B. fremontii*, but these taxa can usually be separated reliably on the basis of thallus colour and cortical features (see Fig. 12).

The holotype collection of *B. oregana* is mixed and comprises intricately entangled (a) typical elongate and fertile thalli of *B. oregana* s. str., (b) a large amount of *B. fuscescens*, (c) some *B. fremontii*, (d) *Letharia columbiana*, and (e) at the base of the specimen, what appears to be *B. abbreviata* with broader more divergent branches. A dissection of the collection would have resulted in the destruction of part of the type and so was not attempted. Isotype material in Nylander's herbarium (H!), undoubtedly sent to Nylander by Tuckerman, is *B. oregana* as interpreted here. The epithet *oregana* thus refers to the pendent rather than the caespitose elements of "*Alectoria oregana* auct." and we have adopted it in this sense.

Selected specimens

Canada. British Columbia. Coastal District: Garibaldi Mountains, Garibaldi, Brodo 8178 (CANL) – Columbia River Basin: Glacier National Park, Ohlsson 395 (MSC) – Fraser River Basin: Southern Cariboo Mountains, Wells Gray Park, Ahti 6517 (H) – Islands South District: Between Mt. Thornhill and Mt. Attree, Ohlsson 2568 (MSC, CANL) – Skagit River Basin: Manning Park, Ahti 15388 (H) – *Alberta.* Waterton Lakes National Park, W of Avion Ridge, Bird 16836 (CANL).

U.S.A. California. Del Norte County: Near Bear Basin, Tucker 6434 (US, COLO) – Riverside County: San Jacinta Mountain (sic) (Jacinto), Hasse s.n., 1904 (US) – San Diego County: San Diego, Orcutt s.n., no date (F) – Santa Cruz County?: Santa Cruz Mountains, Castle Rock, Herre 1144 (F) – *Idaho.* Payette County: Payette Lakes, A. H. Smith 16076C (DUKE, COLO) – *Montana.* Glacier County: Glacier National Park, Sprague Creek, Imshaug 7341 (LAM, US) – Sanders County: Fishtrap Creek, Taylor 7071 (p.p.) (Herb. not indicated) – *Oregon.* Benton County: Mary's Peak W of Corvallis, Pike 3106 (CANL) – Klamath County: Crater Lake National Park, Sipe 1152 (ORE) – *Washington.* Clallam County: Olympic National Park, near Mt. Angeles, Ireland 6898 (US) – Pend Oreille County: Colville National Forest, Layser 1460 (p.p.) (US).

***Bryoria* sect. *Tortuosae* (Bystr.) Brodo & D. Hawksw., comb. nov.**

Bryopogon sect. *Tortuosae* Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 273 (1971), as "Mot."; basionym. – *Alectoria* subgen. *Bryopogon* sect. *Tortuosae* Mot., Fl. Polska, Porosty 5(2): 38 (1962); nom. inval. (Art. 37).

Type species: *Bryoria tortuosa* (Merr.) Brodo & D. Hawksw. (syn. *Alectoria tortuosa* Merr., *Bryopogon tortuosus* (Merr.) Bystr., nom. inval.; holotype).

Thallus subpendent to pendent; emerald-greenish to cervine brown, not blackened. True lateral spinules and isidia absent. Soralia rather rare, tuberculate, emerald-green to greenish yellow. Pseudocyphellae present and abundant or sparse to almost absent, conspicuous, depressed, elongate-fusiform, greenish yellow in one species. Cortex with a moderate amount of matrix, longitudinally orientated (not cellular and knobby) at the surface. Apothecia occasional; margins not ciliate; discs yellowish to emerald-green, often markedly convex. Vulpinic acid known from all species; atranorin and/or chloroatranorin, fumarprotocetraric acid, and other β -orcinol depsidones absent.

Discussion

This section comprises two species, the circum-boreal *B. fremontii* and the western North American *B. tortuosa*, which are unique in *Bryoria* in having pulvinic acid derivatives. (It should be noted that in *B. fremontii* these are restricted to the soralia and apothecia.)

26. *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw., comb. nov.

Alectoria fremontii Tuck., Am. J. Arts Sci., ser. 2, 25: 422 (1858); type: Sierra Nevada, camp of December 5–6, 1845, a piece of moss which is abundant in this region, Fremont (FH-Tuck. 498 holotype!); basionym. – *Bryopogon fremontii* (Tuck.) Rabenh., Flecht. Eur. no. 918 (1871). – *Alectoria jubata* var. *fremontii* (Tuck.) Boist., Nouv. Fl. Lich. 2: 38 (1903).

Alectoria olivacea Räs., Medd. Soc. Fauna Fl. Fenn. 43:4 (1917); type: Fennia, Ostrobothnia borealis, Simo, V. Räsänen, 6 June 1916 (H lectotype!). – *Bryopogon olivaceus* (Räs.) Choisy, Icon. Lich. Univ., ser. 2, 2: sine pagin. (1930). – *Alectoria fremontii* var. *olivacea* (Räs.) H. Magn., Fl. Skand. Busk. Bladl. 100 (1929). – *Alectoria fremontii* subsp. *olivacea* (Räs.) Räs., Lich. Fenn. Exs. no. 162 (1936). – *Alectoria fremontii* f. *olivacea* (Räs.) Mot., Fl. Polska, Porosty 5(2): 76 (1962).

Alectoria corneliae Gyeln., Ann. Crypt. Exot. 4: 171 (1931); type: Oregon, near Brownsville, on pine, L. L. Haskin 1031, 25 May 1930 (US holotype!). – *Bryopogon olivaceus* f. *corneliae* (Gyeln.) Gyeln., Feddes Repert. 38: 230 (1935). – *Alectoria olivacea* f. *corneliae* (Gyeln.) Zahlbr., Cat. Lich. Univ. 10: 559 (1940).

Alectoria fremontii subsp. *erikssonii* DR., Ark. Bot. 20A (11): 8 (1926); nom. nov. for *A. fremontii* sensu Räs., non Tuck. – *Bryopogon fremontii* f. *erikssonii* (DR.) Savicz, Lich. Ross. 4 no. 34 (1935). – *Alectoria fremontii* f. *erikssonii* (DR.) Mot., Fl. Polska, Porosty 5(2): 77 (1962); nom. inval. (Art. 33).

Alectoria fremontii var. *perfertilis* Räs., Ann. Missouri Bot. Gard. 20: 10 (1933); type: British Columbia, Golden, ad corticem arboris (*Pinus*), V. Kujala, September 1931 (H holotype!). – *Bryopogon olivaceus* var. *perfertilis* (Räs.) Gyeln., Feddes Repert. 38: 230 (1935). – *Alectoria olivacea* var. *perfertilis* (Räs.) Zahlbr., Cat. Lich. Univ. 10: 559 (1940).

? *Alectoria fremontii* f. *dealbata* Mot., Fl. Polska, Porosty 5(2): 77 (1962); nom. inval. (Art. 37).

Thallus pendent, often very long, to 45 cm (or exceptionally 90 cm, fide Turner in litt.); branching anisotomic dichotomous to submonopodial, usually frequent from the base; branches uneven in diameter, becoming twisted and foveolate, sometimes becoming dorsiventrally compressed and expanded towards the base, (0.2–) 0.4–1.5(–4.0) mm diam.; yellowish brown to reddish brown or dark brown, colour often

variable within the same specimen, usually shiny.

True lateral spinules absent. Soralia absent or sparse, tuberculate, pale yellow to bright yellow, usually as wide as the branches on which they occur, to 2.0(–4.0) mm long. Pseudocyphellae absent or sparse (perhaps only torsion cracks), depressed and elongate fusiform, white to pale brown.

Apothecia absent or sparse, lateral; excipulum thallinum concoloured with the thallus, thin and soon becoming excluded; disc becoming convex at maturity, 1.0–2.0(–4.0) mm diam., yellow pruinose. Spores 8 per ascus, hyaline, subglobose, simple, 5–8×4–5 μ m. Pycnidia not seen.

Cortex, medulla, apothecia, and soralia K–, C–, KC–, PD–. Contains vulpinic acid in the soralia and apothecia.

Ecology. Mainly on *Pinus ponderosa*, *P. contorta*, *Larix occidentalis*, and *Pseudotsuga menziesii* in open pine or Douglas fir forests (at elevations of 700–2500 m in the Canadian Rockies and 3000–3400 m in the southern Rockies); also on oaks closer to the coast. It seems to prefer somewhat open and rather dry sites (Szczawinski 1953).

Distribution. Western conifer forests from mid-Alberta and British Columbia west to the coast and south throughout California to Baja California, with disjunct populations in Colorado and the Black Hills (Fig. 65A). Wetmore (1968) regards the presence of *B. fremontii* in the Black Hills as a relatively recent (i.e., post-Pleistocene) occurrence due to its rarity. *B. fremontii* shows a classical western American–western European disjunct distribution. In Europe it is known from Fennoscandia and the Caucasus (Krog 1968), and Schwarzwald (Schindler 1974), but it is especially abundant in northern Finland (Ahlner 1948).

Bryoria fremontii was determined from eastern Asia (Saghalien) by Gyelnik (1935, Sato 1936) and has also been reported from Mexico (Williams 1895) and Ellesmereland (Darbishire 1909). These three records require confirmation but we have seen one specimen which may be this species from Ecuador (Gualaquiza [?Guayaquil], 1200 m, Abate M. Allioni, 1910, comm. Sbarbaro [KGY]). Its absence in the British Isles and distribution in the drier Douglas fir

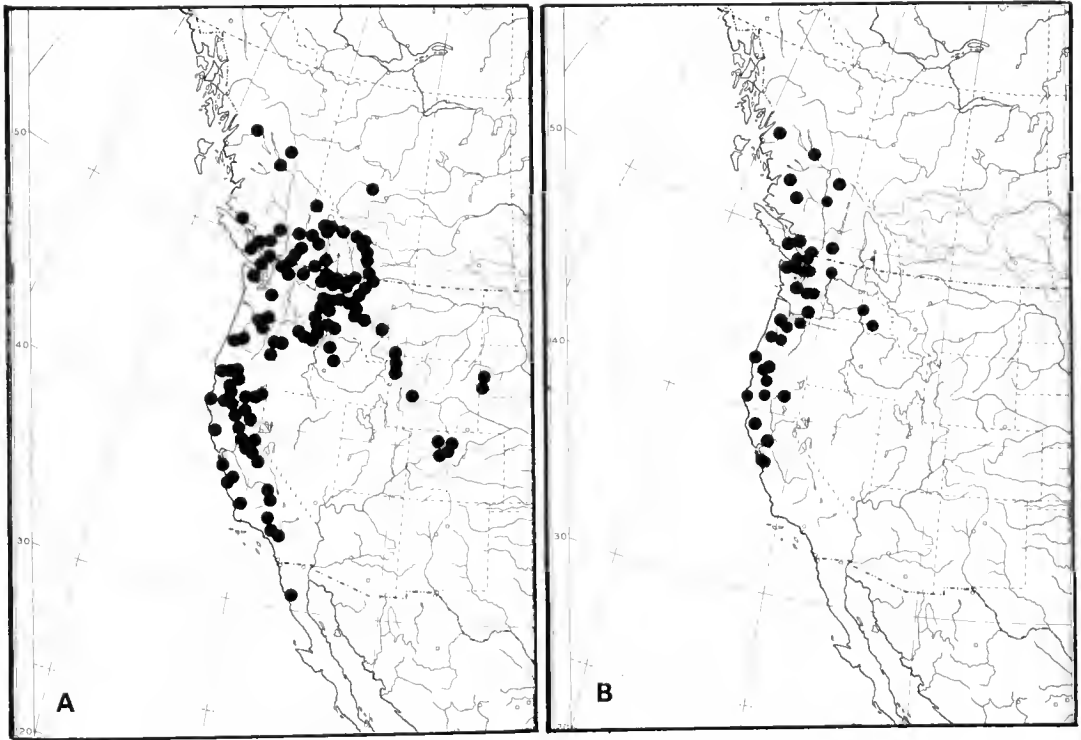


Fig. 65. N. American distribution. – A: *Bryoria fremontii*. – B: *B. tortuosa*.

forests of western America would tend to support Ahlner's (1948) assessment of the species as "northern continental" although he does point to its occasional occurrence in somewhat oceanic localities.

The presence of a northern species like *B. fremontii* in Baja California is apparently not unusual since Stebbins & Major (1965 p. 5) point out that "Boreal plants of holarctic distribution extend southward along the California coast to Monterey, and in the mountains throughout the Sierra Nevada and even into southern California." The jump between southern California and northern Baja California is not very far with regard to distance or climate.

Discussion

Bryoria fremontii is an extremely variable species in some respects but is generally unlikely to be misidentified, even when sterile,

owing to its shiny, broad, and foveolate main stems and its characteristic yellowish brown to dark reddish brown colour. Some confusion can occur with unusually large and acid-deficient plants of *B. trichodes* subsp. *americana*. Very slender, dark specimens can be distinguished from *B. oregana* by examinations of the cortical structure (Fig. 12). Specimens appearing similar to *B. fremontii* but differing in being unusually pale, dull, and quite brittle often prove to be *B. friabilis* on examination by TLC. (The latter species contains gyrophoric acid.)

Specimens of *B. fremontii* with both yellow soralia and yellow-pruinose apothecia are extremely rare in North America, as they are in Europe, though they are more frequent in California than elsewhere. Specimens with only soralia or only apothecia are almost as rare. The most commonly encountered morphotype is dark red-brown to dark brown in colour, with very thick and foveolate, shiny, main branches

and numerous slender side branches. Various infraspecific taxa have been proposed to accommodate the morphotypes with and without soralia, etc. (see Motyka 1962), but these variations seem to be without any taxonomic significance. Material with white soralia (e.g., "f. *dealbata* Mot.") is mentioned in the literature but we have seen none in our investigations and are sceptical as to its existence; such reports may well be based on misidentifications although it is occasionally possible to find old soralia rubbed free of their coating of vulpinic acid so as to appear almost white. (In such cases, typical yellow soralia are invariably present elsewhere on the same specimen.)

On the west coast, there occurs a population of this species with an unusually pale, almost yellow-brown thallus and white incipient pseudocyphellae (perhaps actually "torsion" cracks). Plants belonging to this morphotype, which includes the type specimen of *Alectoria corneliae* Gyeln., are frequently extremely robust and have very thick shiny branches. This morphotype might at first appear to merit recognition at some infraspecific rank, but since a continuous series of intermediate plants exists, we do not consider it to be taxonomically important.

Because the vulpinic acid in this species is restricted to soralia and apothecial discs, it cannot be demonstrated by TLC in material lacking these structures.

Attention is drawn to Ahlner's (1948) important discussion of the variability of this species in Europe.

Selected specimens

Exsiccatae. Cummings, Seymour & Williams; Dec. N. Amer. Lich. 54: *Montana*, Flathead County: Columbia Falls, Williams (CANL, DUKE, MSC, NYBG, US, WIS) – Cummings, Williams & Seymour: Lich. Bor. Amer. 17: (same as above) (COLO) – Merrill: Lich. Exs., Ser. II, 47: *Washington*, Ferry County: Republic, Foster (COLO, F, MSC, NYBG, WIS) – Rel. Tuck. (no number): *Wyoming*, County unknown, Wind River Mountains, Hayden (LAM) – Tuckerman: Lich. Amer. Septentr. Exs. 52: *California*, no specific locality, Fremont (NYBG) – Weber: Lich. Exs. 418 (p.p.): *California*, Shasta County: Burney, Pike & Jackman (CANL).

