

# Synopsis of the genus *Peltigera* (lichenized Ascomycetes) in British Columbia, with a key to the North American species

Trevor Goward, Bernard Goffinet, and Orvo Vitikainen

**Abstract:** Based on extensive field studies, herbarium research and thin layer chromatography, the taxonomy, distribution and ecology of 28 species of *Peltigera* occurring in British Columbia are discussed. Distribution maps are presented for selected species, and a key to the North American taxa is provided. *Peltigera cinnamomea* Goward is described as new, and the blue-green phototype of *Peltigera leucophlebia* (Nyl.) Gyelnik is documented for the first time. *Peltigera scabrosella* Holt.-Hartw. is reported as new for North America based on a collection from the Yukon Territory. *Peltigera hymenina* is new for British Columbia.

**Key words:** lichens, Ascomycotina, *Peltigera*, Peltigeraceae, British Columbia, distribution.

**Résumé :** Sur base de travaux sur le terrain, d'examen d'échantillons d'herbier et de chromatographies sur couche mince, la taxonomie, la distribution et l'écologie de 28 espèces de *Peltigera* présentes en Colombie-Britannique sont discutées. La distribution de certaines espèces est cartographiée et une clé de détermination des taxons nord-américains est proposée. *Peltigera cinnamomea* Goward est une espèce nouvelle pour la science et le phototype à cyanobactérie de *P. leucophlebia* (Nyl.) Gyelnik est décrit pour la première fois. *Peltigera scabrosella* Holt.-Hartw. est nouveau pour le continent nord-américain, tandis que *P. hymenina* est nouveau pour la Colombie-Britannique.

**Mots clés :** lichens, Ascomycotina, *Peltigera*, Peltigeraceae, Colombie-Britannique, distribution.

## Introduction

*Peltigera* Willd. is a diverse assemblage of small to large terricolous foliose lichens characterized by broad lobes, marginal apothecia, and a veined, cottony lower surface. Though readily recognized at the genus level, many *Peltigerae* are notoriously difficult to identify to species.

Earlier this century, *Peltigera* received considerable attention from the Hungarian lichenologist V. Gyelnik, who described more than 200 taxa in this genus between 1926 and 1942 (see Sjödin 1954). Most of these taxa have not withstood critical examination. What is more, the status of most of Gyelnik's names remains uncertain, owing in part to the loss of most of his type specimens during World War II (Wetmore 1960) and in part to a failure on occasion to designate type specimens. Therefore this genus seems likely to

remain nomenclaturally unstable into the foreseeable future.

*Peltigera* in North America was first monographed by Thomson (1950), who recognized 41 taxa. Only 12 of these, however, were accorded specific rank; the rest were distributed among 16 varieties and 13 forms. Recent work on this genus (e.g., Vitikainen 1981, 1985; Tønsberg and Holtan-Hartwig 1983) has resulted in the description of several new taxa, as well as the reassignment of a number of Thomson's varieties to specific rank. The latest North American lichen checklist (Egan 1987, 1991) lists 26 species (and no varieties or forms) of *Peltigera*, though this figure includes *P. erumpens* (Taylor in Hook.) Elenkin, which is actually a synonym of *P. didactyla* (With.) Laundon. More recently, two additional taxa have been recognized as occurring in North America: *Peltigera* sp. 1 sensu Holtan-Hartwig (1993) and *P. didactyla* var. *extenuata* (Nyl. ex Vainio) Goffinet & Hastings (1995).

Compared with other regions of the world, British Columbia contains an unusually rich *Peltigera* flora. With the publication of this paper, all *Peltigera* species hitherto documented for North America are now known or (in the case of *P. scabrosella*) believed to occur in this province. Also present are two taxa previously unknown to science, namely *P. cinnamomea* Goward, and *P. sp. 1* sensu Goward et al., as well as the blue-green phototype of *P. leucophlebia*. A summary discussion of British Columbia's *Peltigera* flora is thus likely to be of general interest to lichenologists.

This paper has five primary objectives: (i) to provide a

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**Trevor Goward**<sup>1</sup> Herbarium, Department of Botany, University of British Columbia, Vancouver, BC V6T 2B1, Canada.

**Bernard Goffinet** Department of Botany, University of Alberta, Edmonton, AB T6G 2E9, Canada.

**Orvo Vitikainen** Botanical Museum (Mycology), P.O. Box 47, FIN-00014 Helsinki University, Finland.

<sup>1</sup> Author to whom all correspondence should be addressed at Edgewood Blue, Box 131, Clearwater, BC V0E 1N0, Canada.

floristic inventory of the *Peltigera* of British Columbia;<sup>2</sup> (ii) to summarize the ecology and distribution of the species; (iii) to comment on the taxonomy and identification of critical species; (iv) to provide an identification key to the *Peltigera* of North America; and (v) to point to taxonomic problems in need of further research.

## Methods

The observations presented below are based on field studies in all portions of British Columbia, as well as on an examination of approximately 1600 specimens of *Peltigera* from ALTA, CANL, H, OSC, UBC, and the personal herbaria of B. Goffinet and T. Goward. These specimens as well as a few specimens of *P. cinnamomea* from the British Columbia Ministry of Forests herbarium in Prince George were studied according to the methods of traditional herbarium taxonomy. In addition, selected specimens were subjected to thin layer chromatography (TLC) following the methods of Culberson (1972), Culberson and Kristinsson (1970), and Walker and James (1980). The lichen substances were extracted in acetone and loaded on precoated Merck Silica gel 60 F254 plates. They were then developed in solvent system G (toluene – ethyl acetate – formic acid = 139:83:8) and (or) system EHF (diethyl ether – hexane – formic acid = 300:100:3).

The chemical data reported here are based primarily on material from British Columbia. However, in species for which local data are lacking, European reports are presented instead. Given the limited amount of data available for many of the taxa, no attempt is made to define chemotypes within species. The symbol  $\pm$  denotes chemical substances that occur in variable amounts within a given species, i.e., that are lacking in certain chemotypes of such species.

## Results

### Morphology

*Peltigera* is a taxonomically difficult group in which accurate identification requires a clear understanding of the idealized morphology of the species. Though it is beyond the scope of this paper to provide a comprehensive glossary of terms, various critical characters are briefly discussed below and are illustrated in Figs. 1–19. Character states for most species are summarized in Tables 1–6. Additional character illustrations and discussions on their variation are provided in Holtan-Hartwig (1993) and Goffinet and Hastings (1994).

#### Upper cortex

In most *Peltigera* the upper cortex is smooth, though in a few species it has a roughened or scabrid appearance, owing to the presence of submicroscopic cortical “warts.” In members of the *P. aphthosa* group and *P. canina* group (Tables 2 and 3), cortical hyphae typically extend beyond the surface of cortex as a minute tomentum of glassy “hairs.” The

tomentum may be either appressed or erect. By contrast, the upper cortex is glabrous in members of the *P. polydactylon* group, except when encrusted with tiny whitish calcium oxalate crystals or pruina. The upper cortex can be broadly classified according to topography as dimpled (Fig. 1), corrugate (Fig. 2, proximal portion of lobe), billowed (Fig. 3), or plane (Fig. 2, distal portion of lobe).

*Peltigera venosa* and members of the *P. aphthosa* group are three-way symbioses between a mycobiont and two photobionts. *Coccomyxa*, a green alga, typically serves as the primary photobiont, whereas *Nostoc*, a cyanobacterium, is localized in scattered cephalodia (Fig. 4). The cephalodia may either be peltate, i.e., have free margins (Fig. 4, top), or be appressed (Fig. 4, bottom) and under humid conditions may enlarge into full-sized lobes. The resulting blue-green phototype may grow completely independent of the original green phototype, though more often the two phototypes grow attached.

In a few species, *Nostoc* is discontinuously distributed beneath the upper cortex, as indicated by the presence of pale laminal flecks or maculae. Maculae form a delicate reticulum that is best developed in thalli growing under sheltered, humid conditions. Even then, however, this reticulum is usually conspicuous only when the thallus is moist, though in blue-green phototypes of *P. aphthosa*, *P. britannica*, and *P. leucophlebia*, the upper surface is strongly maculate.

Lobe tips and their inclination provide a critical character for certain members of the *P. canina* group. In some species (Fig. 2), the extreme tips are upturned, whereas in others they are distinctly downturned (Fig. 3). In interpreting for this character, only well-developed, sterile lobes should be examined. Excessively pressed herbarium specimens may be difficult to assess.

Lobe thickness is correlated to a considerable extent with environmental conditions and can also be species specific. Thalli may be classified as either membranous (i.e., less than 200  $\mu\text{m}$ ), thin (between 200 and 400  $\mu\text{m}$ ), thick (i.e., between 400 and 1000  $\mu\text{m}$ ), and very thick (i.e., over 1000  $\mu\text{m}$ ). Measurements should be taken on thalli in a moist condition.

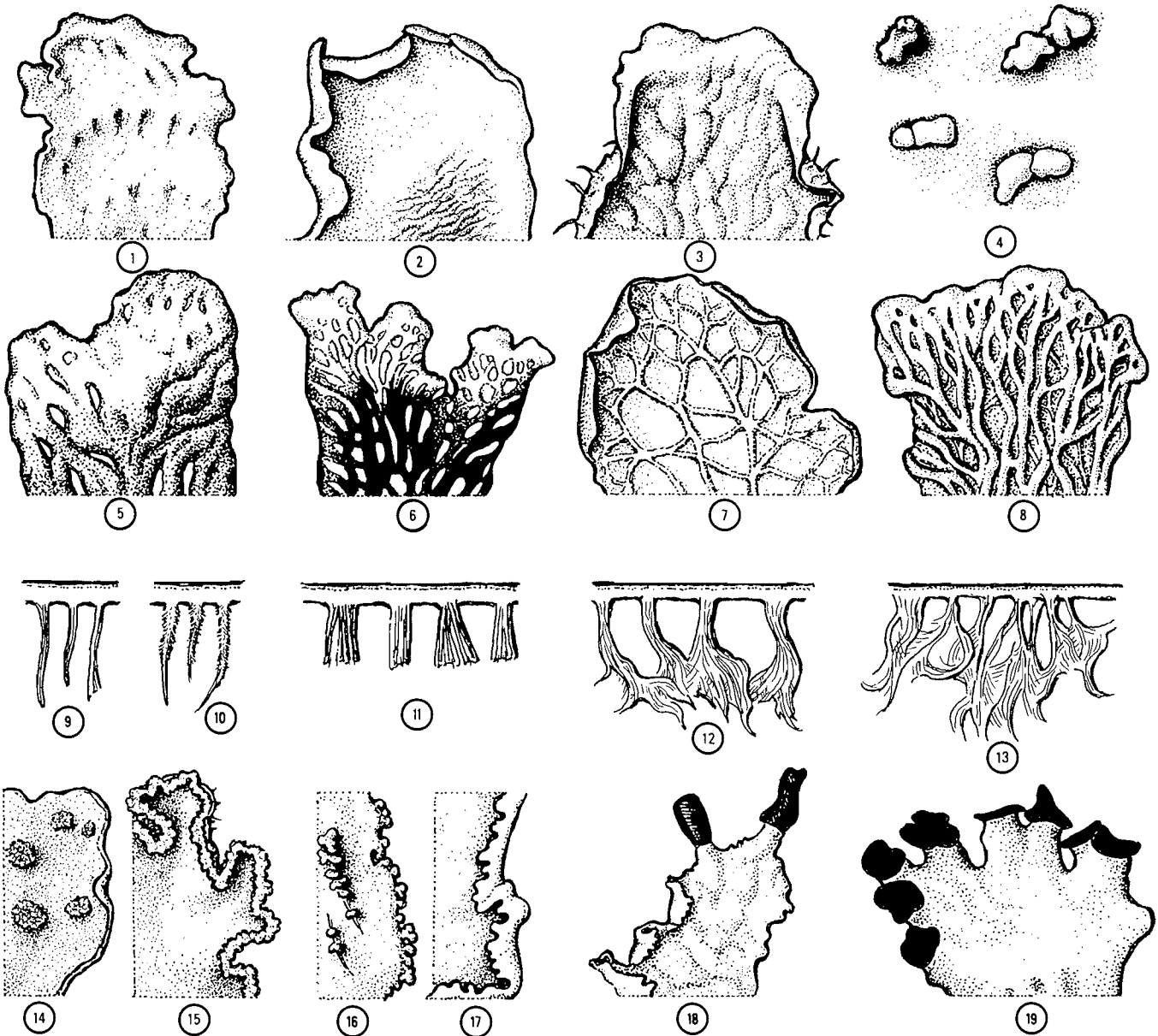
#### Lower surface

The lower surface in *Peltigera* is noncorticate and consists of a dense network of medullary hyphae that in turn accrete to form pale or darkish fusing veins. The veins may be characterized according to habit as indistinct (Fig. 5), broad (Fig. 6), or narrow (Fig. 7). In terms of relief, they can be described as low (Fig. 6), raised (Fig. 7), or ropy and overlapping (Fig. 8). In a few species the veins are covered in short erect hyphae termed tomentum. The interstices separating the veins may be described as polygonal (Fig. 7), lenticular (Fig. 8), or oval (Fig. 6). All of these characters are most satisfactorily assessed on the basis of sterile lobes (see Jahns and Frey 1982).

Extending downward from the veins are numerous rhizines, i.e., medullary outgrowths that attach the thallus to the substrate. In outline the rhizines may be classified as simple (Fig. 9), fasciculate (Fig. 11), penicillate (Fig. 12), or flocculent (Fig. 13). There is, however, considerable intergradation between these categories, and many thalli possess more than one kind of rhizine. In certain species within the

<sup>2</sup> We have refrained from providing an exhaustive list of synonyms as these are given in a taxonomic revision of *Peltigera* in Europe (Vitikainen 1994), which appeared while this paper was in press. Only synonyms not included in the latest checklist of North American lichens (Egan 1987) are presented here.

**Figs. 1–16.** Morphological characteristics in *Peltigera*. Fig. 1. Dimpled upper surface (*P. horizontalis*.  $\times 3$ ). Fig. 2. Plane and corrugate upper surface with upturned lobe tips (*P. occidentalis*.  $\times 3$ ). Fig. 3. Billowed upper surface, with downturned lobe tips (*P. membranacea*.  $\times 2$ ). Fig. 4 (top). Peltate cephalodia (*P. britannica*.  $\times 15$ ). Fig. 4 (bottom). Appressed cephalodia (*P. aphthosa*.  $\times 15$ ). Fig. 5. Indistinct veins (*P. malacea*.  $\times 2$ ). Fig. 6. Broad, low veins with oval interstices (*P. polydactylon*.  $\times 3$ ). Fig. 7. Narrow, raised veins with polygonal interstices (*P. membranacea*.  $\times 2$ ). Fig. 8. Narrow, ropy veins with lenticular interstices (*P. ponojensis*.  $\times 3$ ). Fig. 9. Simple, nontomentose, discrete rhizines (*P. cinnamomea*.  $\times 5$ ). Fig. 10. Simple, erect-tomentose, discrete rhizines (*P. membranacea*.  $\times 5$ ). Fig. 11. Fasciculate, discrete rhizines (*P. scabrosa*.  $\times 10$ ). Fig. 12. Penicillate, confluent rhizines (*P. canina*.  $\times 5$ ). Fig. 13. Flocculent, confluent rhizines (*P. didactyla*.  $\times 10$ ). Fig. 14. Laminal soredia (*P. didactyla*.  $\times 4$ ). Fig. 15. Marginal soredia (*P. collina*.  $\times 3$ ). Fig. 16. Marginal lobules (*P. praetextata*.  $\times 5$ ). **Fig. 17.** Marginal lobules (*P. pacifica*.  $\times 5$ ). **Fig. 18.** Erect, folded apothecia (*P. pacifica*.  $\times 2$ ). **Fig. 19.** Horizontal, plane apothecia (*P. horizontalis*.  $\times 2$ ). Illustrations by T. Goward.