Canada. *British Columbia*. Islands South District: Vancouver Islands: Little Qualicum Falls Provincial Park, Becking s.n., 25 Sept. 1953 (LAM) – Coast Area: Garibaldi Park, Krajina 351-4 (CANL) – Colum-

bia River Basin: Deer Park, Macoun 55 (NYBG, US) – Fraser River Basin: Blue River, Brodo 15791 (CANL, WIS) – Okanagan River Basin: Princeton, Brodo 7812 (CANL) – Peace River Basin: McLeod Lake, Leechman s.n., July 1954 (FH) – Skagit River Basin: Manning Park, Ahti 15389 (H) – Skeena River Basin: E of Hazelton, Ohlsson 2962A (MSC) – *Alberta*. Banff National Park: Trail to Lake Agnes, Imshaug 6866 (WIS).

U.S.A. California. Eldorado County: near Kyburz, Eldorado Nat. Forest, Belshaw 6005 (DUKE, COLO) – Los Angeles County: St. Antonio Mts., Johnston 3085 (FH, F) – *Colorado*. Routt County: Seedhouse Guard Station, Weber 6835 (COLO) – *Idaho*. Latah County: Kendrick, Esslinger 248B (COLO) – *Montana*. Missoula County: S of Alberton, J. W. Thomson 16319 (US, WIS, CANL) – *Oregon*. Klamath County: Crater Lake, Sipe 990 (ORE, F) – *South Dakota*. Custer County: Custer, Wetmore 10053 (MSC) – *Washington*. Asotin County: Fields Spring State Park, Imshaug 16483 (MSC, CANL) – *Wyoming*. Yellowstone National Park: Near Canyon Junction, Imshaug 9441 (WIS, LAM).

Mexico. *Baja California*: Cape San Quentin (sic) (San Quintin), Greene s.n., Feb. 1906 (FH) – Nacho-guero Valley, Schoenfeldt 3427 (US).

27. *Bryoria tortuosa* (Merr.) Brodo & D. Hawksw., comb. nov.

Alectoria tortuosa Merr., Bryologist 12: 5 (1909); type: British Columbia, near Westminster, A. J. Hill, July 1904 (FH holotype!); basionym. – *Eualectoria tortuosa* (Merr.) Gyeln., Ann. Mus. Nat. Hung., Bot. 28: 283 (1934); nom. inval. (Art. 34). – *Bryopogon tortuosus* (Merr.) Gyeln., Feddes Repert. 38: 229 (1935).

Thallus pendent, 10–30 cm long; branching mainly anisotomic dichotomous; angles between the dichotomies acute, with frequent slender, perpendicular side branches arising from the axes; branches uneven in diameter, strongly twisted and tortuous, foveolate and often flattened, 0.4–0.5(–1.0) mm in diam.; dull, dark red-brown to dusky yellow-brown, occasionally becoming bright yellow in thalli having heavy concentrations of vulpinic acid; pale and dark specimens often grow mixed.

Spinules and isidia absent; soredia exceedingly rare. Pseudocyphellae usually abundant, occasionally rare, bright yellow, linear or sometimes short fusiform, slightly raised, twisting around filaments in long yellow spirals (Fig. 5C).

Apothecia rare, lateral, 2–3 mm diam., excipulum thallinum raised, persistent, disc heavily yellow pruinose. Spores 7.5–8.7 × 4.7–5.0 μm, 8 per ascus, hyaline, ellipsoid. Pycnidia unknown.

Cortex and medulla K-, C-, KC-, PD-, but thallus producing a yellowish stain on filter paper with PD in most specimens. Contains vulpinic acid.

Ecology. On trees in well-lighted, open stands. Most frequently on oaks and pines, although it has been collected on a large variety of trees and shrubs.

Distribution. Along the west coast, mainly from southern British Columbia to central California; with scattered localities in central British Columbia, mainly on exposed hillsides or in pine stands (Fig. 65 B). The Idaho localities are also in ponderosa pine stands fitting in well with its known ecology (see above). The only reported locality outside of North America for *B. tortuosa* is in the Carpathian Mountains in Europe (Motyka 1958), but the specimen upon which this record is based has not been seen by us. The distribution of the moss *Crummia latifolia* (common in western North America with a single occurrence in the Caucasus Mountains) is very similar (Schofield & Crum 1972 p. 175, map 26).

Discussion

Bryoria tortuosa is readily recognizable by its red-brown to dusty yellow-brown to almost greenish yellow thallus, and yellow, generally conspicuous, pseudocyphellae. Specimens with very few pseudocyphellae are likely to be confused with *B. fremontii*, so a careful examination of all material of the latter is advisable; in critical cases, TLC always reveals vulpinic acid in *B. tortuosa* while in *B. fremontii* it is only found associated with soralia and apothecia.

The ability to produce vulpinic acid varies considerably in this species and is responsible for the marked variations in the colour of the

thallus. Numerous packets contain mixtures of both greenish yellow thalli with abundant vulpinic acid and dark brown thalli showing only yellow pseudocyphellae; all intergradations occur.

The name *Alectoria virens* Tayl. was incorrectly applied to this species by Howe (1911). *A. virens* is a very different species unknown outside Asia (see Excluded taxa).

A single specimen from Vancouver Island, B. C. (Tibell 5083 [UPS]), was seen with scattered, yellow, tuberculate soralia. It was bright yellow with conspicuous yellow pseudocyphellae and was therefore definitely not *B. fremontii*. Soralia have not previously been reported from *B. tortuosa*.

Selected specimens

Exsiccatae. Brodo: Lich. Can. Exs. 3: *British Columbia*, Vancouver Island, Saanich, Brodo 8096 (CANL) – Brodo: Lich. Can. Exs. 4: *British Columbia*, 29 miles S of Merritt, Brodo 8496 (CANL) – Merrill: Lich. Exs., Ser. 1, 160: *Oregon*, Marion County: Silverton, Foster (BM, CANL, DUKE, MSC, NYBG, US) – Weber: Lich. Exs. 418 (p.p.): *California*, Shasta County: Burney, Pike & Jackman (CANL).

Canada. British Columbia. Coastal District: Earl's Cove, Brodo 8343 (CANL) – Dean River Basin: Along Mosher Creek, Tweedsmuir Provincial Park, Ohlsson 1932A (p.p.) (MSC) – Fraser River Basin: Beaver Lake, Macoun 417 (CANL) – Islands South District: Between Parkville and Port Alberni, Tibell 5083 (UPS) – Skeena River Basin: 30 miles W of New Hazelton, Ohlsson 2887A (MSC).

U.S.A. California. Humboldt County: Near Manila, Lindsay 90 (HSC) – Santa Cruz County: Boulder Creek, Hesse 3056 (CANL, COLO, F, NYBG) – Trinity County: Weaverville, Richards & Drouet 1315 (FH, F, US) – *Idaho.* Idaho County: Stites, Cooke 22967 (WIS) – Latah County: Kendrick, Esslinger 232B (WIS?) – *Oregon.* Jackson County: Eagle Point, Sipe 640 (MSC, ORE) – *Washington.* Clallam County: Dungeness, Foster 12 (US) – Okanogan County: Winthrop, 8 mile Creek, Hasles s.n. (p.p.), 1950 (WIS).

Pseudephebe Choisy

Icon. Lich. Univ., Ser. 2, Fasc. 1: sine pagin. (1930). – *Alectoria* sect. *Pseudephebe* (Choisy) Choisy, Bull. Mens. Soc. Linn. Lyon 24: 26 (1955). – *Parmelia* sect. *Tereiuscula* Hillm., Rabenh. Krypt.-Fl. 9, 5(3): 104 (1936). – *Alectoria* sect. *Tereiuscula* (Hillm.) Lamb, Br. Antarct. Surv. Sci. Rep. 38: 26 (1964). – *Alectoria* subgen. *Tereiuscula* (Hillm.) D. Hawksw., Lichenologist 5: 201 (1972). – *Alectoria* sect. *Subparmelia* Degel., Nyt Mag. Naturvid. 70: 286 (1938).

Type species: *Pseudephebe pubescens* (L.) Choisy (syn. *Lichen pubescens* L.; holotype).

Thallus fruticose, sometimes becoming compacted and subcrustose centrally, prostrate, closely adpressed to the substrate (under 1 cm tall), attached to the substrate by hapters over the whole thallus area and not merely at the base; base sometimes dying so that the thalli form rosettes; branching isotomic-dichotomous, often strictly so, branches terete but tending to become dorsiventrally compressed in one species, minute, even to uneven; brown to dark or black, matt to slightly shiny, usually concolourous except where attached to the substrate.

True lateral spinules, isidia, soralia, and pseudocyphellae absent. Cortex composed of longitudinally orientated hyphae which become prosoplectenchymatous to almost paraplectenchymatous at the surface. The surface itself is smooth or slightly rough. Medullary hyphae not ornamented.

Apothecia lateral, frequent to abundant in both species; excipulum thallinum concolourous with the thallus, becoming excluded or, if persistent, not incurved, sometimes ciliate; disc brown to almost black. Asci clavate, thick-walled, arrested bitunicate, 8-spored. Ascospores ellipsoid, lacking a distinct epispore, hyaline at maturity, simple, $7-12 \times 6-8 \mu\text{m}$. Pycnidia common.

Lichen products absent.

Discussion

The systematic position of the species comprising the genus *Pseudephebe* has long been a cause of controversy, with some authors placing them in *Alectoria*, and others classifying them under *Parmelia*. They cannot really be satisfactorily placed in either of these two genera and are most appropriately regarded as constituting a distinct genus. With regard to *Parmelia*, *Pseudephebe* is clearly allied to the subgenus *Melanoparmelia* Hue, but differs from most species of that subgenus in the fruticose rather than foliose habit and in the absence of lichen substances. It is probable that some species with almost fruticose "lobes" currently generally placed in *Melanoparmelia* may eventually prove to be additional members of *Pseudephebe*. We have not investigated those species in view of work in progress elsewhere.

In *Pseudephebe* the cortex is composed of longitudinally orientated hyphae as reported by Degelius (1937). However, where the hyphae reach the surface, a "layer" of short almost isodiametric cells is formed (Fig. 13) quite unlike that seen in other taxa treated here, with the possible exception of species placed in *Bryoria* sect. *Subdivergentes*. In that section of *Bryoria*, the superficial cortical cells are extremely irregular in shape and project above the surface to produce a dull, matt texture and appearance. In *Pseudephebe* the surface of the cortex, although "cellular", is only very slightly roughened by unevenness of the cells.

1. *Pseudephebe minuscula* (Nyl. ex Arnold) Brodo & D. Hawksw., comb. nov.

Imbricaria lanata var. *minuscula* Nyl. ex Arnold, Ver. Zool.-Bot. Ges. Wien 28: 293 (1878); type: Fennia, Lapponia enontekiensis, Enontekio, in alpe

Pietsovaara prope Kilpisjärvi, J. P. Norrlin, 1867 (H-Nyl. 34255 lectotype!); basionym. – *Parmelia minuscula* (Nyl. ex Arnold) Nyl., Bull. Soc. Linn. Normand., sér. 4, 1: 205 (1887). – *Cornicularia lanata* var. *minuscula* (Nyl. ex Arnold) Hue, Deux. Exped. Antarct. Fr., Lich.: 41 (1915). – *Alectoria minuscula* (Nyl. ex Arnold) Degel., Nyt Mag. Naturvid. 78: 286 (1938).

Parmelia pubescens var. *congesta* Zahlbr., Dtsch. Südpol. Exped. 8: 52 (1928); type: Antarctica, Kaiser Wilhelm II Land, Gaussberg, Drygalsky's Expedition, 1901–03 (BM lectotype!). – *Alectoria congesta* (Zahlbr.) Dodge, B.A.N.Z. Antarct. Res. Exped. 1929–31, B, 7: 195 (1948). – *Alectoria minuscula* f. *congesta* (Zahlbr.) Lamb, Lilloa 14: 244 (1948).

Parmelia minuscula subsp. *minutissima* Räs., Medd. Soc. Fauna Fl. Fenn. 43: 118 (1919); type: Finland, Ostrobothnia borealis, Simo, Onkalo, kiviadala, V. Räsänen, 26 June 1915 (H holotype!).

Alectoria antarctica Dodge & Baker, Ann. Missouri Bot. Gard. 25: 599 (1938) p.p.; type: Antarctica, Marie Byrd Land, Edsel Ford Range, Mt. Rea-Cooper, P. Siple et al. R-1 (herb. Dodge, holotype slide!); nom. illegit. (Art. 70).

Parmelia minuscula f. *aperta* Lyngé, in Lyngé & Scholander, Skr. Svalbard Ishavet 41: 71 (1932); type: Greenland, Kapp Humboldt, B. Lyngé, 3 August 1929 (O lectotype!).

Parmelia minuscula f. *applanata* Lyngé, in Lyngé & Scholander, Skr. Svalbard Ishavet 41: 71 (1932); type: Greenland, Østgrønland, Kjerulfjorden, B. Lyngé, 13 August 1929 (O lectotype!). – *Alectoria minuscula* f. *applanata* (Lyngé) Lamb, Nyt Mag. Naturvid. 80: 264 (1939).

Parmelia minuscula f. *crustacea* Lyngé, in Lyngé & Scholander, Skr. Svalbard Ishavet 41: 71 (1932); type: Greenland, Østgrønland, Jacksonoya, B. Lyngé, 31 July–1 August 1929 (O lectotype!). – *Alectoria minuscula* f. *crustacea* (Lyngé) Degel., Bot. Notiser 1943: 108 (1943).

Parmelia minuscula f. *luxurians* Lyngé, in Lyngé & Scholander, Skr. Svalbard Ishavet 41: 71 (1932); type: Greenland, Østgrønland, Kjerulfjorden, B. Lyngé, 13 August 1929 (O holotype!).

Parmelia pubescens f. *biformis* Vain., Res. Voy. S. Y. Belgica 1897–99, Lich.: 14 (1903); type: Antarctica (TUR syntypes; not seen; see Lamb, 1948: 243). – *Alectoria minuscula* f. *biformis* (Vain.) Lamb, Lilloa 14: 243 (1948). – *Alectoria biformis* (Vain.) Dodge, Lich. Fl. Antarct.: 219 (1973).

Parmelia almqvistii f. *opaca* Lyngé, Rep. Scient. Results Norw. Exped. Nova Zemlya 43: 197 (1928); type: Nova Zemlya, Belushi Bay, B. Lyngé, 1921 (O holotype; not seen).

For further information on the synonymy of this species, see Lamb (1948, 1964).

Thallus prostrate and decumbent, in extreme forms becoming almost subfoliose or even crustose and pulverulent, generally forming more or less circular adpressed thalli up to 7 cm diam.; branches always somewhat flattened, especially on older portions, up to 1.0 mm broad,

tapering irregularly to 0.2–0.5 mm on main stems and 0.1 mm at tips where the branches are very uneven, but more or less terete; branching irregularly isotomic dichotomous with numerous short lateral branches often present giving thallus a “ciliate” appearance; internodal distance short, usually c. 0.2–0.5(–1.0) mm; dark brown to black, shiny or dull, occasionally pale brown at the base.

True lateral spinules absent, but simple or branched isidioid adventitious branches are not uncommon in one morphotype. Soralia and pseudocyphellae absent (or brown and inconspicuous in one specimen?).

Apothecia frequent, disc dark red-brown to black, flat, to 3 mm diam.; margins persistent, smooth or verrucose; spores 8 per ascus, 7.7–8.0 × 6.7–9.0 μm, hyaline. Pycnidia very abundant, embedded in the thallus and opening to the surface through broad ostioles; conidia 6–8 × 2–1 μm.

All tissues of thallus K–, C–, KC–, PD–; no lichen substances present.

Ecology. On siliceous, or sometimes lime-containing rocks in alpine or arctic habitats. John Thomson (in litt.) considers it to be characteristic of windswept gravels and rock outcrops. Imshaug (1957) pointed out that *P. minuscula* is more abundant in drier, more exposed localities than is *P. pubescens*.

Distribution. Circumpolar arctic-alpine (Fig. 66). There seems to be a tendency for *P. minuscula* to be more continental in its distribution than *P. pubescens*, although the two are often found together. Weber (in litt.) has observed the same thing. *P. minuscula* is almost entirely absent from the mountains on the British Columbia coast and is fairly common in the southern Rockies. It was growing luxuriantly on one of the dry subalpine summits of the San Francisco Mountains in Arizona. The species is also known from a number of localities in the Southern Hemisphere. In Antarctica, it is circumpolar, whereas *P. pubescens* is restricted to the milder Antarctic Peninsula no further south than the Marguerite Bay area (Lamb 1964).

Discussion

Pseudephebe minuscula, like other lichens growing under extremely rigorous conditions, is

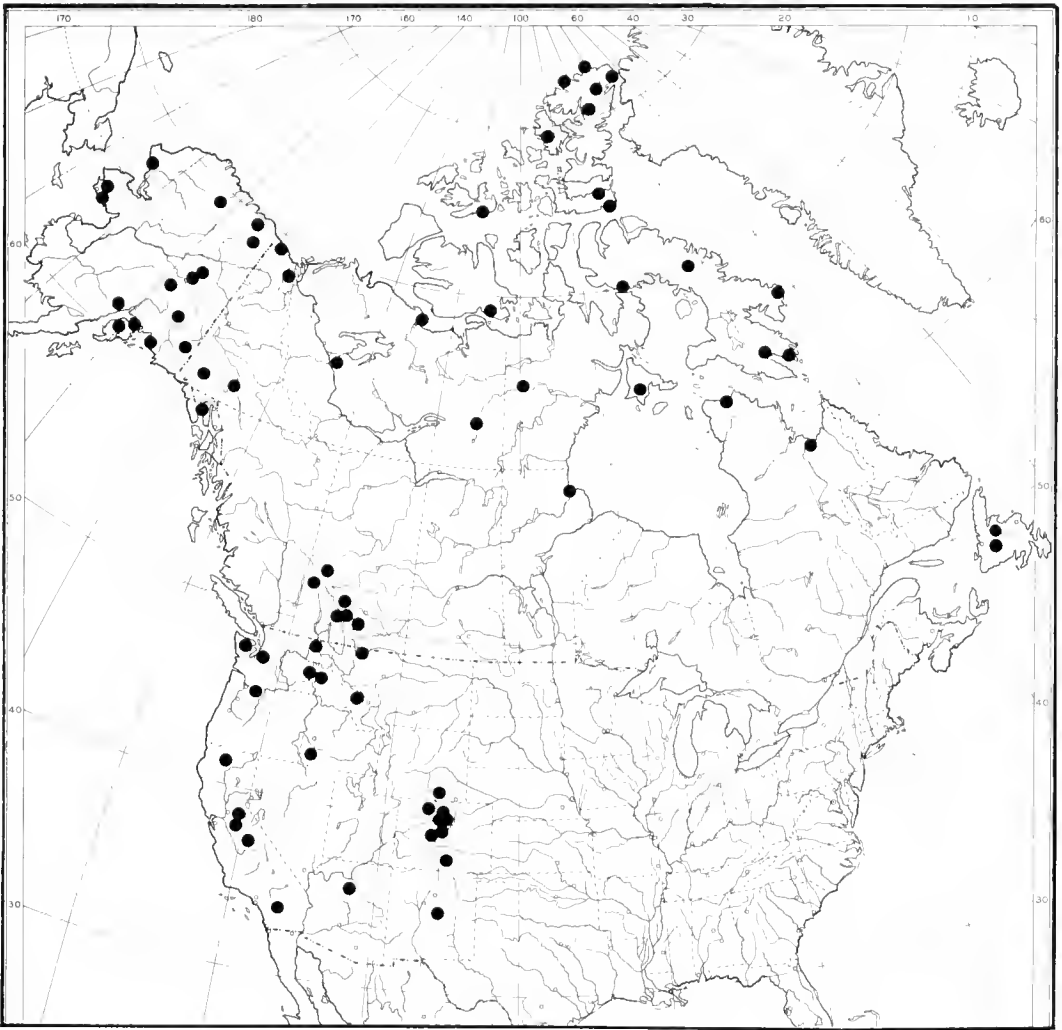


Fig. 66. *Pseudephebe minuscula*. N. American distribution.

very variable in its superficial appearance, depending on the protection and moisture available to the thallus. Typically, the thallus is conspicuously flattened and very minute, but robust specimens can become almost ascendent and develop terete branches which appear very like those of *P. pubescens*. Similarly, under extremely severe conditions, *P. pubescens* can become very adpressed and approach *P. minuscula*. As a result of environmental pressures tending to induce a similar phenotype, as Imshaug (1957) has already pointed out, some

thalli will always remain difficult to refer to one species or the other. Imshaug (1957) accurately described the situation with regard to the difficulties in the taxonomy of this pair of species.

The environmental modifications in both species have been given a large number of infraspecific names, mainly at the rank of variety or form (e.g., Lynge & Scholander 1932, Hillman 1936, Lamb 1948, 1964, Motyka 1960a). Most of these are probably of little taxonomic importance and we have not attempted to differentiate one from another and assess their relative

importance in this study. One morphotype of *P. pubescens*, f. *subciliata* (see p. 156), may, however, be genotypically distinct (see Hawksworth 1972) but that form appears to be extremely rare in North America.

Dodge (1973 p. 218) endeavoured to separate five species in this group on the basis of differences in habit, branching, and measurements of various anatomical characters. In our view, his system is impractical, being mainly based on characters of dubious taxonomic value.

Selected specimens

Canada. British Columbia. Fraser River Basin: Wells Gray Provincial Park, Ahti 14158 (H) – Kootenay River Basin: Lake Oesa, MacFadden 62 (US) – *Alberta.* Jasper National Park, Queen Elizabeth Ranges, Scotter 7797 (CANL) – *Manitoba.* Churchill, J. W. Thomson 3772 (CANL) – *Quebec.* Territoire du Nouveau Québec: Fort Chimo, J. W. Thomson 13778 (CANL, US) – *Newfoundland.* Grand Falls District: Summit of Hodges Hill, Ahti 7740 (H) – *Yukon.* 62°39'N, 134°45'W, Bostock 34 (CANL) – Kluane Lake, Murray L-41336 (FH) – *Northwest Territories.* District of Franklin: Axel Heiberg Island: White Glacier, Kuc 85 (CANL) – Devon Island: Dundas Harbour, Innes-Taylor 11 (CANL) – Melville Island: Bridport Inlet, Tener 395 (CANL) – Mackenzie District: Bernard Harbour, Johansen s.n., June 1914 (FH) – Keewatin District: Southampton Island, Salmon Pond, Parker SP-70-16C (CANL).

U.S.A. Alaska. Alaska Range District: E fork of the Kuskokwim River, Viereck 5117A (ALA) – Arctic Coast District: Okpilak Lake, J. W. Thomson & Shushan 10159 (US) – Eastern Pacific Coast District: Muir Glacier, Kincaid s.n., 13 July 1897 (CANL) – *Arizona.* Coconino County: San Francisco Peaks, Nash 7561 (CANL, MIN) – *California.* Amador County: Silver Lake, Thiers 17241 (HSC) – Calaveras County: Ebbetts Pass, Thiers 17664 (CANL) – Riverside County: San Jacinto Mts., Darrow 305 (WIS) – Siskiyou County: Mt. Shasta, Cooke 25701 (WIS) – *Colorado.* Summit County-Clear Creek County: NE of Loveland Pass, Shushan SL-1593 (US) – *Idaho.* Owyhee County: Silver City, Anderegg 1437 (WIS) – *Montana.* Glacier County: Glacier National Park, Altyn Peak, Imshaug 5488 (CANL) – *New Mexico.* Santa Fe County: Santa Fe, Egan EL-1652 (US, WIS) – *Oregon.* Hood River County: Mt. Hood, Shushan SL-2500 (WIS) – *Washington.* Clallam County: Olympic National Park, Obstruction Peak, Brodo 14401 (CANL) – Pend Oreille County: Newport, Schroeder L-305 (WIS) – *Wyoming.* Albany County: Medicine Bow Mts., Cain 25736 (WIS).

2. *Pseudephebe pubescens* (L.) Choisy

Icon. Lich. Univ., ser. 2, 1: sine pagin. (1930). – *Lichen pubescens* L., Sp. Pl. 2: 1155 (1753); type: sine loc., herb. C. Linnaeus (LINN 1273.286 lectotype!).

– *Alectoria pubescens* (L.) R. Howe, Class. Fam. Usneaceae: 23 (1912) et Bull. Torrey Bot. Club 39: 201 (1912).

Alectoria pacifica Stiz., Proc. Calif. Acad. Sci. 5(2): 537 (1895); type: Mexico, Island of Guadalupe, E. Palmer, 1875 (ZT holotype! US isotype!).

For further synonyms see Hawksworth (1972 pp. 235–236).

Thallus decumbent to ascendent and shrubby; branches generally very uneven in diameter but more or less terete throughout their length, with diameters near the base 0.1–0.2 mm and at the tips 0.05–0.1 mm; branching isotomic to anisotomic dichotomous with short lateral branches rare; internodal distance generally long, (0.6–)1–3(–5) mm; dark red-brown to black, satiny to shiny.

True lateral spinules, soredia, and isidia absent, although adventitious outgrowths similar to those on *P. minuscula* are found on rare occasions. Pseudocyphellae absent. Pycnidia abundant and conspicuous, as in *P. minuscula*.

Apothecia infrequent, disc black, flat, 1.2–1.6 mm diam.; margin thick, red-brown when young, excluded when old; spores 8 per ascus, broadly ellipsoid, c. $10 \times 7.5 \mu\text{m}$, hyaline.

All thallus tissues K–, C–, KC–, PD–; no lichen substances present.

Ecology. On dry, sandy, or stony ground and acid rocks, especially igneous rocks, sometimes shale; usually on exposed rocky ridges or boulders soon free of snow in the spring. The species tends to be found in moister sites in regions having a continental climate (Weber in litt.).

Distribution. Low to high arctic, subalpine to alpine; frequent on exposed habitats along the west coast and in the Districts of Keewatin and Mackenzie (N.W.T.) as well as on the arctic islands; many more occurrences in the humid coastal ranges than the similar *P. minuscula*. It ranges as far south as Guadalupe (type of *Alectoria pacifica*). It is circumpolar in both the Northern and Southern Hemispheres (Hawksworth 1972).

Discussion. See under *P. minuscula*.

Selected specimens

Exsiccatae. Merrill: Lich. Exs., Ser. I, 88: *Washington*, Spokane County: Crater Basin, Bosner (BM, CANL, DUKE) – Merrill: Lich. Exs., Ser. II, 135:

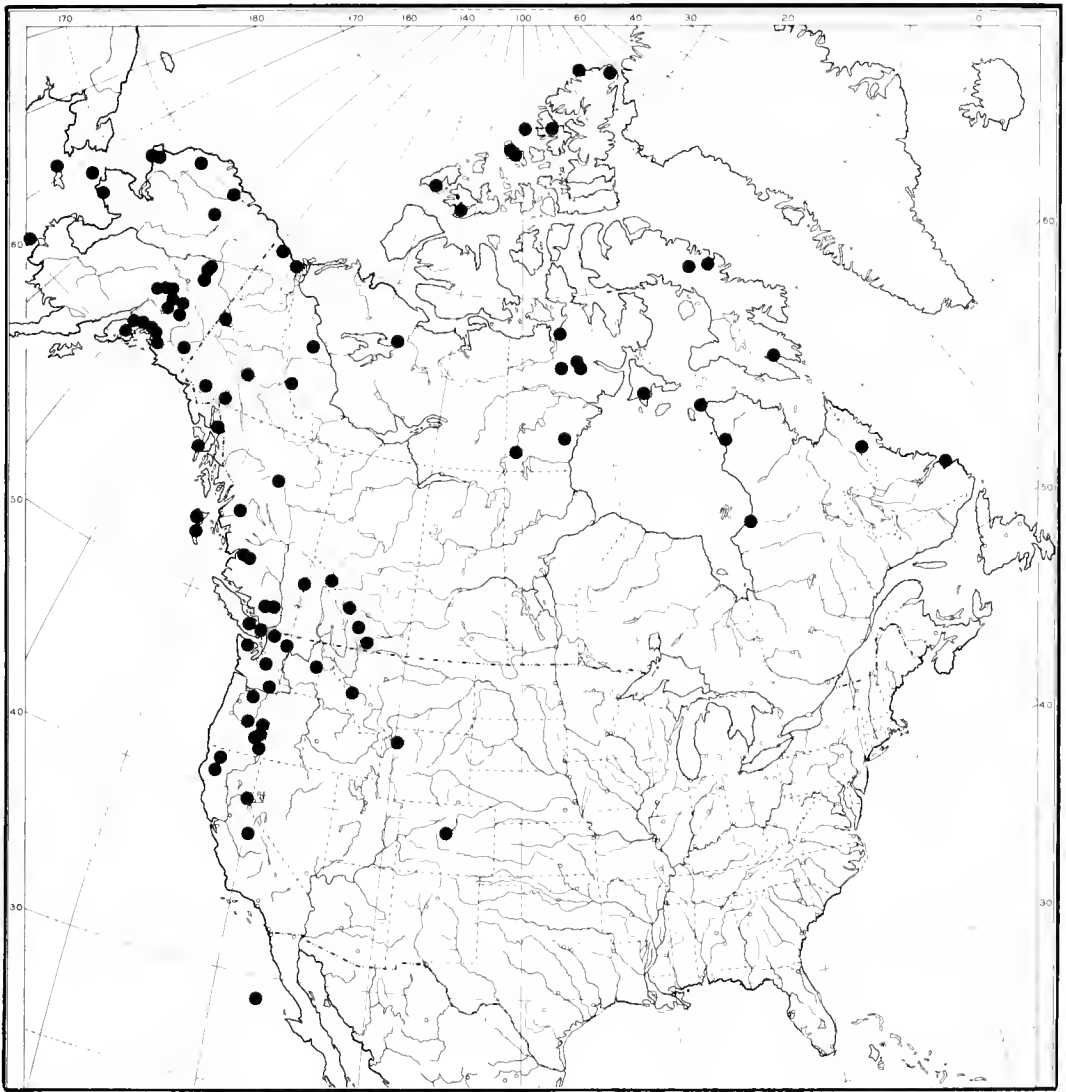


Fig. 67. *Pseudephebe pubescens*. N. American distribution.

Washington, Klickitat County, Goldendale, Foster (BM, DUKE, US) – Thomson: Lich. Arct. 55: *N.W.T.*, District of Keewatin: Rossby Lake, J. W. Thomson (CANL, DUKE, MSC) – Weber: Lich. Exs. 219: *N.W.T.*, District of Mackenzie: Mackenzie Mountains, O'Grady Lake, Cody 16816 (CANL, DUKE).