*P. canina* group, the rhizines are covered in short, erect hyphae and are said to be erect-tomentose (Fig. 10). When considered collectively, rhizines may be discrete (Figs. 9, 10, and 11) or confluent (Figs. 12 and 13). In *P. elisabethae* and *P. horizontalis* the outermost rhizines are arranged in concentric rows, presumably reflecting annual growth incre-

ments of the thallus. No such alignment is seen in other species.

*Vegetative propagules*

Asexual reproduction occurs via laminal or marginal soredia (Figs. 14 and 15), laminal isidia, laminal lobules, or margi-

Fig. 20. The distribution of *Peltigera leucophlebia* in British Columbia.

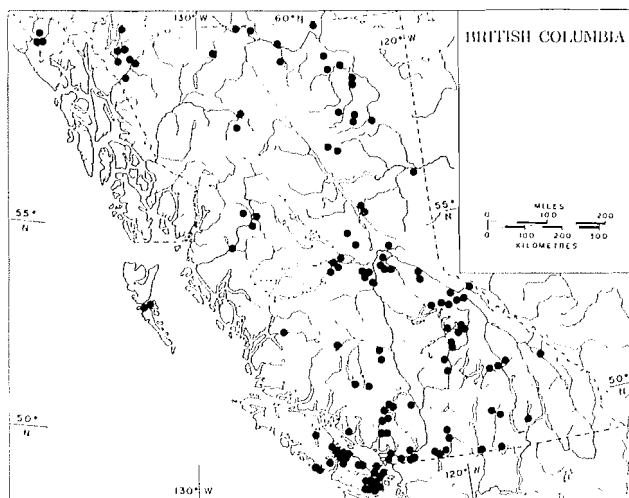
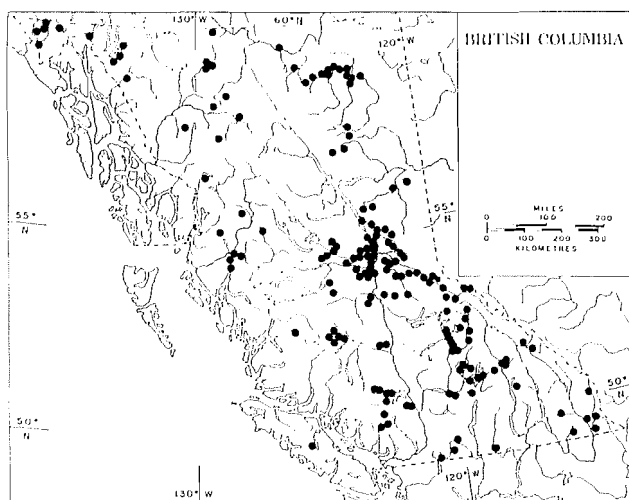


Fig. 21. The distribution of *Peltigera aphthosa* in British Columbia.

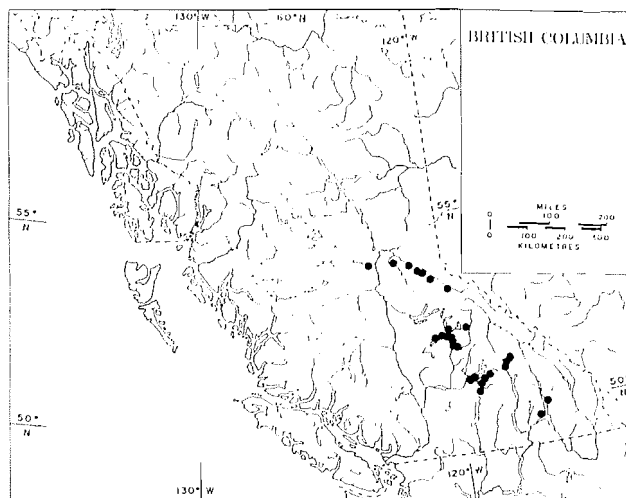


nal lobules (Figs. 16 and 17). Marginal lobules have been observed in a majority of the species discussed here but are diagnostic in only about six species. Marginal lobules are not homologous structures in all species: in *P. pacifica* and *P. polydactylon*, for example, they represent lobe margins in a crisped condition (Fig. 17), whereas in *P. praetextata* they are true thalline outgrowths (Fig. 16) and are sometimes called phyllidia (Holtan-Hartwig 1993). In some species these structures occur both along the lobe margins and along stress cracks of the laminal surface (see Thomson 1948); in the latter case, they must be distinguished from laminal isidia or lobules, which are not associated with stress cracks.

#### Apothecia

Apothecia have been observed in all local species excepting *P. evansiana*, *P. lactucifolia*, and *P. lepidophora*. Spores are eight per ascus, acicular to narrowly elliptical, typically four-celled, hyaline, and of little taxonomic value at the species level. In a majority of species the apothecia themselves

Fig. 22. The distribution of *Peltigera horizontalis* in British Columbia.



are erect and longitudinally folded (Fig. 18), the lower surface is noncorticate, and the disc is brown. Exceptions include the following: *P. elisabethae*, *P. horizontalis*, and *P. venosa*, in which the apothecia are horizontally oriented and more or less plane (Fig. 19); *P. leucophlebia*, in which the lower surface is patchy-corticate versus continuously corticate in *P. aphthosa*, *P. britannica*, and *P. sp. 1*; and *P. collina* and *P. neckeri*, in which the apothecial discs are black.

#### Distribution and ecology

In British Columbia, several major mountain systems, intervening valleys, plains, and plateaux occur in close proximity (Demarchi et al. 1990). The mountains, aligned perpendicular to the prevailing westerly flow of moist Pacific air, create a strong climatic gradient from west to east. Lowlands along the Pacific coast have a distinctly hypermaritime and temperate climate, whereas in northeastern regions a much more continental and boreal climate prevails (Tuhkanen 1984). The mountains themselves introduce additional (oroboreal and oroarctic) elements to the climate, but as these are of a more local nature, they will not be discussed in detail here. For notes on the orographic distributions of various *Peltigera* species, see Goward and Ahti (1992).

Given this climatic heterogeneity, it is hardly surprising that comparatively few *Peltigera* species are ubiquitous in British Columbia. It is possible in fact to recognize five broad categories of distribution: (i) widespread, (ii) inland, (iii) intermontane, (iv) humid, and (v) coastal.

Taxa with a more or less widespread distribution include *P. didactyla* var. *didactyla*, *P. ponojensis*, *P. rufescens*, and *P. venosa*. Even these species, however, are obviously more abundant in some parts of the province than in others (*P. rufescens*, for example, has yet to be reliably reported from the Queen Charlotte Islands). With the exception of the mesophytic *P. venosa*, these taxa are distinctly xerophytic and depend on the presence of exposed, often somewhat disturbed sites. Other mesophytic species also probably belonging here are *P. leucophlebia* (Fig. 20), and to a lesser extent *P. praetextata*, though the distributions of these are possibly limited by the availability of calcium-rich soils.

Species that are widespread in inland regions but are essentially absent from coastal localities (e.g., Fig. 21) include *P. aphthosa*, *P. canina*, *P. cinnamomea*, *P. didactyla* var. *extenuata*, *P. elisabethae*, *P. evansiana*, *P. lepidophora*, *P. malacea*, *P. neckeri*, *P. polydactylon*, *P. retifoveata*, and *P. scabrosa*. Within this group, *P. retifoveata*, *P. scabrosa*, and *P. evansiana* are primarily boreal in distribution. A few of the species occur on the southeastern tip of Vancouver Island, which has a distinctly mediterranean climate.