Canada. British Columbia. Coastal District: W of Hagensburg, Ohlsson 2289 (CANL) – Fraser River Basin: E of Hazelton, Ohlsson 2973 (CANL) – Islands North District: Moresby Island: Laing Point, Brodo 10795 (CANL) – Islands South District: Vancouver

Island: Mount Benson, Nanaimo, Macoun 49 (US) – Saltspring Island, Brodo 13890 (CANL) – Skeena River Basin: Terrace, Ohlsson 2798 (CANL) – Alberta. Oldham River Watershed, Beauvais Lake, Bird 14754 (CANL) – Quebec. Territoire du Nouveau Québec: Porvungnituk (sic) (Povungnituk), Thompson 30 (CANL) – Poste-de-la-Baleine, Brisson & Forest 20342 (CANL) – Newfoundland. Labrador North District: Crater Lake vicinity, 52 miles WSW of Hebron, Gillett 9415A (CANL) – Labrador South District: Pack's Harbour, Waghorne 25 (US) – Yukon. Dezadeash Lake, Douglas 5355 (CANL) –

34 miles from West Dawson, Calder & Billard 3320 (CANL) – *Northwest Territories*. Mackenzie District: NE corner of Great Bear Lake, Wisensel JW18B (SASK) – District of Keewatin: Ennadai Lake, Brown 1327 (CANL) – Franklin District: Baffin Island, Dutch Polar Station, Soper 152 (CANL, DUKE, NYBG).

U.S.A. Alaska. Alaska Range District: Denali Highway, mile 28, Krog 3805 (O) – Aleutian Islands: Unalaska, Captain's Bay, Eyerdam s.n., 1 May 1932 (FH) – Bering Strait District: Ogotoruk Creek Drainage, Johnson, Viereck & Melchior 106 (ALA, US) – Central Yukon River District: Steese Highway, Eagle Summit, Krog 2546 (O) – Eastern Pacific Coast District: Sitka, Harbour Mountain, Krog 6266 (O) – Western Pacific Coast District: Cold Bay, 55°12'N, 162°40'W, MacCartney s.n., 6 Aug. 1971 (WIS) – *California*. Mariposa County: Yosemite Valley, Herb. H. E. Hasse 571 (US) – Sierra County:

E of Yuba Pass, Tavares 621 (US) – Siskiyou County: Trail to Sugar Lake, Salmon Mountains, Largent 4495 (HSC, WIS) – *Colorado*. Clear Creek County: Summit Lake, Mount Evans, Sushan & Weber S 1598A (CANL, FH) – *Montana*. Ravalli County: St. Mary Peak, Stevensville, Stickney 1559 (WIS) – *Oregon*. Deschutes County: Lava Butte, near Bend, Pojar s.n., 8 Aug. 1970 (UBC) – Hood River County: Mt. Hood, Foster 571 (FH) – Lake County: Near Fort Rock, Horse Ranch, Pike L-106 (OSC) – *Washington*. Okanogan County: Slate Peak, near Winthrop, Imshaug 18568 (CANL) – Whatcom County: Mt. Baker, Herre s.n., 14 Aug. 1914 (US) – *Wyoming*. Yellowstone National Park: Shoshone Lake, Coulter 3 (US).

Mexico. Baja California. Guadalupe Island, Palmer s.n., 1875 (US, ZT).

Sulcaria Bystr.

Ann. Univ. Mariae Curie-Skłodowska, C, 26: 275 (1971). – *Alectoria* sect. *Sulcaria* Mot., Fl. Polska, Porosty 5(2): 39 (1962); nom. inval. (Art. 37). – *Alectoria* subsect. *Sulcata* DR., Ark. Bot. 20A (11): 5, 19 (1926). – *Alectoria* subgen. *Sulcata* (DR.) D. Hawksw., J. Jap. Bot. 46: 335 (1971). – *Alectoria* sect. *Coelocaulopsis* Choisy, Bull. Mens. Soc. Linn. Lyon 24: 26 (1955); nom. inval. (Art. 36).

Type species: *Sulcaria sulcata* (Lév.) Bystr. ex Brodo & D. Hawksw. (syn. *Cornicularia sulcata* Lév.; holotype).

Thallus fruticose, erect and caespitose to decumbent or pendent; branching variable; branches generally terete, but in one species bursting open longitudinally and forming dorsiventrally compressed and expanded flattened areas; greyish-brown, badious, or emerald green.

Lateral spinules present consistently in some species, rarer or absent in others. Isidia and soralia absent. Pseudocyphellae present in the form of a single longitudinal furrow (Fig. 5D), \pm continuous from the base to the apex of the thallus, deeply depressed, sometimes appearing almost scalariform, white or emerald green, sometimes bursting open to expose the medulla, occasionally tending to become weakly sorediate. Cortex not disintegrating, not differentiated and rough at the surface. Medullary hyphae not ornamented.

Apothecia lateral, often appearing geniculate owing to the death of the branch distal to them, common in one species, unknown in the others; excipulum thallinum concolourous with the thallus, persistent and incurved, sometimes becoming ciliate; disc brownish-black, often distinctly blue-grey pruinose. Asci clavate, thick-walled, arrested bitunicate, 6–8-spored. Ascospores ellipsoid, yellowish to brown at maturity, 1- or later 3-septate when mature, $22\text{--}40 \times 8\text{--}15 \mu\text{m}$. Pycnidia unknown.

Usnic acids absent; atranorin abundant in two species, chloroatranorin absent; β -orcinol dep-

sidone present in two species; pulvinic acid derivatives known in two species; orcinol depsidone known in one specimen of one species; orcinol depsides, tridepsides, β -orcinol depsides and hydroxyanthraquinones absent.

Discussion

Of the three species we are accepting in this genus, only one (*S. badia*) is known from North America; the others (*S. sulcata* and *S. virens*) are confined to southeast Asia. Only *S. sulcata* is known fertile but this species is regularly so. The distinctive pseudocyphellate furrow serves to separate sterile members of this genus from the other genera treated here. Two species which we have placed in *Bryoria* (*B. pseudocapillaris* and *B. spiralifera*), and which are only known sterile, may be allied to it. In fact, the section *Implexae* of *Bryoria* seems to be closely allied to the genus *Sulcaria* to judge by their similarities in chemistry (the frequency of β -orcinol depsidones), colour (as in *B. spiralifera* and the European *B. kuennerleana*), and long pseudocyphellae.

It is of interest to note that, whereas atranorin is usually present in only trace amounts in *Bryoria* so that it is only detectable by TLC, in two of the species of *Sulcaria* it is so abundant that a yellow reaction with K is readily obtained and the compound easily demonstrated by microcrystal tests.

1. *Sulcaria badia* Brodo & D. Hawksw., sp. nov.

Thallus pendulus, 20–50 cm longus, flaccidus; rami praecipue iso-dichotomiter fastigiati, frequentes e basi emergentes, in angulos praecipue acutos rotundos divergentes, valde compressi et tortuosi, conspicue sulcati, diametro aequales, basi 0.25–0.4(–1.0) mm diam., ramis lateralibus brevibus et gracilibus fere perpendiculariter frequenter instructi; tota planta

opaca castanea vel badia vel partim flavo-brunnea.

Rami laterales spiniformes veri, isidia, et soralia desunt. Pseudocyphellae conspicuae, albae, lineatae, longissimae, in sulcos profundos immersae.

Apothecia et pycnidia ignota.

Cortex K+ flavescens, C-, KC+ flavescens, PD+ brunneolus; medulla K-, C-, KC-, PD-; in charta separata K+ flavescens et PD+ flavescens reagens. Thallus solum atranorium continens.

Holotypus: America septentrionalis, U.S.A., Oregon, Philomath, in Malis veteribus, F. P. Sipe 669 p.p. (ORE). Fig. 68.

The holotype is a portion of the same number designated by Gyelnik as the holotype of *B. pseudofuscens* (Gyeln.) Brodo & D. Hawksw. in BP (i.e., an arithmotype). The specimen in BP is, however, quite distinct in both morphology and chemistry from that in ORE. See also the discussion under *B. pseudofuscens*.

Thallus pendent, 20–50 cm long, flaccid; branching mainly isotomic dichotomous, frequent from the base, angles between the dichotomies mainly acute and rounded; branches markedly flattened and twisted, conspicuously sulcate, even, 0.25–0.4(–1.0) mm diam. at the base, with short, slender almost perpendicular lateral branches; very dull chestnut-brown to almost badius or yellowish brown in parts.

True lateral spinules, isidia and soralia absent. Pseudocyphellae conspicuous, white, linear, extremely long, most developing into deep furrows (Fig. 5D).

Apothecia and pycnidia unknown.

Cortex K+ yellow, C-, KC+ yellow, PD+ brownish; medulla K-, C-, KC-, PD-; on filter paper K+ yellow and PD+ yellow. Contains atranorin alone. A specimen from California (Pike & Rhoades 2245 [OSU]) contains, in addition, an unidentified PD- substance having relative Rf classes (C. Culberson 1972) of 5.5–5.

Ecology. On trees, especially apple and oak trees, in well-lighted *Quercus garryana* communities.

Distribution. Along the west coast from Washington to Northern California (Fig. 69). Endemic to North America.

Discussion

This previously undescribed species is easily recognized by its very distinctive colour. The colour of the thallus is not unlike that of the Asian *S. sulcata* which is almost always fertile,



Fig. 68. *Sulcaria badia*, Oregon, Hall, 1871 (FH-Tuck, 504). Scale 0.5 mm.

caespitose, and contains psoromic acid in addition to atranorin.

A morphologically typical specimen of *Sulcaria sulcata* var. *sulcata* from China (Krypt. Exs. Vindobon., No. 2766, Handel-Mazzetti, prov. Yunnan [CANL]) was found to contain virensic acid instead of psoromic acid with TLC and microchemical tests (Hawksworth 1971). The frequency of this chemical strain is unknown at present. It is intriguing that the locality of this specimen is the same as the type locality of *S. sulcata* f. *vulpinoides*, a form differing from f. *sulcata* in being yellow-green in colour, due to vulpinic acid (Hawksworth 1971).

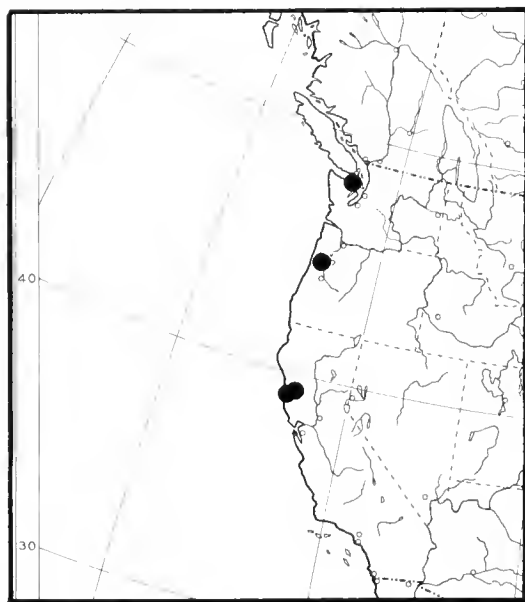


Fig. 69. *Sulcaria badia*. Known distribution.

Large amounts of atranorin occur in this species: a K+ yellow reaction is easily obtained, and this compound can be readily confirmed by micro-crystal tests in GAO-T.

We are referring this species to the genus *Sulcaria* because of the characteristic sulci, although this feature is perhaps less well developed in *S. badia* than it is in either *S. sulcata* or *S. virens*. In the absence of apothecia, the placing of this North American species in the genus *Sulcaria* should be regarded as tentative.

Specimens

U.S.A. California. Mendocino County: Round Valley. Chesnut s.n., 20 July–3 Aug. 1897 (US) – 2 miles W of Willits, Pike & Rhoades 2245 (OSC) – *Oregon*. Benton County: near Philomath, Sipe s.n., no date (ORE, F) – Philomath, Sipe 669 (CANL) – Locality unknown: Hall s.n., no date (FH-Tuck., US) – *Washington*. Clallam County: near Dungeness. Foster 2552A (FH).

Excluded taxa

Alectoria achariana Gyeln.

Nyt Mag. Naturvid. 70: 54 (1932).

This species was reported by Gyelnik (1931) prior to the valid publication of the name from "Canada, Lake Louise, alt. 5665 ft. (SEIGFRID, sub *Alectoria Fremontii*. A1-9)". Gyelnik, however, later reconsidered his determination and treated this collection as the holotype of *Bryopogon negativus* f. *canadensis* Gyeln., which is discussed separately below.

The identity of *A. achariana* itself remains uncertain in the absence of the holotype collection which is not in BP (Versegny in litt.). Hawksworth (1972 p. 219) noted that an isoparatype of this taxon in BM was *Bryoria fuscescens* var. *positiva*.

Alectoria californica (Tuck.) Merrill

Lich. Exs. no. 82 (1908). – *Cetraria californica* Tuck., Am. J. Arts Sci., ser. 2, 28: 203 (1859).

Although this taxon shows a strong resemblance to some morphotypes of *Bryoria abbreviata*, it is more appropriately placed in the genus *Cornicularia* (as *C. californica* (Tuck.) DR.) on the basis of the anatomy of the cortex (see general section Anatomy and morphology: Cortex). The characters most useful for the separation of these two species are discussed under *B. abbreviata*.

Alectoria cetrariza Nyl.

Bull. Soc. Linn. Normand., sér. 4, 1: 270 (1887); type: U.S.A., Oregon, Millamak, on *Pinus contorta*, Herb. Nylander no. 35973 (H holotype!). – *Coelocaulon cetrariza* (Nyl.) Gyeln., Ann. Mus. Nat. Hungar., Bot. 28: 282 (1934).

An examination of the holotype of this taxon showed it to be conspecific with *Cornicularia californica*.

Alectoria crinalis Ach.

Lich. Univ.: 594 (1810).

This epithet was taken up by Hale (1969 p. 191) for the species treated under the name *Ramalina crinalis* (Ach.) Gyeln. by Motyka (1964). As pointed out below under *Alectoria thrausta*, *R. thrausta* (Ach.) Nyl. is the nomenclaturally correct combination for this species. Although we have not seen the material under this name in Acharius' main herbarium in H, authentic material of it in BM (!) is *R. thrausta*.

Alectoria divergens (Ach.) Nyl.

Mém. Soc. Imp. Sci. Nat. Cherb. 3: 171 (1855); et Bot. Notiser 1855: 136 (1855). – *Cornicularia divergens* Ach., Meth. Lich.: 305 (1803); type: Sweden, Lapponia, Herb. Acharius (H lectotype!); basionym.

This species was accepted in *Alectoria* by Howe (1911), but on the basis of its cortical structure must be placed in *Cornicularia* at the present time (Hawksworth 1972). The separation of *C. divergens* from *Bryoria nitidula*, a species with which it has sometimes been confused, is discussed under the latter species.

Cornicularia fibrillosa (Ach.) Halsey

Ann. Lyceum Nat. Hist. N. Y. 1: 20 (1823). – *Cornicularia pubescens* γ. *fibrillosa* Ach., Syn. Lich.: 303 (1814); type: Amer[ica] bor[éal]is, Muhlenberg (H-Ach holotype); basionym.

This name was applied by Halsey (1823) to a species "Common on fences" in the vicinity of New York. He clearly based his name on

that of Acharius (1814) and intended to treat it as distinct species ("Certainly a distinct species"). Acharius, however, gave the habitat as "ad saxa" and an examination of the only specimen under this name in his main herbarium (presumed to be the holotype) by Dr. T. Ahti (in litt.) revealed that this was a member of the genus *Epliebe* Fr. Its small size renders a determination to the species level difficult. The epithet *fibrillosa* was not mentioned by Henssen (1963). From Halsey's description and comments there can be little doubt that he misapplied the Acharian name to *Bryoria furcellata*. A specimen under this name from Tuckerman's herbarium (New England, "ad septimenta lignea, vulg., sterilis" [BM]) is also *B. furcellata*.