The intermontane species are restricted primarily to southern inland regions west of the Coast Mountains and east of the Rocky Mountains (e.g., Fig. 22). Included here are the hygrophytic *P. horizontalis* and the more mesophytic *P. kristinssonii*.

Not surprisingly, species restricted to humid coastal or inland localities are invariably hygrophytic in ecology: *P. britannica*, *P. collina*, *P. degenii*, *P. membranacea*, and *P. pacifica*. Based on its distribution in western Europe (Vitikainen 1987), *P. neopolydactyla* s.str. might also be included here, but this species is rather broadly circumscribed in North America and may include more than one taxon.

Only *P. hymenina* is known exclusively from coastal localities, though future segregates of *P. neopolydactyla* will probably also display this pattern.

### Chemistry

*Peltigera* is a chemically complex and varied genus in which numerous compounds remain to be identified (Holtan-Hartwig 1993). Its species produce the secondary metabolites of two major pathways: the acetate-polymalonate

pathway (tenuiorin, methyl gyrophorate, and gyrophoric acid) and the mevalonic acid pathway (several hopane triterpenoids). Representatives of both of these metabolite series are found in all species groups. Chemical diversity and evolution in the Peltigerales was recently reviewed by Galloway (1991).

Though many *Peltigera* display characteristic chemical patterns, these vary in taxonomic importance from species to species and indeed from group to group. For example, most members of the *P. canina* group (exceptions: *P. malacea*, *P. retifoveata*, and *P. didactyla* var. *extenuata*) lack any identifiable substances at all. The *P. polydactylon* group, by contrast, is chemically highly diverse. Within this group, some species (e.g., *P. neckeri*) are chemically distinct, whereas others (e.g., *P. elisabethae* and *P. horizontalis*) have overlapping chemical patterns. Some species, including *P. occidentalis*, display various chemical patterns and in the absence of correlating morphological or ecological characters are said to contain two or more chemical races. Some chemical races, especially within *P. neopolydactyla*, might better be treated as distinct taxonomic entities, but such decisions must await thorough chemical, morphological, and ecological investigations on a global scale.

Spot tests are of little or no diagnostic value in *Peltigera*, and the identification of lichen substances must be based exclusively on thin layer chromatography. Even gyrophoric acid, though present in many species of the *P. polydactylon* group, varies considerably in concentration and therefore fails to yield a consistent reaction with C and KC (see Goffinet and Hastings 1995 for further discussion).

### Key to the North American species of *Peltigera*

- 1a. Two photobionts present: primary photobiont green (*Coccomyxa*); secondary photobiont blue-green (*Nostoc*), confined to cephalodia, these scattered over the upper or lower surface ..... 2
- 1b. One photobiont present: blue-green (*Nostoc*); cephalodia absent ..... 6
- 2a (1a). Cephalodia present over lower surface; thallus fan-shaped, attached to the substrate at a single point along the margin, averaging <2 cm in diameter ..... *P. venosa*
- 2b. Cephalodia present over the upper surface; thallus more or less lobate, broadly attached, averaging >3 cm in diameter ..... 3
- 3a (2b). Lower surface darkening abruptly toward thallus centre; lower surface of apothecia continuously corticate; veins broad to indistinct ..... 4
- 3b. Lower surface darkening gradually toward thallus centre and (or) the lower surface of the apothecia patchy-corticate, the noncorticate areas appearing whitish; veins broad ..... 5
- 4a (3a). Mature cephalodia peltate (check sheltered lobes), usually flat or concave, often detaching and leaving white scars; humid localities at lower elevations. .... *P. britannica*
- 4b. Mature cephalodia appressed throughout, usually convex or flat, not detaching; widespread ..... *P. aphthosa*
- 5a (3b). Lower surfaces of apothecia continuously corticate; lobes few; lobe margins even or weakly crisped; cephalodia in central portions of thallus up to 2 mm in diameter; restricted to snowy districts, usually at higher elevations (but also along the coast) ..... *P. sp. 1*
- 5b. Lower surfaces of apothecia patchy-corticate to noncorticate; lobes many; lobe margins strongly crisped; cephalodia seldom >1 mm in diameter; widespread ..... *P. leucophlebia*
- 6a (1b). Attached to lobes containing a green alga and (or) upper surface distinctly maculate; restricted to humid localities ..  
..... (blue-green phototype of) *P. aphthosa*, *P. britannica*, or *P. leucophlebia*<sup>3</sup>
- 6b. Not attached to lobes containing a green alga; upper surface not maculate; ecology various ..... 7

<sup>3</sup> These phototypes overlap morphologically (Table 2) and can only be reliably identified on the basis of the associated *Coccomyxa*-containing thallus.

- 7a (6b). Soredia present ..... 8  
 7b. Soredia absent ..... 10
- 8a (7a). Soredia primarily marginal; apothecial disk black, on short extensions of vegetative lobes ..... *P. collina*  
 8b. Soredia entirely laminal; apothecial disk usually brownish, on rather elongate extensions of the vegetative lobes ... 9
- 9a (8b). Rhizines white-flocculent in central portions of thallus, sparse and simple toward margins; mature thallus often deeply concave, consisting of a single lobe (occasionally several-lobed), averaging < 1 cm in diameter; medulla KC-; methyl gyrophorate absent. .... *P. didactyla* var. *didactyla*  
 9b. Rhizines white-flocculent throughout, or sparse or lacking toward thallus centre; mature thallus typically flat to at most weakly concave, multilobate, averaging > 1 cm in diameter; medulla KC+ reddish (flash) or KC-; methyl gyrophorate present ..... *P. didactyla* var. *extenuata*
- 10a (7b). Laminal isidia and (or) lobules present ..... 11  
 10b. Laminal isidia and lobules absent (note: marginal lobules may, however, be present along laminal stress cracks in some species) ..... 12
- 11a (10a). Isidia dorsiventral, more or less appressed; mature lobes < 0.8 cm wide; lobe tips upturned; usually over soil .... *P. lepidophora*  
 11b. Isidia cylindrical or rarely dorsiventral, predominantly erect; mature lobes > 1 cm wide; lobe tips often downturned; over moss in sheltered sites ..... *P. evansiana*
- 12a (10b). Upper surface bearing scattered greenish lobules, these laminally tomentose, containing a green alga; humid localities ..... (blue-green phototype of) *P. aphthosa*, *P. britannica*, or *P. leucophlebia*<sup>3</sup>  
 12b. Greenish lobules absent; ecology various ..... 13
- 13a (12b). Upper surface tomentose, the hairs either closely appressed or erect and felt-like (note: in *P. malacea* and *P. kristinssonii*, the hairs are often confined to the immediate vicinity of the lobe tips and may be difficult to observe) ..... 14  
 13b. Upper surface scabrid or pruinose in some specimens, but never tomentose ..... 25
- 14a (13a). Upper surface dark greenish when wet (check sheltered lobes), bearing erect, felt-like tomentum, especially near lobe tips; lower surface lacking veins, or with few and indistinct veins; medulla thick ..... *P. malacea*  
 14b. Upper surface bluish or greyish when wet, bearing appressed or erect tomentum near the lobe tips; lower surface distinctly veined; medulla thin or thick ..... 15
- 15a (14b). Veins low, very dark brown toward thallus centre, strikingly contrastive with the interstices; upper surface in part scabrid, bearing erect tomentum near the lobe tips; lobe tips mostly downturned ..... *P. kristinssonii*  
 15b. Veins low or raised, pale throughout or dark toward thallus centre, moderately contrastive to occasionally strikingly contrastive with the interstices; upper surface rarely scabrid, generally covered in appressed tomentum near the lobe tips; lobe tips upturned or downturned ..... 16
- 16a (15b). Lobes < 1.5 cm wide at maturity; lobe tips mostly upturned ..... 17  
 16b. Lobes > 1.5 cm wide at maturity; lobe tips mostly downturned ..... 20
- 17a (16a). Mature apothecia averaging 3–5(–6) mm long; most lobes fertile, soralial scars often present on sterile portion of thallus ..... *P. didactyla* var. *didactyla*  
 17b. Mature apothecia > 4–8(–12) mm long; thallus often entirely sterile; upper surface lacking scars ..... 18
- 18a (17b). Rhizines becoming confluent toward thallus centre; veins rather felt-like, uniformly (and often abruptly) darkening toward thallus centre, mostly forming a netlike pattern ..... *P. rufescens*  
 18b. Rhizines mostly discrete; veins with a compact appearance, not felt-like, pale throughout or more often irregularly darkening toward thallus centre, often apparently overlapping ..... 19
- 19a (18b). Lobe margins and (or) margins of stress cracks usually lobulate (check mature lobes); upper surface often somewhat broadly billowed ..... *P. praetextata*  
 19b. Lobe margin and margins of stress cracks lacking lobules; upper surface plane or at least not broadly billowed .... *P. ponojensis*
- 20a (16b). Veins lacking erect tomentum ..... 21  
 20b. Veins densely and usually conspicuously covered in minute, erect tomentum ..... 23
- 21a (20a). Rhizines richly penicillate or flocculent, usually confluent toward thallus centre; upper surface appressed-tomentose more or less throughout ..... *P. canina*  
 21b. Rhizines generally simple and discrete (except flaring toward the tips in some specimens); upper surface usually abruptly glabrous toward thallus centre ..... 22
- 22a (21b). Veins distinctly rusty cinnamon-coloured toward thallus centre; lobe margins more or less even; lobe margins and margins of stress cracks lacking lobules ..... *P. cinnamomea*  
 22b. Veins pale to dark brown, but not distinctly cinnamon-coloured; lobe margins more or less crisped; lobe margins and margins of stress cracks usually lobulate (check mature lobes) ..... *P. praetextata*
- 23a (20b). Veins broad, strongly raised, apparently overlapping; interstices deeply pitted, mostly oval; rhizines stout; primarily boreal ..... *P. retifoveata*

- 23b. Veins narrow, low to strongly raised, generally fusing; interstices not deeply pitted, polygonal to more often lenticular; rhizines simple; distribution various ..... 24
- 24a (23b). Lobe margins and margins of stress cracks usually lobulate (check mature lobes); interstices mostly lenticular; veins raised or more often rather low; rhizines generally lacking erect tomentum ..... *P. praetextata*
- 24b. Lobe margins and margins of stress crack lacking lobules; interstices lenticular to polygonal; veins strongly raised; rhizines bearing erect tomentum ..... *P. membranacea*
- 25a (13b). Upper surface conspicuously scabrid (at least toward lobe tip), never pruinose ..... 26
- 25b. Upper surface smooth and occasionally pruinose near lobe tip ..... 29
- 26a (25a). Veins dark toward thallus centre, strikingly contrastive with the interstices; upper surface apparently glabrous but actually bearing minute erect tomentum near lobe tips (check sheltered lobes) ..... *P. kristinssonii*
- 26b. Veins dark or pale, not strikingly contrastive with the interstices; upper surface glabrous throughout ..... 27
- 27a (26b). Rhizines simple, elongate; upper cortex indistinctly scabrid or scabrid in patches; widespread in humid coastal localities ..... (scabrid form of) *P. neopolydactyla*
- 27b. Rhizines fasciculate, proportionally short; upper surface distinctly and uniformly scabrid; inland ..... 28
- 28a (27b). Lower surface dark toward thallus centre; rhizines dark throughout ..... *P. scabrosa*
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 45b. Lobe margins neither lobulate nor strongly crisped; mature lobes >20 mm wide; upper surface plane or somewhat broadly billowed ..... *P. neopolydactyla*

## The taxa

*Peltigera aphthosa* (L.) Willd. (green phototype), Flora Berol. Prodr. 347. 1787

*Lichen aphthosus* L., Sp. Pl. 2: 1148. 1753

*Peltigera* species having laminal cephalodia and a green primary photobiont belong to the *P. aphthosa* group. In British Columbia this group consists of four species: *P. aphthosa*, *P. britannica*, *P. leucophlebia*, and *P. sp. 1*. The following characters are useful for distinguishing among these species: (i) degree of marginal crisping; (ii) degree of cortication on the lower surface of the apothecia; (iii) distinctness of the veins; (iv) abruptness with which the veins darken toward the thallus centre; and (v) the habit of the cephalodia (Fig. 4). These and other points of separation are summarized in Table 1. See also the comments under *P. aphthosa* (blue-green phototype) below.

Common over soil, moss, duff, logs, and rock in open to somewhat shady inland localities, also rare in coastal localities (Fig. 21); xerophytic to hygrophytic; circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid (traces); phlebic acids  $\pm$  A and B, zeorin and  $\pm$  unidentified triterpenoids; or two unidentified triterpenoids as in *P. leucophlebia*. Tønsberg and Holtan-Hartwig (1983) and Holtan-Hartwig (1993) further report dolichorrhizin (their chemotype II).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Mt. Revelstoke National Park, Clachnacudann Creek, Fairbarns MF3 017 (ALTA); Fraser River Basin, Willow River, Goward 91-1679; Taku River Basin, Sinwa Eddy, Goward 82-811; Stuart River Basin, Fort St. James, MacKinnon 8206610.

*Peltigera aphthosa* (L.) Willd. (blue-green phototype)

Blue-green phototypes of *P. aphthosa*, *P. britannica*, and *P. leucophlebia* are all bluish grey and in this regard closely resemble certain forms of *P. malacea*, *P. collina*, *P. hymenina*, and *P. neckeri*. However, the blue-green phototypes are distinctly maculate above and typically bear at least a few scattered green *Coccomyxa*-containing lobes and lobules.

Distinguishing among these blue-green phototypes is much more difficult and usually involves identifying the associated green thalli. Whereas the blue-green phototypes of *P. aphthosa* and *P. leucophlebia* are virtually identical,

the blue-green phototype of *P. britannica* is somewhat distinctive owing to its association with *Coccomyxa*-containing lobes typically larger than itself, as well as its partly lobulate lobe margins. See also Table 2.

Rare over moss and mossy logs in open, humid inland forests at lower elevations; hygrophytic; western North America and western Eurasia.

Chemistry: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid (traces); phlebic acids  $\pm$  A and B, zeorin, unidentified triterpenoids. Unlike Tønsberg and Holtan-Hartwig (1983) we failed to detect dolichorrhizin in our material.

Selected specimens examined (all UBC): CANADA: British Columbia: Moyie River Basin, Moyie Falls, Goward 81-1677, Kispiox River Basin, Date Creek, Goward 92-319, Fraser River Basin, Legrand Creek, Goward 92-1289.

*Peltigera britannica* (Gyelnik) Holtan-Hartwig & Tønsb. (green phototype), Nord. J. Bot. 3: 685. 1983

*P. variolosa* f. *britannica* Gyelnik, Ann. Mycol. 30: 453. 1932

*P. avenosa* Gyelnik, Bryologist, 34: 18, 1931; Ann. Crypt. Exot. 4: 168. 1931

Tønsberg and Holtan-Hartwig (1983) recently synonymized the name *P. avenosa* Gyelnik against the blue-green phototype of *P. aphthosa*. They argued that the chemistry of the holotype of *P. avenosa* agrees with their chemotype II of *P. aphthosa*. In our opinion, *P. avenosa* is much more likely to belong to *P. britannica*. Our chemical studies now reveal that *P. avenosa* conforms not only with *P. aphthosa* but also with one of the local chemotypes of *P. britannica*. Moreover, *P. britannica* is expected to be much more common than *P. aphthosa* in the type locality of *P. avenosa*, which is actually Vancouver Island and not "southeastern Alaska" as previously reported by Tønsberg and Holtan-Hartwig (1983).