It should also be pointed out that Zahlbruckner (1930 p. 604) erroneously attributed the name *Cornicularia fibrillosa* to Eaton (1829 p. 188); Eaton did employ this name and even provided a description at least five years earlier (Eaton 1824 p. 273; editions of this work prior to the fourth have not been seen by us). Since Eaton did not cite the names of authors of lichen taxa in the fourth edition, and as *C. fibrillosa* was listed after *C. pubescens* and stated to occur "on rocks", it seems that he was simply following Acharius but adopting specific rank as proposed by Halsey in the previous year.

***Bryoria intricans* (Vain.) Brodo & D. Hawksw., comb. nov.**

Alectoria chalybeiformis f. *intricans* Vain., Termezetr. Fuzetek 22: 276 (1899); type: Caucasus, in rupe ad Adisch, 1885, H. Lojka, Herb. Vainio no. 01010 (TUR no. 001244 holotype!); basionym. — *Alectoria intricans* (Vain.) Mot., Fragm. Florist. Geobot. 3: 228 (1958).

Gyelnik (1931) reported this species from Idaho on the basis of a collection from the "Upper Priest River, on *Pinus* (STILLINGER, sub *Alectoria jubata*, *sorediata*, Al-11)" which we have not been able to locate. Motyka later tentatively referred one of Krog's Alaskan collections to this taxon but Krog (1968) did not accept his determination; in our view, Krog's specimen is a slender plant of *B. chalybeiformis*.

The holotype collection of this taxon is poorly developed but there seems little doubt that the interpretation of it adopted by Krog (1971), and

Dahl & Krog (1973), is correct. We have not seen any North American material definitely referable to this taxon although young thalli and fragmentary specimens of *B. chalybeiformis* resemble it in part but differ in being prostrate to decumbent rather than pendent. It is possible that *B. intricans* is a saxicolous morphotype of *B. lanestris* and it is of interest to note in this respect that Motyka (1958 a) applied the epithet *lanestris* to a saxicolous taxon apparently identical to *B. intricans*.

***Alectoria jubata* (L.) Ach.**

Lich. Univ.: 592 (1810). — *Lichen jubatus* L., Sp. Plant. 2: 1155 (1753); type: sine loc., Herb. Linnaeus no. 1273.281 p.p. (LINN lectotype!).

The name *Alectoria jubata* has been applied by both North American and European lichenologists at various times to numerous pendent species of *Bryoria* and has tended to be used as a "blanket" name for this taxonomically difficult group. As the name has been taken up in different senses, its rejection under Art. 69 now appears to be justifiable.

The lectotype specimen is extremely squashed and is in a poor state of preservation. It may either correspond to the concept of "*A. proluxa*" (an illegitimate name; see below) adopted by Motyka (1958 a), as pointed out by Hawksworth (1970), or even a very poor and maltreated specimen of *A. fremontii*. "*A. proluxa*", as interpreted by Motyka (1958a), appears to be a taxon restricted to eastern Europe and of dubious taxonomic validity. In view of the state of the type specimen and the uncertainty surrounding it, and since the name has been used in different senses, it seems preferable to reject this name altogether as a *nomen confusum*.

***Alectoria jubata* var. *philadelphiae* Gyeln.**

Nyt Mag. Naturvid. 70: 58 (1932). — *Bryopogon jubatus* var. *philadelphiae* (Gyeln.) Gyeln., Feddes Repert. 38: 225 (1935). — *Bryopogon fuscescens* var. *philadelphiae* (Gyeln.) Gyeln., Ann. Mus. Nat. Hungar., Bot. 32: 153 (1939).

This variety was described on the basis of a specimen from British Columbia (Selkirk, Shaw 977) but this collection has not been located in BP (Verseghe in litt.). Gyelnik's diagnosis of

this taxon was "*Thallus pendulus, opacus, levis, 4-8 cm longus, olivaceofuscus, sorediis lateralibus maculiformibus, fuscocaeasis, granuloso-pulverulentis instructus*". From Gyelnik (1935) it appears that the taxon must have been K- , KC- and C- . While these data suggest that this variety may well belong to *B. fuscescens*, Räsänen, who corresponded with and sent material to Gyelnik, determined some North American collections of *B. pseudofuscescens* in H as var. *philadelphiiae*. The true application of this epithet must consequently remain in doubt until the holotype collection is found.

Alectoria loxensis (Fée) Nyl.

Mém. Soc. Imp. Sci. Nat. Cherb. 5: 98 (1857). – *Cornicularia loxensis* Fée, Essai Crypt.: 137 (1825); lectotype: loc. cit. Pl. 31 fig. 7.

This species is most satisfactorily accommodated in the genus *Oropogon* Th. Fr., of which it is the holotype species (i.e., as *O. loxensis* (Fée) Th. Fr.). *Oropogon* differs from the other Alectorioid genera in having single-spored asci, massive brown submuriform ascospores, "cyphella-like" cortical perforations, and a characteristic chemistry. Considerable morphological and chemical variation occurs in what has been called *O. loxensis* and, as pointed out by Jørgensen (1972), the group is in need of a thorough taxonomic revision. *O. loxensis* s. lat. has not been correctly reported from either Canada or the United States but is very common on trees and rocks in the moist mountains of Central and South America. The thalli of *O. loxensis* are chestnut brown and shiny to very pale whitish-grey (var. *atroalbicans* (Nyl.) DR.; see Dodge & Vareschi 1956) and are very frequently referred to *Alectoria* s. lat. by collectors. Sterile plants of *O. loxensis* are, however, easily separated from similar *Bryoria* and *Sulcaria* species by the conspicuous fusiform "cyphella-like" perforations in the cortex (illustrated by Hawksworth 1972). The world distribution of *Oropogon* was discussed and mapped by Sato (1967).

Bryopogon negativus f. *canadensis* Gyeln.

Acta Geobot. Hungar. 2: 165 (1937). – *Bryopogon lanestrus* f. *canadensis* Gyeln., Acta Geobot. Hungar. 2: 165 (1937); nom. inval. (Art. 34).

This form was described on the basis of a collection from Lake Louise (near Banff, Alberta) which Gyelnik (1932) had determined as *Alectoria achariana* (see this name). Gyelnik's original diagnosis of this form was "*Similis f. barbato* Gyeln. *sed ramis primariis thalli crassi (usque ad 1 mm), minus contorti, angulosi, irregulariter lacunosi. Thallus K- , C- , KC- , P- "*. Although Gyelnik indicated that the type material was preserved in BP, it cannot be located there now (Verseghy in litt.), and so the identity of this taxon must remain in doubt.

Alectoria proluxa (Ach.) Nyl.

Medd. Soc. Fauna Fl. Fenn. 2: 14 (1878). – *Alectoria jubata* α. *prolaxa* Ach., Lich. Univ.: 592 (1810).

The name *Alectoria proluxa*, which was applied to North American collections by several early authors (e.g., Nylander 1885, Hulting 1896, Macoun 1902), was used by Motyka (1958 a, 1962) for a species he considered to be essentially eastern European. As pointed out by Hawksworth (1970), however, a number of nomenclatural difficulties surround this name. It can be treated as (a) illegitimate under Art. 63 as it was a superfluous name for [var.] *jubata*, and (b) a name to be rejected under Art. 70 as based on discordant elements. In fact, as Art. 63 applies, this epithet is automatically typified by the type of [var.] *jubata* under the provisions of Art. 7. Thus the name "*A. proluxa*" is an obligate synonym of *A. jubata*, a name which itself is best rejected (see this name). As is the case with *A. jubata*, this name has been applied to diverse dark-coloured species of the genus by North American authors.

Alectoria sarmentosa var. *dichotoma* (Hoffm.) Gyeln.

Ann. Mus. Nat. Hung., Bot. 28: 283 (1934). – *Usnea dichotoma* Hoffm., Deutsch. Fl. 2: 134 (1796); type: Sine loc., Herb. Hoffmann no 8573 (MW neotype!).

This taxon was reported from North America by Gyelnik (1934) but, as pointed out by Hawksworth (1970 p. 240, 1972 p. 239), Hoffmann's only extant collection of this proves to be *Ramalina thrausta* (Ach.) Nyl. In the absence of further evidence, this epithet is thus most appropriately treated as a synonym of *R. thrausta*. This does not affect the nomenclature

of *R. thransta* as there is already a *R. dichotoma* Hepp ex Zoll. validly published in 1854 (fide Zahlbruckner 1930 p. 524). We have not seen the material referred to this taxon by Gyelnik, so the sense in which he used the name remains uncertain.

***Bryoria setacea* (Ach.) Brodo & D. Hawksw., comb. nov.**

Alectoria jubata ♂. *setacea* Ach., Lich. Univ.: 594 (1810); type: sine loc. (H-Ach., upper left-hand specimen, lectotype!); basionym. – *Alectoria setacea* (Ach.) Mot., Fragm. Florist. Geobot. 3: 216 (1958).

This species was recorded for North America by both Ahti (1964) and Krog (1968) on the basis of collections determined by Motyka which we have reexamined and consider to be conspecific with *Bryoria capillaris*. Motyka (1964), however, indicated that this species did not occur in North America and so appears to have reconsidered these determinations himself. As pointed out by Hawksworth (1973), *B. setacea* seems to represent a "vexillifera"-like morphotype of *B. capillaris* with robust main stems which are often markedly foveolate and exceed 1 mm in diameter, sparse branching, and a prostrate habit. The true *B. setacea* appears to be an exclusively European species most frequent in upland areas of Scandinavia, although it is occasionally encountered in the mountainous regions of central Europe.

Motyka has tended to use the name in a rather broad sense applying it also to large pendent specimens of *B. capillaris* in which the basal branches are unusually stout, tending to become somewhat foveolate. Such a difference appears to be mainly environmentally controlled and thus of no taxonomic importance. Collections from North America falling within this broadened concept of *B. setacea* have been found during the present studies, and the following may be cited as representative (all on trees and treated as belonging to *B. capillaris*): British Columbia, Victoria, 1908, Macoun (CANL 16194); Ontario, Geraldton District, 1958, Ahti 3927, 3932 (H); Quebec, Gaspé Peninsula, 1907, Macoun (CANL 16181). In addition we examined one specimen from an uncertain locality ("on rocks by the Rim"), collected by Merrill (FH) and containing alectorialic and barbatolic acids together with

atranorin (?) and some unknown compounds, but this is perhaps merely an abnormal specimen of *B. nadvornikiana*.

***Bryoria smithii* (DR.) Brodo & D. Hawksw., comb. nov.**

Alectoria smithii DR., Ark. Bot. 20A (11): 15 (1926); basionym.

Alectoria bicolor var. *berengeriana* Massal. ex Stiz., Ann. Naturh. Mus. Wien 7: 127 (1892).

For further synonyms and typifications see Hawksworth (1972 p. 246).

This species was reported for North America by Stizenberger (1892) on the basis of a collection made in Newfoundland (ZT!) which has been redetermined as *B. fuscescens* var. *positiva* (Jørgensen & Ryvarden 1970, Ahti & Hawksworth 1974). Keissler (1958 p. 151) also considered this species to occur in North America on the basis of material distributed by Merrill, Lich. Exs. no. 211 (sub *Alectoria chalybeiformis*), but, as pointed out by Jørgensen & Ryvarden (1970), material under this number proves to be *B. furcellata*.

The distribution of *B. smithii* is centered in Asia, but extends through the moister parts of Europe and onto the Pacific Islands. Although we have seen no North American material of this distinctive species, it is conceivable that it may occur at least near the east or west coasts.

B. smithii is perhaps most similar to *B. bicolor* from which it differs in the presence of minute soralia bearing tufts of isidioid spinules (not unlike those seen in *B. furcellata*), the complete absence of fumarprotocetraric acid (i.e., PD- throughout), and a decumbent rather than ± erect habit. For further information on this species see Jørgensen & Ryvarden (1970) and Hawksworth (1972).

***Bryopogon spadiceus* Choisy**

Icon. Lich. Univ., Ser. II, Fasc. 2, sine pagin. (1931).

This is a superfluous name for *Alectoria jubata* (L.) Ach., as that epithet was placed as a synonym of *B. spadiceus* by Choisy (1931). The latter is therefore typified by the type of *Lichen jubatus* L. (see under *Alectoria jubata*), and so is illegitimate and must be rejected (Art. 63).

The name *Bryopogon spadiceus* was applied by Choisy (1931) to two North American collections: one from Alberta, Cypress Hills, J. Macoun, 1880 (Macoun, Lich. Exs. no. 19 [herb. Choisy, herb. Gandoger]) and one from the Bering Sea, St. Paul Island, J. (M.?) Macoun, June–July 1897 [herb. Gandoger]. As Macoun's exsiccata no. 19 consists of material from several localities and the St. Paul Island material has not been located, the identity of these specimens remains uncertain.

***Bryoria subdivergens* (Dahl) Brodo & D. Hawksw., comb. nov.**

Alectoria subdivergens Dahl, Medd. Gronl. 150(2): 145 (1950); type: Greenland, Julianehaab District, Quagssimuit, E. Dahl, 4 July 1937 (O holotype! O isotype!); basionym. – *Bryopogon subdivergens* (Dahl) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C. 26: 271 (1971); nom. inval. (Art. 33).

Thallus subcaespitose to decumbent or trailing, to 25–30 mm long; branching anisotomic dichotomous, angles between the branches mainly obtuse; main branches longitudinally foveolate and pitted, angular in cross section, mainly even in diameter, to 0.8 mm diam. (1–2 mm diam. fide Dahl 1950); red-brown throughout, matt.

True lateral spinules, soralia and pseudocyphellae absent; branches sometimes appearing spinulose due to the occurrence of short, pointed, lateral branches.

Apothecia infrequent, lateral; excipulum thallinum concolourous with the thallus, becoming excluded as the ascocarps mature, eciliate; disc red-brown becoming markedly convex with age, 1.5–2.5 mm diam. Ascospores 8 per ascus, subglobose, thin-walled, hyaline, 6–8 µm diam. Pycnidia not seen.

Cortical hyphae as in *B. oregana*.

Cortex and medulla K–, C–, KC–, PD–; contains no lichen substances.

Ecology. In its type locality *B. subdivergens* occurred growing amongst mosses and lichens in a tundra lichen-heath.

Distribution. This species was reported from four additional sites in Greenland and one in Labrador by Dahl (1950). Dahl considered the species as easily mistaken for *Cornicularia divergens* but this appears to have been due to his referring material of the latter to *B. sub-*

divergens. All Greenland material apart from that from the type locality proves to be *C. divergens*. The report from Labrador was based on material collected by Tanner at Hebron but this collection has not been located in H, O, S or UPS. *B. subdivergens* was also recorded for North America by Thomson (1960) on the basis of a collection from Baffin Island (Pangnirtung Fjord, Soper 74 [CANL]) which has been redetermined as *Cornicularia divergens*. Motyka (1964) stated that he had seen a collection of this species from Cornwallis Island (Resolute Bay, Collins [K]), but this specimen has not been located amongst the lichen collections transferred to BM from K. We have seen some unusually dark specimens of *Alectoria nigricans* collected by Collins at Resolute Bay (in herb. US), and these may be duplicates of the specimen seen by Motyka at Kew.

This species is thus only known with certainty from the type locality but should be searched for elsewhere in Greenland and in arctic North America.

Discussion

Bryoria subdivergens is extremely similar to *B. abbreviata*, a corticolous western species, and were it not for their very disjunct localities and different habitats we would have been inclined to treat them as conspecific. The type material of *B. subdivergens*, upon which the above description is based, is rather sparse and additional collections of this species are urgently required. The similarity of the cortices in these two species, *B. oregana*, and probably also *B. divergens* is discussed in the general section Anatomy and morphology.