If synonymy with *P. britannica* is accepted, then *P. avenosa* would take priority. We refrain, however, from advancing this innovation, which would not be in the best interests of nomenclatural stability. Recent changes to the Nomenclatural Code now make it possible to conserve species names (Nicholson and Greuter 1994, example 3); a proposal to conserve *P. britannica* over *P. avenosa* is in preparation by one of us (O.V.).

Until recently, *P. britannica* was treated variously within



**Table 1.** Comparison of *Peltigera* species containing a green alga (*Coccomyxa*) as primary photobiont.

	<i>P. aphthosa</i>	<i>P. britannica</i>	<i>P. leucophlebia</i>	<i>P. sp. 1</i>
Lobes				
Width (cm)	2–4	2–3	2–3.5	3–4(–5.5)
Thickness	(Thin) <b>very thick</b>	(Thin) <b>very thick</b>	Thin to thick	<b>Thin</b>
Cephalodia	<b>Appressed</b>	Peltate	Appressed	Appressed
Lobe margins	Even	Even to crisped	Crisped	Even to crisped
Veins				
Breadth	<b>Indistinct</b>	Even to crisped	Broad	Broad
Inward darkening	<b>Abrupt</b>	<b>Abrupt</b>	<b>Gradual</b>	<b>Gradual</b>
Apothecia				
Frequency	<b>Frequent</b>	<b>Rare</b>	Frequent	Rare
Underside	<b>Continuously corticate</b>	<b>Continuously corticate</b>	<b>Discontinuously corticate</b>	<b>Continuously corticate</b>
Ecology	Xeric to hygic	Hygic	Xeric to hygic	Hygic (to mesic)
Distribution	Mostly inland	Widespread in humid regions	Widespread	Widespread in snowy regions

NOTE: Main diagnostic characters are in boldface.

**Table 2.** Comparison of *Peltigera* species containing *Nostoc* as primary photobiont and bearing erect tomentum on the upper surface (check sheltered lobe tips).

	<i>P. aphthosa</i> (blue-green phototype)	<i>P. britannica</i> (blue-green phototype)	<i>P. leucophlebia</i> (blue-green phototype)	<i>P. kristinssonii</i>	<i>P. malacea</i>
Lobes					
Width (cm)	1–1.5(–2)	0.5–1.0	1–1.5(–2)	1–1.5(–2)	<b>1.5–2.5(–3)</b>
Thickness	Thin	Thin	Thin	Thin to thick	<b>Thick to very thick</b>
Upper surface					
Tomentum	Present near lobe tip	<b>Absent</b> or present near tip	Present near lobe tip	Present near lobe tip	Present near lobe tip
Colour	Greyish blue	Greyish blue	Greyish blue	<b>Brownish</b>	<b>Greenish</b>
Texture	Smooth	Smooth	Smooth	<b>Scabrid</b>	Smooth
Maculae	<b>Conspicuous</b>	<b>Conspicuous</b>	<b>Conspicuous</b>	Absent	Absent
Marginal lobules	Absent	<b>Present</b>	Absent	Absent	Absent
Veins					
Width	Indistinct	Indistinct	Indistinct	<b>Broad</b>	Very broad to indistinct
Contrast	Weak	Weak	Weak	<b>Striking</b>	Weak
Surface	Smooth	Smooth	Smooth	<b>Erect-tomentose</b>	Smooth
Interstices					
Shape	Lenticular	Lenticular	Lenticular	Lenticular	Lenticular
Relief	Moderate	Moderate	Moderate	Low	Moderate
Rhizines	Irregular	Irregular	<b>Simple</b>	<b>Fasciculate</b>	Irregular
Green lobes	<b>Typically subordinate</b>	<b>Typically dominant</b>	<b>Typically subordinate</b>	Absent	Absent
Chemistry	Present	Present	Present	<b>Absent</b>	Absent
Habitat	Hygic	Hygic	Hygic	Mesic	<b>Xeric</b> to mesic

NOTE: Main diagnostic characters are in boldface.

*P. aphthosa* and *P. leucophlebia* (including *P. variolosa* Gyelnik). It may be distinguished from both those species on the basis of its peltate cephalodia (Fig. 4, top), the margins of which are somewhat raised or free from the upper cortex, especially on sheltered lobes. Peltate cephalodia are unknown in either of the other species. See also Table 1.

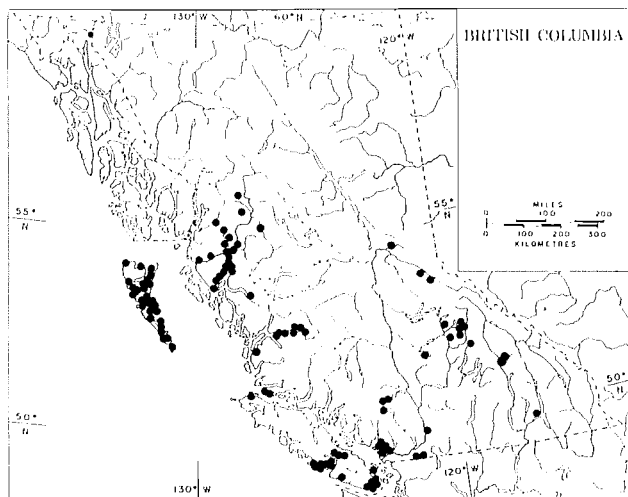
According to Holtan-Hartwig (1993), apothecia are unknown in *P. britannica* in Norway. Brodo and Richardson (1978) also noted the absence of fruiting bodies in material

from British Columbia. Our own observations reveal that *P. britannica* does produce apothecia but that these are rare and confined to specimens collected at or near the limits of the range.

Frequent over moss and mossy logs and rocks in sheltered to shaded coastal localities at lower elevations; also infrequent in similar habitats in humid inland forests (Fig. 23); hygrophytic; probably incompletely circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate, ± gyrophoric

**Fig. 23.** The distribution of *Peltigera britannica* in British Columbia.



acid; phlebic acid B, dolichorrhizin, zeorin or phlebic acid B, and an unidentified triterpenoid. The European material seems to differ in the presence of trace amounts of phlebic acid A and the absence of dolichorrhizin and zeorin (Holtan-Hartwig 1993).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Chilliwack River Basin, Sleese Creek, Goward 78-1277; Kootenay River Basin, Kokanee Creek Park, Goward 81-1605b; Kitlope River Basin, Tasytis River, Goward 91-1290; Vancouver Island, East Sooke Park, Horton 20595 (ALTA).

*Peltigera britannica* (Gyelnik) Holtan-Hartwig & Tønsh. (blue-green phototype)

For points of separation with blue-green *P. aphthosa* and related species, see Table 2 and also the discussion under the blue-green phototype of *P. aphthosa*.

Apparently in keeping with the detachable cephalodia and distinctly hygric ecology of *P. britannica*, this phototype is much more common than the blue-green phototypes of *P. aphthosa* and *P. leucophlebia*. Joined specimens of green and blue-green lobes are typical in this species. In many such specimens, it is possible to trace the development of the blue-green lobes from the laminal cephalodia of the green phototype.

Infrequent over moss and mossy logs in humid coast forests at lower elevations, also rare in humid inland forests; hygrophytic; western North America and western Eurasia.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric

acid; phlebic acid B, dolichorrhizin, zeorin or phlebic acid B, and an unidentified triterpenoid.

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Vancouver Island, Ucluelet, Goward 83-355; Kispiox River Basin, Date Creek, Goward 91-999; Skeena River Basin, Mudflat Creek, Goward 81-1908.

*Peltigera canina* (L.) Willd., Flora Berol. Prodr.: 347. 1787

*Lichen caninus* L., Sp. Pl. 2: 1149. 1753

The combination of broad lobes (1.5–3.0 cm wide), downturned lobe tips, broadcast laminal tomentum (disappearing

only gradually toward the thallus centre), and strongly penicillate and confluent rhizines (Fig. 12) distinguish typical specimens of *P. canina* from all other *Peltigera*. Small specimens may approach (i) *P. ponojensis*, which has upturned lobe tips, discrete, mostly simple rhizines, and compact, often distinctly raised veins, and (ii) *P. rufescens*, in which the lobe tips are upturned and the rhizines (and veins) darken abruptly inward of the lobe tips. Larger specimens of *P. canina* may sometimes be confused with *P. cinnamomea*, in which the central portions of the lower surface are distinctly cinnamon-coloured, and the rhizines are essentially simple, or at least not confluent. For points of separation with other similar species, see Table 3.

Common over soil, moss, duff and logs in open to somewhat sheltered inland localities; weakly xerophytic to mesophytic; circumpolar.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Kootenay National Park, McKay Creek, Dupuis SD2 012 (ALTA); Thompson River Basin, Lac du Bois, Goward 83-508; Fort Nelson River Basin, Fort Nelson, Goward 82-1048; Moyie River Basin, Lumerton, Goward 81-1676a.

*Peltigera cinnamomea* Goward sp. nov.

Thallus foliosus, *Peltigerae praetextatae* similis sed pagina inferna cinnamomea et marginibus lobulis carentis differt. Apothecia revoluta disco longo ca. 6–10 mm; sporae bacillari-aciculares, (38–)40–49(–55)  $\times$  3–5  $\mu$ m, triseptatae. Terricola. Holotypus Goward 82-2b in UBC.

TYPE: CANADA: BRITISH COLUMBIA: Clearwater River Basin, 0.5 km S Philip Creek, elev. 675 m, 51°52'N, 120°01'W, over mossy boulder in boulder bed, in open, mixed forest, 13 April 1985, Goward 85-2b (Holotype UBC; Isotypes ALTA, CANL, H).

Thallus foliose, loosely appressed, large, 10–30 cm across; lobes somewhat leathery, stiff, averaging to (1–)1.5–3 cm wide, elongate, loosely overlapping, irregularly branching; lobe tips rounded, plane to downturned; lobe margins essentially even; upper surface pale bluish grey to pale brownish grey or infused in part with cinnamon brownish, dull, often somewhat broadly billowed, tomentose, the tomentum appressed, usually disappearing abruptly toward thallus centre; soredia absent; isidia and marginal lobules absent; lower surface veined; veins pale tan, grading inward to rusty brown, distinct, narrow, in part raised, glabrous; interstices whitish, lenticular, moderately deep; rhizines concolorous with veins, abundant, simple to becoming penicillate, discrete.

Cortex 50–80  $\mu$ m thick; photobiont layer 20–80  $\mu$ m thick, containing *Nostoc*; medulla white, 70–180  $\mu$ m thick.

Apothecia common, marginal, located on narrow, elongate lobes; disc medium brown, longitudinally folded, averaging to 6–10 mm long, erect; spores hyaline, 8 per ascus, (38–)40–49(55)  $\times$  3–5  $\mu$ m, 3-septate. Conidiomata unknown.

The name *cinnamomea* refers to the typically cinnamon-coloured veins.

Photographs of *P. cinnamomea* are given in Goffinet and Hastings (1994, Figs. 24 and 25).

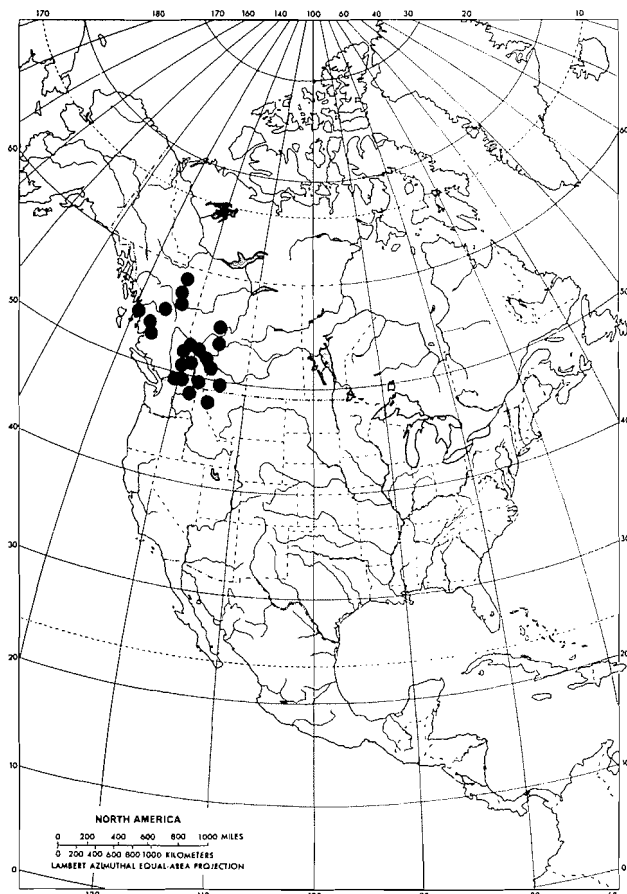
*Peltigera cinnamomea* is easily recognized in the field but has until now escaped taxonomic notice. Most of the specimens examined by us had previously been filed under

**Table 3.** Comparison of *Peltigera* species containing *Nostoc* as primary photobiont and bearing appressed (i.e., non-erect) laminal tomentum.

	<i>P. canina</i>	<i>P. cinnamomea</i>	<i>P. didactyla</i>	<i>P. membranacea</i>	<i>P. ponojensis</i>	<i>P. praetextata</i>	<i>P. retifoveata</i>	<i>P. rufescens</i>
Lobes								
Width (cm)	<b>1.5–2(–3)</b>	<b>1.5–3</b>	<b>0.7–1</b>	<b>1.5–3</b>	<b>0.5–1.5</b>	1–1.5(–2)	1.5–2(–3)	<b>0.5–1</b>
Thickness	Thin	Thin	Thin	<b>Membranous</b>	Thin (to thick)	(Membranous to) thin	<b>Thick to very thick</b>	Thin to thick
Upper surface								
Tomentum	<b>Broadcast</b>	±Broadcast	Near lobe tip	<b>Near lobe tip</b>	<b>Broadcast</b>	<b>Near lobe tip</b>	Near lobe tip	<b>Broadcast</b>
Lobe tips	<b>Downturned</b>	Plane to downturned	Downturned	<b>Downturned</b>	<b>Uprturned</b>	Plane to upturned	Downturned	<b>Uprturned</b>
Marginal lobules	<b>Absent</b>	<b>Absent</b>	Absent	Absent	Absent	<b>Often present</b>	Absent	Absent
Soredia	Absent	Absent	<b>Present</b>	Absent	Absent	Absent	Absent	Absent
Veins								
Width	Narrow	Narrow	Narrow	Narrow	Narrow	Narrow	<b>Broad</b>	Narrow
Relief	Low to raised	Low to partly raised	Low	<b>Strongly raised</b>	Raised to <b>ropy</b>	Raised	<b>Strongly raised</b>	<b>Low</b>
Colour	Pale to dark brown	Pale to <b>cinnamon</b>	Pale to dark brown	Pale to dark brown	<b>Pale</b> to dark brown	Pale to medium brown	Pale to dark brown	Dark brown to <b>black</b>
Surface	Smooth	<b>Smooth</b>	Smooth	<b>Erect-tomentose</b>	Smooth	Smooth or <b>erect-tomentose</b>	<b>Erect-tomentose</b>	Smooth
Interstices								
Shape	Lenticular	Lenticular	Lenticular	Lenticular to <b>polygonal</b>	Lenticular	Lenticular	Lenticular to <b>oval</b>	Lenticular
Impress	Moderate	Moderate	Moderate	Moderate	<b>Deep</b>	Moderate	<b>Deep</b>	Moderate
Rhizines								
Habit	<b>Penicillate to flocculent</b>	Simple	±Simple to flocculent	Simple	± <b>Simple</b>	± <b>Simple</b>	Simple	<b>Flocculent</b>
Growth	<b>Confluent</b>	Discrete	Discrete	Discrete	<b>Discrete</b>	<b>Discrete</b>	Discrete	Confluent
Surface	Smooth	Smooth	Smooth	<b>Erect-tomentose</b>	Smooth	Smooth	<b>Erect-tomentose</b>	Smooth
Colour	Pale to brown	Pale to <b>cinnamon</b>	Pale to brown	Pale to brown	Pale to brown	Pale to brown	Brown	Brown to <b>Black</b>
Apothecia	Frequent	Frequent	<b>Very frequent</b>	Frequent	Frequent	Frequent	Infrequent	Frequent
Chemistry	Absent	Absent	Absent or <b>present</b>	Absent	Absent	Absent	<b>Present</b>	Absent
Habitat	Xeric to mesic	Mesic to hygic	Xeric to mesic	Mesic to hygic	Xeric (to mesic)	Mesic	Mesic	Xeric

NOTE: Main diagnostic characters are in boldface.