***Alectoria thrausta* Ach.**

Lich. Univ.: 596 (1810); type: Helvetia (H-Ach, lectotype!).

This species, which is often confused with *A. sarmentosa*, has been treated as belonging to the genus *Ramalina* (*R. thrausta* (Ach.) Nyl.) by most recent authors. Its retention in *Ramalina* is justified, in the absence of apothecia, by (a) the occurrence of apical soralia, (b) the presence of only (+)-usnic acid, (c) the presence of occasional net-like tips (as in young *R. menziesii*), and (d) the presence of a partially prosoplec-

tenchymatous cortex (see general section on Anatomy and morphology). Interestingly, the very similar *Ramalina chondrina* Steiner, a species described from the Canary Islands, produces apothecia with the 1-septate hyaline ascospores characteristic of that genus.

The most useful characters for the separation of *R. thrausta* from *Alectoria sarmentosa* are its generally more delicate habit, the infrequency of convex pseudocyphellae, its tendency to assume a characteristic orange-yellow colour in the herbarium, the presence of minute apical soralia on short and often hook-like branchlets, and the consistently C-, KC-, PD- medulla (but note that some chemotypes of *A. sarmentosa* have these reactions).

Motyka (1960, 1962, 1964) adopted the name *R. crinalis* (Ach.) Gyeln. (syn. *A. crinalis* Ach.) for this species but, as pointed out by Ahti (1964), this is nomenclaturally incorrect; the name *R. thrausta* is the one which must be used for this taxon.

Alectoria trichodes Bach. Pyl.

Mém. Soc. Linn. Paris 4: 432, 505 (1826).

This name was applied by Bachelot de la Pylaie (1826) to some pendent *Bryoria* he saw in Newfoundland. No description was provided and there was no indication that he intended to introduce a new combination based on Michaux's name (see Discussion under *Bryoria trichodes* subsp. *trichodes*), so this name was not validly published by him (Arts. 32-34). In a resumé of Bachelot de la Pylaie's paper, Arnold (1826 p. 128) also referred to this name but failed to validate it either as a new species or a new combination. The nomenclatural situation here is comparable to that of Du Rietz's use of the name "*Haematomma ochroleucum*" discussed by Laundon (1970).

Some of Bachelot de la Pylaie's material is now preserved in FH and there is one specimen from "E. Newfoundland" under the name "*Setaria trichodes* Michx." mounted on a sheet including a collection made by Despréaux, probably in 1828, which might have been collected

by Bachelot de la Pylaie; this belongs to *Bryoria trichodes* subsp. *americana* (see Ahti & Hawksworth 1974).

Alectoria tristis (Web.) Th. Fr.

Lich. Scand. 1: 28 (1871). – *Lichen tristis* Web., Spicil. Fl. Goett.: 209 (1778).

This name has been treated as a synonym of *Cornicularia normoerica* (Gunn) DR. by most authors since Du Rietz (1926). This species is clearly not an *Alectoria* on the basis of its anatomical structure. It does occupy a very isolated position within the genus *Cornicularia* (Schreb.) Ach. which, in any case, seems to be a heterogeneous group.

Alectoria usneoides (Ach.) Ach.

Lich. Univ.: 594 (1810). – *Parmelia usneoides* Ach., Meth. Lich.: 270 (1803).

Parmelia usneoides is a superfluous name introduced by Acharius for *Lichen usnea* L., the basionym of *Ramalina usnea* (L.) R. Howe, which is a true species of *Ramalina* with uniseptate ascospores. The typification of *L. usnea* is discussed by Imshaug (1972).

Sulcaria virens (Tayl.) Bystr. ex Brodo & D. Hawksw., comb. nov.

Alectoria virens Tayl., Hook. Lond. J. Bot. 6: 188 (1847); type: India, Sheopore, Wallich, January 1821 (FH holotype! BM isotype!); basionym. – *Sulcaria virens* (Tayl.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 276 (1971); nom. inval. (Art. 33).

This name was incorrectly taken up by Howe (1911) for *A. tortuosa* Merr. (= *Bryoria*), and he has been followed by several later North American authors. *Sulcaria virens*, however, is a very distinctive species which is restricted to the Himalayan region (including parts of India, Nepal and China) and Taiwan. *Bryoria tortuosa* and *Sulcaria virens* are perhaps most easily separated on the basis of the single longitudinal furrow which characterizes all branches of the latter, but they also differ in several other respects (see Hawksworth 1971).

New combinations for non-North American and some infraspecific taxa

Bryoria asiatica (DR.) Brodo & D. Hawksw., comb. nov. – *Alectoria asiatica* DR., Ark. Bot. 20A (11): 18 (1926); type: China, Prov. Sze-ch'uan, reg. bor.-occid., mellan Tsagogamba och Tamba, alt. 4000 m.s.m., på *Juniperus*, *Picea* eller *Rhododendron*, H. Smith 5018, 2 October 1922 (UPS holotype!); basionym.

Bryoria chalybeiformis f. *prostratosteola* (Gyeln.) D. Hawksw., comb. nov. – *Alectoria prostratosteola* Gyeln., Nyt Mag. Naturvid. 70: 58 (1932); type: U.S.S.R., Kasachskaja S.S.R., Altanigeb rupe, Koton, Karagny, P. Kwaszmikowa, 1926 (BP 48575 lectotype!); basionym. – For further synonyms see Hawksworth (1972 p. 215).

Bryoria confusa (Awasthi) Brodo & D. Hawksw., comb. nov. – *Alectoria confusa* Awasthi, Proc. Indian Acad. Sci., B. 72: 152 (1970); type: E. Nepal, Mewakhola valley, alt. c. 11,500 ft, D. D. Awasthi 2278, 28 May 1953 (herb. Awasthi, holotype; not seen); basionym.

Bryoria cornicularioides (P. Jorg.) Brodo & D. Hawksw., comb. nov. – *Alectoria cornicularioides* P. Jorg., Bryologist 78: 77 (1975); type: China, Prov. Shensi Kuan-tou-san, among mosses, G. Giraldi, 1896 (FI holotype!).

Bryoria dahlia (P. Jorg.) Brodo & D. Hawksw., comb. nov. – *Alectoria dahlia* P. Jorg., Svensk Bot. Tidskr. 66: 192 (1972); type: New Guinea, Chimbu District, Mt. Wilhelm, Pinaunde Valley, E. Dahl, 1970 (BM isotype!).

Bryoria divergens (Nyl.) Brodo & D. Hawksw., comb. nov. – *Alectoria divergens* Nyl., Flora, Jena 69: 466 (1886); type: China, Prov. Yunnan, in monte Tsang-chan, supra Ta-li, supra ramulos, alt. 4,000 m, R. P. Delavay, 1885 (H-Nyl. 35972 holotype!); basionym. – For further synonyms see Hawksworth (1970 p. 237).

Bryoria fuscescens f. *pallida* (Savicz) D. Hawksw., comb. nov. – *Bryopogon chalybeiform* f. *pallidum* Savicz, Not. Syst. Inst. Crypt. Horti Petrop. 1: 64 (1922); type: Poland, Prov. Suwalki, distr. Augustov, V. P. Savicz, 9 May 1914 (I.E holotype!); basionym. – For further synonyms see Hawksworth (1972 p. 218).

Bryoria fuscescens var. *positiva* (Gyeln.) Brodo & D. Hawksw., comb. nov. – *Bryopogon positivus* Gyeln., Acta Geobot. Hung. 2: 164 (1937); type:

U.S.S.R., Siberia, Altaigebirge, Dorf Tscherga, N. Lawrow, 18 June 1927 (BP 33,974 holotype!); basionym. – For further synonyms see Hawksworth (1972 p. 219).

Bryoria himalayensis (Mot.) Brodo & D. Hawksw., comb. nov. – *Alectoria himalayensis* Mot., Fragm. Florist. Geobot. 6: 450 (1960); type: Himalaya, Sikkim, T. Thomson 299 (BM isotype!); basionym.

Bryoria indonesica (P. Jorg.) Brodo & D. Hawksw., comb. nov. – *Alectoria indonesica* P. Jorg., Svensk Bot. Tidskr. 66: 194 (1972); type: Indonesia, Celebes, south-west slope of Mt. Rautemario, on large *Quercus*, alt. 3,100 m, A. C. Jermy 7448, 1969 (BM holotype!); basionym.

Bryoria kuemmerleana (Gyeln.) Brodo & D. Hawksw., comb. nov. – *Alectoria kuemmerleana* Gyeln., Nyt Mag. Naturvid. 70: 49 (1932); type: Hungary, Comit. Szepes, Fenyveserdő alomján a "Stösschen" lejtőjén a M. Tátrában, c. 1380 m, Timkő Györgye, 17 July 1917 (BP 33,952 holotype!); basionym.

Bryoria lactinea (Nyl.) Brodo & D. Hawksw., comb. nov. – *Alectoria lactinea* Nyl., Lich. Jap.: 23 (1890); type: Japonia, Itjigome, E. Almqvist, 1879 (H-Nyl. 35882 holotype!); basionym.

Bryoria motykae (D. Hawksw.) Brodo & D. Hawksw., comb. nov. – *Alectoria motykae* D. Hawksw., Bot. Notiser 124: 124 (1971); type: Kenya, Mt. Kenya, Teleki Valley, on vertical surface of boulders, alt. 4,200 m, O. Hedberg 1720b, 28 July 1948 (UPS holotype!); basionym.

Bryoria osteola (Gyeln.) Brodo & D. Hawksw., comb. nov. – *Alectoria osteola* Gyeln., Nyt Mag. Naturvid. 70: 49 (1932); type: Hungary, Comit. Gömör, in monte Kiralyhegy, Filarszky & Kümmerle, 3 July 1906 (BP 33,955 holotype!); basionym.

Bryoria perspinosa (Bystr.) Brodo & D. Hawksw., comb. nov. – *Alectoria perspinosa* Bystr., Khumbu Himal. 6: 21 (1969); type: E. Nepal, Vorhimalaya, *Abies-Rhododendron*-Bergwald, östlich Junbesi, J. Poelt L778, 9 October 1962 (M isotype!); basionym.

Bryoria poeltii (Bystr.) Brodo & D. Hawksw., comb. nov. – *Alectoria poeltii* Bystr., Khumbu Himal. 6: 20 (1969); type: E. Nepal, Himalaya, Mahalangur Himal, Khumbu, bei Bibre, J. Poelt L805, September 1962 (M isotype!); basionym.

Bryoria ruwenzoriensis (D. Hawksw.) Brodo & D. Hawksw., comb. nov. – *Alectoria ruwenzoriensis* D. Hawksw., Bot. Notiser 124: 124 (1971); type: Uganda, Ruwenzori, Mijusi Valley, alt. 3,900 m, O. Hedberg 521f, 27 March 1948 (UPS holotype!); basionym.

Bryoria variabilis (Bystr.) Brodo & D. Hawksw., comb. nov. – *Alectoria variabilis* Bystr., Khumbu Himal. 6: 22 (1969); type: E. Nepal, Himalaya, Khumbu, *Abies-Rhododendron*-Wald, J. Poelt L798, 9 October 1962 (M isotype!); basionym.

Pseudephebe pubescens f. *subciliata* (Nyl.) D. Hawksw., comb. nov. – *Parmelia lanata* var. *subciliata* Nyl., Flora, Jena 51: 346 (1868); type: Scotland, ad rupes calcareosus monti Morrone in regione Braemar, J. M. Crombie, 1867 (H-Nyl. 34350 holotype!; BM isotype!); basionym. – For further synonyms see Hawksworth (1972 p. 236).

Sulcaria sulcata (Lév.) Bystr. ex Brodo & D. Hawksw., comb. nov. – *Cornicularia sulcata* Lév., in Jacquin, Fr.-Voy. Inde, Descr. Coll. 4: 179 (1844); type: loc. cit. 2: pl. 180 fig. 3(2) lectotype!; basionym. – *Sulcaria sulcata* (Lév.) Bystr., Ann. Univ. Mariae Curie-Skłodowska, C, 26: 276 (1971); nom. inval. (Art. 33).

Sulcaria sulcata f. *vulpinoides* (Zahlbr.) D. Hawksw., comb. nov. – *Alectoria sulcata* var. *vulpinoides* Zahlbr., in Handel-Mazzetti, Symb. Bot. Sin. 3: 202 (1930); type: China, Prov. Yunnan, prope urbem Lidjiang [Likiang], imprimis in monte Yülung-schan, "von Einheimischen" 3606, 1914–18 (W holotype!); basionym.

Sulcaria sulcata var. *barbata* (D. Hawksw.) D. Hawksw., comb. nov. – *Alectoria sulcata* var. *barbata* D. Hawksw., Taxon 19: 242 (1970); type: Formosa, Mt. Shi-San, Mt. Shin-Kao-San, alt. 3,300–3,600 m, S. Kurokawa 337, 1 January 1964 (TNS holotype!); basionym.

Sulcaria virens f. *decolorans* (Asah.) D. Hawksw., comb. nov. – *Alectoria virens* var. *decolorans* Asah., in Hara, Fl. E. Himal.: 604 (1966); type: India, Sikkim, Darjeeling, Phalut, M. Togashi, 9 May 1960 (TNS holotype!); basionym.

Sulcaria virens var. *forrestii* (D. Hawksw.) D. Hawksw., comb. nov. – *Alectoria virens* var. *forrestii* D. Hawksw., Misc. Bryol. Lichen., Nichinan 5: 1 (1969); type: China, Prov. Yunnan, Jhi Shan east of Tali Lake, 25°48' N, alt. 10,000 ft, on rocks in dry open situations, G. Forrest 13471, August 1914 (E holotype!); basionym.

References

- Acharius, E. 1798: *Lichenographiae Svecicae Prodromus*. Linköping.
- 1810: *Lichenographia Universalis*. Göttingen.
- 1814: *Synopsis Methodica Lichenum*. Lund.
- Ahlner, S. 1948: Utbredningstyper bland nordiska barrträds-lavar. *Acta Phytogeogr. Suec.* 22: 1–257.
- Ahti, T. 1959: Studies on the caribou lichen stands on Newfoundland. *Ann. Bot. Soc. Vanamo* 30(4): 1–44.
- 1964: Macrolichens and their zonal distribution in boreal and arctic Ontario, Canada. *Ann. Bot. Fenn.* 1: 1–35.
- 1966: *Parmelia olivacea* and the allied non-isidiate and non-sorediate corticolous lichens in the Northern Hemisphere. *Acta Bot. Fenn.* 70: 1–68.
- 1973: Taxonomic notes on some species of *Cladonia* subsect. *Unciales*. *Ann. Bot. Fenn.* 10: 163–184.
- Ahti, T. & Hawksworth, D. L. 1974: Notes on the lichens of Newfoundland. 4. *Alectoria*. *Ann. Bot. Fenn.* 11: 189–196.
- Ahti, T. & Hepburn, R. L. 1967: Preliminary studies on woodland caribou range, especially on lichen stands in Ontario. *Ont. Dep't Lands Forest Research Report (Wildlife) No. 74*: 1–134.
- Andrews, J. T. & Webber, P. J. 1964: A lichenometrical study of the north-western margin of the Barnes ice cap: a geomorphological technique. *Geogr. Bull.* 22: 80–104.
- 1969: Lichenometry to evaluate changes in glacial mass budgets: as illustrated from north-central Baffin Island, N.W.T. *Arctic Alp. Res.* 1: 188–194.
- Arnold, F. G. C. 1896: Lichenologische Fragmente. 35. Neufundland. *Österr. Bot. Z.* 46: 128–131, 176–182, 213–220, 245–251, 286–292, 326–332, 359–363.
- Asahina, Y. 1936: Mikrochemischer Nachweis der Flechtenstoffe II. *J. Jap. Bot.* 12: 25–38.
- Atlas of Canada 1958: Geographic Branch, Ministry of Mines and Tech. Services. Ottawa.
- Awasthi, D. D. 1970: On *Alectoria acanthodes* Hue, *Alectoria confusa* sp. nov. and systematic position of *Alectoria*. *Proc. Indian Acad. Sci., B*, 72: 149–155.
- Bachelot de la Pylaie, A. J. M. 1826: Notice sur l'île de Terre Neuve et quelques îles voisines. *Mém. Soc. Linn. Paris* 4: 417–547.
- Banfield, A. W. F. 1974: *The mammals of Canada*. Toronto.
- Barkman, J. J. 1958: *Phytosociology and ecology of cryptogamic epiphytes*. Assen.
- Bergerud, A. T. 1972: Food habits of Newfoundland caribou. *J. Wildl. Manag.* 36: 913–923.
- Bergerud, A. T. & Russell, L. 1964: Evaluation of rumen food analysis for Newfoundland caribou. *J. Wildl. Manag.* 28: 809–814.
- Beschel, R. E. 1963: Geobotanical studies on Axel Heiberg Island in 1962. In E. Müller (ed.), *Axel Heiberg Island Preliminary Report*, pp. 1–18. Montreal. (Original volume not seen.)
- Briquet, J. 1935: *International rules of botanical nomenclature adopted by the International Botanical Congresses of Vienna, 1905, and Brussels, 1910, revised by the International Botanical Congress of Cambridge, 1930*. Jena.
- Brodo, I. M. 1968: The lichens of Long Island, New York: A vegetational and floristic analysis. *N. Y. State Museum & Science Service Bull.* 410: 1–330.
- 1973: The lichen genus *Coccotrema* in North America. *Bryologist* 76: 260–270.
- Bystrek, J. 1963: De variabilitate *Alectoriae fuscicentis* Gyel. *Ann. Univ. Mariae Curie-Skłodowska C*, 18: 411–418.
- 1969: Die Gattung *Alectoria*. *Khumbu Himal.* 6: 17–24.
- 1971: Taxonomic studies on the genus *Alectoria*. *Ann. Univ. Mariae Curie-Skłodowska C*, 26: 265–279.
- 1974: *Alectoria stigmata*, lichenum nova species in Alaska inventa. *Frag. Flor. Geobot.* 20: 255–256.
- Calder, J. A. & Taylor, R. L. 1968: *Flora of the Queen Charlotte Islands. Part I*. [Research Branch, Canada, Dept. of Agr. Monogr. 4(1): 1–659.] Ottawa.
- Choisy, M. 1931: *Icones lichenum universalis, Ser. II, Fasc. 2*. Oullins.
- Clements, F. E. & Shear, C. L. 1931: *The genera of fungi*. New York.
- Crangan, A. T. 1957: History, food habits and range requirements of the woodland caribou of continental North America. *Trans. N. Amer. Wildl. Conf.* 22: 485–501.
- Crum, H. 1966: Evolutionary and phytogeographic patterns in the Canadian moss flora. In R. L. Taylor & R. A. Ludwig (ed.), *The evolution of Canada's flora*, pp. 28–42. Toronto.
- Culberson, C. F. 1969: *Chemical and botanical guide to lichen products*. Chapel Hill.
- 1970: Supplement to "Chemical and botanical guide to lichen products". *Bryologist* 73: 177–377.
- 1972: Improved conditions and new data for the

- identification of lichen products by a standardized thin-layer chromatography method. *J. Chromatogr.* 72: 113–125.
- 1974: Conditions for the use of Merck silica gel 60F₂₅₄ plates in the standardized thin-layer chromatographic technique for lichen products. *J. Chromatogr.* 97: 107–108.
 - Culberson, C. F. & Hale, M. E., Jr. 1973: Chemical and morphological evolution in *Parmelia* sect. *Hypotrachyna*: Product of ancient hybridization? *Brittonia* 25: 162–173.
 - Culberson, C. F. & Kristinsson, H. 1970: A standardized method for the identification of lichen products. *J. Chromatogr.* 46: 85–93.
 - Culberson, W. L. 1958: Variation in the pine-inhabiting vegetation of North Carolina. *Ecology* 39: 23–28.
 - 1969: The use of chemistry in the systematics of the lichens. *Taxon* 18: 152–166.
 - 1969 a: Norstictic acid as a hymenial constituent of *Letharia*. *Mycologia* 61: 731–736.
 - 1972: Disjunctive distributions in the lichen-forming fungi. *Ann. Missouri Bot. Gard.* 59: 165–173.
 - Culberson, W. L. & Culberson, C. F. 1968: The lichen genera *Cetrelia* and *Platismatia* (Parmeliaceae). *Contr. U.S. Nat. Herbarium* 37(7): 449–558.
 - 1970: A phylogenetic view of chemical evolution in the lichens. *Bryologist* 73: 1–31.
 - 1973: Parallel evolution in lichen-forming fungi. *Science* 180: 196–198.
 - Dahl, E. 1950: Studies in the macrolichen flora of South West Greenland. *Meddel. Grøn.* 150(2): 1–176.
 - Dahl, E. & Krog, H. 1973: *Macrolichens of Denmark, Finland, Norway and Sweden*. Oslo, Bergen and Tromsø.
 - Dahl, E., Lyngø, B. & Scholander, P. F. 1937: Lichens from southeast Greenland. *Skr. om Svalbard og Ishavet* 70: 1–76.
 - Darbishire, O. V. 1909: Lichens collected during the 2nd Norwegian Polar Expedition in 1898–1902. *Rept. 2nd Norw. Arct. Exped.* 21: 1–68.
 - Daubenmire, R. 1969: Ecologic plant geography of the Pacific Northwest. *Madroño* 20: 111–128.
 - Degelius, G. 1934: Flechten aus Nordfjord und Sunnfjord (Norwegen). *Bergens Mus. Årbok* 1934(3): 1–31.
 - 1935: Das ozeanische Element der Strauch- und Laubflechtenflora von Skandinavien. *Acta Phytogeogr. Suec.* 7: 1–411.
 - 1937: Lichens from southern Alaska and the Aleutian Islands, collected by Dr. E. Hultén. *Acta Horti Gothob.* 12: 105–144.
 - 1941: Contributions to the lichen flora of North America. 2. The lichen flora of the Great Smoky Mountains. *Ark. Bot.* 30A (3): 1–80.
 - DesMeules, P. & Heyland, J. 1969: Contribution to the study of the food habits of caribou. Part 1. Lichen preferences. *Naturaliste Can.* 96: 317–331.
 - Dey, J. P. 1974: *Parmelia commensurata*, a lichen new to North America. *Bryologist* 77: 250–252.
 - Dodge, C. W. 1973: *Lichen flora of the Antarctic continent and adjacent islands*. Canaan (New Hampshire).
 - Dodge, C. W. & Vareschi, V. 1956: Resultados liquenológicos de excursiones efectuadas en Venezuela No. 1. *Acta Biol. Venez.* 2(1): 1–12.
 - Dove, M. 1933: *Coyote stories*. Caldwell, Idaho.
 - Du Rietz, G. E. 1926: Vorarbeiten zu einer "Synopsis lichenum". 1. Die Gattungen *Alectoria*, *Oropogon* und *Cornicularia*. *Ark. Bot.* 20A (11): 1–43.
 - Eaton, A. 1824: *A manual of botany, for the northern and middle states of America*. Fourth edition. Albany.
 - 1829: *A manual of botany, for the northern and middle states of America*. Fifth edition. Albany.
 - Edwards, R. Y., Soos, J. & Ritcey, R. W. 1960: Quantitative observations on epidendric lichens used as food by caribou. *Ecology* 41: 425–431.
 - Frey, E. 1936: Vorarbeiten zu einer Monographie der Umbilicariaceen. *Ber. Schweiz. Bot. Gesell.* 44: 198–230.
 - 1952: Die Flechtenflora und -Vegetation des Nationalparks im Unterengadin. I. Die diskokarpen Blatt- und Strauchflechten. *Ergebn. Wiss. Untersuch. Schweiz. Nationalparks* 3: 361–503.
 - Fries, Th. M. 1860: Lichenes Arctoi Europae Groenlandiaeque hactenus cogniti. *Nova Acta Soc. Regiae Sci. Upsal., ser. 3*, 3: 103–398. [Reprint issued 1860; journal issued 1861.]
 - 1871: *Lichenographia Scandinavica* 1. Uppsala.
 - Galløe, O. 1947: *Natural history of the Danish lichens* 7. Copenhagen.
 - 1950: *Natural history of the Danish lichens* 8. Copenhagen.
 - 1954: *Natural history of the Danish lichens* 9. Copenhagen.
 - Gyelnik, V. 1931: Additamenta ad cognitionem lichenum extraeuropaeorum. *Ann. Crypt. Exot.* 4: 166–174.
 - 1932: *Alectoria* Studien. *Nyt Mag. Naturvid.* 70: 35–62.
 - 1934: Lichenes Sipeani ex Oregon. *Ann. Mus. Nat. Hung.* 28: 278–284.
 - 1935: Conspectus Bryopogonum. *Feddes Repert.* 38: 219–255.
 - Hale, M. E., Jr. 1955: Studies on the chemistry and distribution of North American lichens. *Bryologist* 58: 242–246.
 - 1969: *How to know the lichens*. Dubuque, Iowa.
 - 1973: Fine structure of the cortex in the lichen family Parmeliaceae viewed with the scanning electron microscope. *Smithsonian Contr. Bot.* 10: i–iii, 1–92.
 - 1974: *Bulbothrix*, *Parmelina*, *Relicina*, and *Xanthoparmelia*, four new genera in the Parmeliaceae (Lichens). *Phytologia* 28: 479–490.
 - 1976: The structure of lichens viewed with the scanning electron microscope. In D. H. Brown, D. L. Hawksworth & R. H. Bailey (eds.), *Lichenology: progress and problems*, pp. 1–15. London, New York and San Francisco.
 - Hale, M. E., Jr. & Culberson, W. L. 1970: A fourth checklist of the lichens of the continental United States and Canada. *Bryologist* 73: 499–543.
 - Halsey, A. 1823: Synoptical view of the lichens growing in the vicinity of the City of New York. *Ann. Lyceum Nat. Hist. N. Y.* 1: 1–21.
 - Hawksworth, D. L. 1969: Chemical and nomenclature

- tural notes on Alectoria (Lichenes) I. *Taxon* 18: 393-399.
- 1969 a: The scanning electron microscope. An aid to the study of cortical hyphal orientation in the lichen genera Alectoria and Cornicularia. *J. Microscopie* 8: 753-760.
 - 1970: Chemical and nomenclatural notes on Alectoria (Lichenes) II. *Taxon* 19: 237-243.
 - 1971: Chemical and nomenclatural notes on Alectoria (Lichenes) III. The chemistry, morphology and distribution of Alectoria virens Tayl. *J. Jap. Bot.* 46: 335-342.
 - 1971 a: Regional studies in Alectoria (Lichenes) I. The central and southern African species. *Bot. Notiser* 124: 122-128.
 - 1972: Regional studies in Alectoria (Lichenes) II. The British species. *Lichenologist* 5: 181-261.
 - 1973: Ecological factors and species delimitation in the lichens. In V. H. Heywood (ed.), *Taxonomy and ecology*, pp. 31-69. London and New York.
 - 1974: *Mycologist's handbook*. Kew.
 - 1976: Lichen chemotaxonomy. In D. H. Brown, D. L. Hawksworth & R. H. Bailey (eds.), *Lichenology: progress and problems*, pp. 139-184. London, New York and San Francisco.
- Hawksworth, D. L. & Coppins, B. J. 1976: Alectoria nidulifera Norrl. discovered in Scotland. *Lichenologist* 8: 95-96.
- Hawksworth, D. L. & Moore, D. M. 1969: Some lichens from Tierra del Fuego with notes on their chemical constituents. *Bryologist* 72: 247-251.
- Hawksworth, D. L. & Rose, F. 1976: *Lichens as pollution monitors*. London.
- Henssen, A. 1963: Eine Revision der Flechtenfamilien Lichinaceae und Ephebeaceae. *Symb. Bot. Upsal.* 18(1).
- Henssen, A. & Jahns, H. M. 1973 (1974): *Lichenes. Eine Einführung in die Flechtenkunde*. Stuttgart.
- Hillmann, J. 1936: Parmeliaceae. *Rabenh. Krypt.-Fl.* 9, 5(3): 1-309, 1-10.
- Holmgren, P. K. & Keuken, W. 1974: Index herbariorum. The herbaria of the world. Ed. 6. *Regnum Veg.* 92: 1-397.
- Howe, R. H. 1911: American species of Alectoria occurring north of the fifteenth parallel. *Mycologia* 3: 106-150.
- Hulting, J. 1896: Beiträge zur Flechtenflora Nordamerikas. *Hedwigia* 35: 186-193.
- Huneck, S. & Follmann, G. 1970: Mitteilungen über Flechteninhaltsstoffe. LXXXI. Zur Phytochemie und Chemotaxonomie der Usneaceengattung Alectoria. *Österr. Bot. Z.* 118: 486-498.
- Imshaug, H. A. 1956: Catalogue of Mexican lichens. *Rev. Bryol. Lichénol.* 25: 321-385.
- 1957: Alpine lichens of western United States and adjacent Canada. I. The macrolichens. *Bryologist* 60: 177-272.
 - 1972: Typification of Ramalina usnea (L.) R. H. Howe. *Lichenologist* 5: 317-318.
- Imshaug, H. A. & Brodo, I. M. 1966: Biosystematic studies on Lecanora pallida and some related lichens in the Americas. *Nova Hedwigia* 12: 1-59.
- Jahns, H. M. 1974 (1973): Anatomy, morphology, and development. In V. Ahmadjian & M. E. Hale (eds.), *The lichens*, pp. 3-58. New York.
- James, P. W. 1965: A new check-list of British lichens. *Lichenologist* 3: 95-153.
- 1973: The effect of air pollutants other than hydrogen fluoride and sulphur dioxide on lichens. In B. W. Ferry, M. S. Baddely & D. L. Hawksworth (eds.), *Air pollution and lichens*, pp. 143-175. Toronto, London.
- James, P. W. & Henssen, A. 1976: The morphological and taxonomic significance of cephalodia. In D. H. Brown, D. L. Hawksworth & R. H. Bailey (eds.), *Lichenology: progress and problems*, pp. 27-76. London, New York, and San Francisco.
- Jobin, L. 1973: L'arpenreuse de la pruche. *Environnement Canada, Centre de Recherches Forestières des Laurentides, Feuillet d'Information CRFL* 4: 1-6.
- Jørgensen, P. M. 1972: Further studies in Alectoria sect. Divaricatae DR. *Svensk Bot. Tidskr.* 66: 191-201.
- 1975: Further notes on Asian Alectoria. *Bryologist* 78: 77-80.
- Jørgensen, P. M. & Ryvarden, L. 1970: Contribution to the lichen flora of Norway. *Årbok Univ. Bergen, Mat.-Naturv. Ser. 10* (1969): 1-24.
- Karev, T. I. 1956: *Korma i pastbislichia severnogo olenya. (Forage and pastures of the reindeer.)* Gosud. Izdat. Sel'skhoz. Liter., Moskva and Leningrad. 100 pp. (Not seen: cited from Ahti & Hepburn 1967).
- Keissler, K. von 1958-60: Usneaceae. *Rabenh. Krypt.-Fl.* 9, 5(4): i-xiii, 1-755.
- Kershaw, K. A. 1975: Studies on lichen-dominated systems. XII. The ecological significance of thallus color. *Can. J. Bot.* 53: 660-667.
- Kershaw, K. A. & Larson, D. W. 1974: Studies on lichen-dominated systems. IX. Topographic influences on microclimate and species distribution. *Can. J. Bot.* 52: 1935-1945.
- Körber, G. W. 1855: *Systema Lichenum Germaniae*. Breslau.
- Krajina, V. J. 1965: Biogeoclimatic zones and biogeocoenoses of British Columbia. In V. Krajina (ed.), *Ecology of western North America* 1, pp. 1-17. Vancouver.
- Kristinsson, H. 1969: Chemical and morphological variation in the Cetraria islandica complex in Iceland. *Bryologist* 72: 344-357.
- Krog, H. 1968: The macrolichens of Alaska. *Norsk Polarinst. Skr.* 144: 1-180.
- 1971: En lavekursjon til Rogaland. *Blyttia* 29: 161-168.
- Krog, H. & Swinscow, T. D. V. 1974: Ramalina species with a hollow thallus (Fistularia) in East Africa. *Norw. J. Bot.* 21: 111-124.
- - 1975: Parmeliaceae, with the exclusion of Parmelia and Usnea, in East Africa. *Norw. J. Bot.* 22: 115-123.
- Krusenstjerna, E. von & Santesson, R. 1950: *Bryological, lichenological and mycological excursion to Jämtland*. (VII Internat. Bot. Congr. Excursion Guide 104.) Stockholm.
- Küchler, A. W. 1964: Potential natural vegetation of the conterminous United States. *Amer. Geogr. Soc. Special Publ.* 36: 1-116.
- Kurokawa, S. 1959: Notulae miscellaneae lichenum japonicorum (6). *J. Jap. Bot.* 34: 23-24.

- 1967: On the occurrence of diffractaic, physodalic, and psoromic acids in Parmeliae. *Bull. Nat. Sci. Mus. (Tokyo)* 10: 369-376.
- Lamb, I. M. 1948: New, rare or interesting lichens from the Southern Hemisphere. *Lilloa* 14: 203-251.
- 1964: Antarctic lichens I. The genera *Usnea*, *Ramalina*, *Himantormia*, *Alectoria*, *Cornicularia*. *Brit. Antarctic Survey Sci. Rep.* 38: 1-34.
- Lanjouw, J. (ed.) 1966: International code of botanical nomenclature. *Regnum Veg.* 46.
- Larson, D. W. & Kershaw, K. A. 1975: Studies on lichen-dominated systems. XI. Lichen-heath and winter snow cover. *Can. J. Bot.* 53: 621-626.
- Laundon, J. R. 1970: Lichens new to the British flora: 4. *Lichenologist* 4: 297-308.
- LeBlanc, F., Rao, D. N. & Comeau, G. 1972: The epiphytic vegetation of *Populus balsamifera* and its significance as an air pollution indicator in Sudbury, Ontario. *Can. J. Bot.* 50: 519-528.
- LeBlanc, F., Robitaille, G. & Rao, D. N. 1974: Biological response of lichens and bryophytes to environmental pollution in the Murdochville Copper Mine area, Québec. *J. Hattori Bot. Lab.* 38: 405-433.
- Letrouit-Galinou, M. A. 1974 (1973): Sexual reproduction. In V. Ahmadian & M. E. Hale (eds.), *The lichens*, pp. 59-90. New York and London.
- Llano, G. A. 1948: Economic uses of lichens. *Econ. Bot.* 2: 15-45.
- 1951: A contribution to the lichen flora of Alaska. *J. Wash. Acad. Sci.* 41: 196-200.
- Lynge, B. 1928: Lichens from Novaya Zemlya. *Rep. Scient. Results Norw. Exped. Nova Zemlya* 43.
- Lynge, B. & Scholander, P. F. 1932: Lichens from North East Greenland collected on the Norwegian Scientific Expeditions in 1929 and 1930. I. *Skr. om Svalbard og Ishavet* 41: 1-116, 7 pl., 1 map.
- Macoun, J. 1902: *Catalogue of Canadian plants, Part VII. Lichenes and Hepaticae*. Ottawa.
- Mägdefrau, K. 1957: Flechten und Moose im baltischen Bernstein. *Ber. Deutsch. Bot. Ges.* 70: 433-435.
- Magnusson, A. H. 1955: A catalogue of the Hawaiian lichens. *Ark. Bot., Ser. 2, 3*: 223-402.
- Marie-Victorin, Fr. 1964: *Flore Laurentienne*. Montreal.
- Michaux, A. 1803: *Flora Boreali-Americana* 1-2. Paris and Strasbourg.
- Miller, G. H. 1973: Variations in lichen growth from direct measurements: preliminary curves for *Alectoria minuscula* from eastern Baffin Island, N. W. T., Canada. *Arctic Alp. Res.* 5: 333-339.
- Moore, B. J. 1968: The macrolichen flora of Florida. *Bryologist* 71: 161-266.
- Morisset, P. 1971: Endemism in the vascular plants in the Gulf of St. Lawrence region. *Naturaliste Can.* 98: 167-177.
- Motyka, J. 1958: Odkrycie *Alectoria tortuosa* Merrill w Karpatach Wschodnich. - *Alectoria tortuosa* Merrill in Carpatibus Orientalibus inventa. *Fragm. Florist. Geobot.* 3: 201-203.
- 1958 a: Lichenum generis *Alectoria* Ach., subgenus *Bryopogon* (L.) Th. Fr. in Europa media (Descriptiones specierum). *Fragm. Florist. Geobot.* 3: 205-231.
- 1960: De speciebus generis *Alectoria* Ach. minus cognitis et novis. *Fragm. Florist. Geobot.* 6: 441-452.
- 1960 a: *Flora Polska, Porosty (Lichenes)*, 5(1). Warsaw.
- 1962: *Flora Polska, Porosty (Lichenes)*, 5(2). Warsaw.
- 1964: The North American species of *Alectoria*. *Bryologist* 67: 1-44.
- Müller Argoviensis, J. 1878: Lichenologische Beiträge VII. *Lichen, Jena* 61: 481-496.
- Nuno, M. 1971: A preliminary note on the *Alectoria asiatica*-group in Asia. *Misc. Bryol. Lichenol.* 5: 157-158.
- Nylander, W. 1885: Liste de quelques lichens recoltés à l'île Miquelon par le Compté de Saint-Phalle, Commandant des îles et parent due président. *Rev. Hort. Bouches-du-Rhône* 1885: 132-133.
- Oxner, A. M. 1956: *Flora Lishainikiv Ukraini (Lichen flora of the Ukraine)* I. Kiev.
- Ozenda, P. 1963: *Lichens. Handbuch der Pflanzen-anatomie* 6(9). Berlin-Nikolassee.
- Packer, J. G. 1971: Endemism in the flora of western Canada. *Naturaliste Can.* 98: 131-144.
- Persson, B. & Santesson, J. 1970: The structure of the depside alectorialic acid. *Acta Chem. Scand.* 24: 345-346.
- Poelt, J. 1965: Zur Systematik der Flechtenfamilie Physciaceae. *Nova Hedwigia* 9: 21-32.
- 1969: *Bestimmungsschlüssel europäischer Flechten*. Lehre.
- 1970: Das Konzept der Artenpaare bei den Flechten. *Vortr. Gesamtgeb. Bot., N. F.* 4: 187-198.
- 1972: Die taxonomische Behandlung von Artenpaaren bei den Flechten. *Bot. Notiser* 125: 77-81.
- Porsild, A. E. 1958: Geographical distribution of some elements in the flora of Canada. *Geogr. Bull.* 11: 57-77.
- Rabenhorst, L. 1845: *Deutschlands Kryptogamen-Flora* 2. Leipzig.
- Rao, D. N. & LeBlanc, F. 1967: Influence of an iron-sintering plant on corticolous epiphytes in Wawa, Ontario. *Bryologist* 70: 141-157.
- Räsänen, V. 1933: Contribution to the lichen flora of North America. *Ann. Missouri Bot. Gard.* 20: 7-21.
- 1939: Die Flechtenflora der nördlichen Küstengegend am Laatokka-See. *Ann. Bot. Soc. Vanamo* 12: 1-240.
- Richardson, D. H. S. 1974: *The vanishing lichens*. New York.
- Rickett, H. W. & Stafleu, F. A. 1959: Nomina generica conservanda et rejicienda Spermatophytorum. *Taxon* 8: 213-243.
- Roland, A. E. & Smith, E. C. 1969: The flora of Nova Scotia. Part II. The Dicotyledons. *Proc. Nova Scotia Inst. Sci.* 26: 71-73.
- Rose, F. 1976: Lichenological indicators of age and continuity in woodlands. In D. H. Brown, D. L. Hawksworth & R. H. Bailey (eds.), *Lichenology: progress and problems*, pp. 279-307. London, New York, and San Francisco.
- Sato, M. 1936: Notes on the lichen flora of Minami-Karafuto, or the Japanese Saghalien. *Bull. Biogeogr. Soc. Japan* 6: 97-121.

- 1965: *Catalogus Lichenum Japonicorum* (ed. 2). Japan.
- 1967: Distribution and substratum of the Japanese lichens. 3. The genus *Oropogon* Th. Fr. *Misc. Bryol. Lichenol.* 4: 129-131.
- Schauer, T. 1965: Ozeanische Flechten im Nordalpenraum. *Portugaliae Acta Biol. (B)* 8: 17-229.
- Schauer, T. & Brodo, I. M. 1966: *Lecanora insignis* und *L. degelii*. Zwei verwandte Flechten der Alpen und der Appalachen aus der *Lecanora-subfusca*-Gruppe. *Nova Hedwigia* 9: 527-533.
- Schindler, H. 1974: Die Flechte *Alectoria fremontii* Tuck. im Nordschwarzwald. *Beitr. Naturk. Forsch. Südwestdeutschl.* 33: 103-106.
- Schofield, W. B. 1969: Phytogeography of north-eastern North America: bryophytes and vascular plants. *Madroño* 20: 155-207.
- Schofield, W. B. & Crum, H. A. 1972: Disjunctions in bryophytes. *Ann. Missouri Bot. Gard.* 59: 174-202.
- Scotter, G. W. 1962: Productivity of arboreal lichens and their possible importance to barren-ground caribou (*Rangifer arcticus*). *Arch. Soc. Zool. Bot. Fenn. Vanamo* 16: 155-161.
- 1964: Effects of forest fires on the winter range of barren-ground caribou in northern Saskatchewan. *Can. Wildl. Serv., Wildl. Manag. Bull., Ser. 1*, 18: 1-109.
- 1965: Chemical composition of forage lichens from northern Saskatchewan as related to use by barren-ground caribou. *Can. J. Plant Sci.* 45: 246-250.
- Sernander-Du Rietz, G. 1957: Om yttre faktorerers inverkan på apotheciebildningen hos *Parmelia tiliacea*. *Svensk Bot. Tidskr.* 51: 454-488.
- Sharp, A. J. 1966: Some aspects of Mexican phytogeography. *Ciencia (México)* 24: 229-232.
- Sjödin, A. 1954: Gyelnik's new lichen names. *Acta Horti Gothob.* 19: 113-156.
- Sjörs, H. 1963: Amphi-Atlantic zonation, nemoral to arctic. In A. Löve & D. Löve (eds.), *North Atlantic biota and their history*, pp. 109-125. Oxford.
- Skye, E. & Hallberg, I. 1969: Changes in the lichen flora following air pollution. *Oikos* 20: 547-552.
- Solberg, Y. J. 1956: Dyeing of wool with lichens and lichen substances. *Acta Chem. Scand.* 10: 1116-1123.
- 1967: Studies on the chemistry of lichens. VI. Chemical investigations of the lichen species *Alectoria nigricans* (Ach.) Nyl. and *Parmelia alpicola* Th. Fr. *Z. Naturf.* 22 b: 777-783.
- 1975: Studies on the chemistry of lichens. XI. Chemical investigations of five Norwegian *Alectoria* species. *Acta Chem. Scand. B* 29: 145-152.
- Stebbins, G. L. & Major, J. 1965: Endemism and speciation in the California flora. *Ecolog. Monogr.* 35: 1-35.
- Stein, B. 1879: Flechten. In F. Cohn (ed.), *Kryptogamen-Flora von Schlesien* 2(2): 1-400. Breslau.
- Stizenberger, E. 1892: Die *Alectoria*-arten und ihre geographische Verbreitung. *Ann. Naturhist. Mus. Wien* 7: 117-134.
- Szczawinski, A. 1953: *Corticolous and lignicolous plant communities in the forest associations of the Douglas fir forest on Vancouver Islands*. Unpubl. Ph. D. thesis, Univ. of British Columbia, Vancouver (Not seen: cited from Edwards et al. 1960).
- Thompson, M. G. 1958: Egg sampling for the western hemlock looper. *Forest Chron.* 34: 248-256.
- Thomson, J. W. 1960: Lichens of arctic America. IV. Lichens collected mainly by A. Innes-Taylor in Greenland and the Canadian Archipelago. *Bryologist* 63: 181-188.
- 1972: Distribution patterns of American arctic lichens. *Can. J. Bot.* 50: 1135-1156.
- Turner, N. L. (in press): Food plants of British Columbia Indians. Part II. Interior peoples. *British Columbia Prov. Mus. Handb.*, Victoria.
- Wade, A. E. 1959: The British species of *Alectoria*. *Lichenologist* 1: 89-97.
- Webber, P. J. & Andrews, J. T. 1973: Lichenometry: a commentary. *Arctic Alp. Res.* 5: 295-302.
- Wetmore, C. M. 1960: The lichen genus *Nephroma* in North and Middle America. *Publ. Museum, Michigan State Univ., Biol. Ser.*, 1(11): 369-452.
- 1968: Lichens of the Black Hills of South Dakota and Wyoming. *Publ. Museum, Michigan State Univ., Biol. Ser.* 3(4): 209-464.
- Williams, T. A. 1895: Notes on Mexican lichens. I. *Amer. Naturalist* 29: 480-485.
- Yoshimura, I. 1968: The phytogeographical relationships between the Japanese and North American species of *Cladonia*. *J. Hattori Bot. Lab.* 31: 227-246.
- 1974: *Lichen flora of Japan in colour*. Osaka.
- Young, S. B. 1971: The vascular flora of St. Lawrence Island with special reference to floristic zonation in the arctic regions. *Contr. Gray Herb. Harvard Univ.* 201: 11-115.
- Zahlbruckner, A. 1929-30: *Catalogus Lichenum Universalis* 6. Leipzig.

Index

This index comprises, in addition to epithets of accepted North American Alectorioid taxa (**bold type**) and ones listed as synonyms of these here, other synonyms mentioned in North American publications (with author and their accepted name prefixed by “=”; mostly discussed in detail by Hawksworth 1972), epithets of extra-North American taxa mentioned, and those excluded from the Alectorioid genera. Pages where treatments of accepted North American species and subspecies start are indicated in bold type, and ones with figures indicated by an asterisk (*).

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Key to the species of *Bobartia*

1. Inflorescence lax, paniculate. Stem subterete, leaves flat 2
2. Inflorescence dense, more or less capitate. Stem and leaves externally very similar 3
3. Flowers mauve 15. *B. lilacina*
4. Flowers yellow 14. *B. paniculata*



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