Fig. 24. The world distribution of *Peltigera cinnamomea*.



*P. praetextata*. That species, however, has brownish or occasionally tan-coloured veins that are also often at least partially erect-tomentose. Additionally, *P. praetextata* tends to have somewhat crisped lobe margins that are lined, at least in older parts of the thallus, with lobules. Though both species are rather widely distributed in inland British Columbia, *P. cinnamomea* is most common in localities subject to prolonged snow cover (e.g., where snow cover persists until May or June), whereas *P. praetextata* is absent from such localities. For points of separation with other species of the *P. canina* group, see Table 3.

*Peltigera cinnamomea* is also very close in appearance to the isidiate species *P. evansiana*. These species may represent the primary and secondary species, respectively, of a species pair (Poelt 1972).

Frequent over moss and mossy rocks and logs in open to somewhat sheltered inland forests at all forested elevations; mesophytic to hygrophytic; western North America (Fig. 24). Together with *P. sp. 1*, *P. cinnamomea* is among the most tolerant of the local *Peltigerae* to prolonged snow cover.

CHEMISTRY: No lichen substances detected, except trace amounts of unidentified chemical substances.

SELECTED ADDITIONAL SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: ALBERTA: Swan Hills, Ostafichuk 330-1 (ALTA). BRITISH COLUMBIA: Clearwater River Basin, Trophy Mountains, Goward 84-850; Skeena River

Basin, Cleanza Creek Provincial Park, Goward 91-1060; Skagit River Basin, Lightning Lake, Goward 85-78; Fraser River Basin, Mount Robson Station, Otto 6289; Nechako River Basin, Ootsa Lake, Goward 81-1767. UNITED STATES OF AMERICA: MONTANA: Lake County, Soup Creek, McCune 7440 and 8664 (OSU); WASHINGTON: Pend Oreille County, Newport, Schroeder L438 (ALTA).

*Peltigera collina* (Ach.) Schrader, J. Bot. 1: 78. 1801  
*Lichen collinus* Ach., Lich. Suec. Prodr.: 162. 1799

Specimens *P. collina* with characteristic marginal soralia (Fig. 15) cannot be confused with any other species of *Peltigera*. Nonsorediate specimens, however, are occasionally encountered and have been referred to *P. nylanderii* Gyelnik (Gyelnik 1927). Such specimens are similar to *P. neckeri* and *P. elisabethae* but differ in having a pale lower surface and distinct veins. Additionally, *P. collina* is particularly common over trees in humid localities, whereas *P. neckeri* and *P. elisabethae* are essentially terricolous, muscicolous or rarely epixylous. See Table 4 for additional points of separation.

In two specimens from northwest British Columbia (Goward 92-1084 and 92-1110, UBC), the upper surface is distinctly greenish when wet, and the soralia are primarily laminal. This material may represent a distinct taxon.

Infrequent over mossy rocks and conifers in sheltered forests at lower elevations in humid regions throughout; hygrophytic; incompletely circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate;  $\pm$  dolichorhizin, zeorin, and  $\pm$  one unidentified triterpenoid. Holtan-Hartwig (1993) reports zeorin as the only triterpenoid.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Selwyn Range, Kinbasket Lake, Parmigan Creek, Goffinet 1273 (herb. Goffinet); Chilliwack River Basin, Chilliwack Lake, Goward 91-2074; Kitsumkalum River Basin, Kitsumkalum Lake, Goward 91-1132; Vancouver Island, Victoria, Goward 82-155.

*Peltigera degenii* Gyelnik, Mag. Bot. Lapok, 25: 253. 1927

Typical material of *P. degenii* may be distinguished from all other species of *Peltigera* by its glossy, glabrous upper surface, membranous lobes, narrow veins and rather broad interstices. Rare glabrous specimens of *P. membranacea* are similar, but in that species the veins and rhizines are erect-tomentose. In glabrous (or essentially glabrous) forms of *P. ponojensis* the lobes are distinctly thick, the upper surface is never glossy, the veins are thick and ropy, and the ecology is xerophytic. For further points of separation see Table 5.

Though lacking tomentum, *P. degenii* apparently belongs to the *P. canina* group rather than the *P. polydactylon* group, an observation suggested both by its narrow veins and by its lack of chemical substances (see also Holtan-Hartwig 1993).

Rare over moss and mossy logs in humid coastal localities at lower elevations, also rare in sheltered, humid inland forests; hygrophytic; probably incompletely circumpolar.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Chilliwack River Basin, Slease Creek,

**Table 4.** Comparison of *Peltigera* species containing *Nostoc* as primary photobiont and having a scabrid upper surface.

	<i>P. collina</i>	<i>P. kristinssonii</i>	<i>P. neopolydactyla</i>	<i>P. scabrosa</i>	<i>P. scabrosella</i>
<b>Lobes</b>					
Width (cm)	0.7–1.5(–2)	1–1.5(–2)	2–3(–4)	2–3(–4)	1.5–2.5
Margins	Even	Even	Even	<b>Even</b>	<b>Crisped</b>
<b>Upper surface</b>					
Detail	Plane	±Billowed	Plane to billowed	± <b>Billowed</b>	± <b>Plane</b>
Tomentum	Absent	Near lobe tip, erect	Absent	Absent	Absent
Pruina	<b>Near lobe tip</b> or absent	Absent	Absent	Absent	Absent
<b>Veins</b>					
Width	±Broad	Broad	Broad (to narrow)	Broad to <b>indistinct</b>	<b>Indistinct</b>
Relief	Low	Low to raised	Low to raised	Low to raised	Low
Contrast	Moderate	<b>Striking</b>	Moderate	Moderate	<b>Weak</b>
Surface	Smooth	Erect-tomentose	Smooth	Smooth	Smooth
<b>Rhizines</b>					
Habit	Simple to flocculent	±Fasciculate	± <b>Simple</b>	<b>Fasciculate</b>	± <b>Simple</b>
Colour	Pale to brown	Brown	Pale to brown	<b>Dark throughout</b>	Pale to brown
<b>Apothecia</b>					
Frequency	<b>Very frequent</b>	Infrequent	Frequent	Frequent	Frequent
Colour	<b>Black</b>	Brown	Brown	Brown	Brown
Chemistry	Present	<b>Absent</b>	Present	Present	Present

NOTE: Main diagnostic characters are in boldface.

**Table 5.** Comparison of glabrous *Peltigera* species containing *Nostoc* as primary photobiont and having distinct, narrow veins.

	<i>P. degenii</i>	<i>P. membranacea</i> (glabrous morph)	<i>P. neopolydactyla</i> (see text)	<i>P. pacifica</i>	<i>P. ponojensis</i> (glabrous morph)
<b>Lobes</b>					
Width (cm)	0.7–1.5(–2)	0.7–1(–1.5)	0.7–1(–1.5)	1.5–2(–3)	0.7–1(–2)
Thickness	Thin	<b>Membranous</b>	Thin (to thick)	Thin to thick	Thin (to thick)
<b>Upper surface</b>					
Gloss	<b>Shiny</b>	Shiny	Shiny to dull	<b>Shiny</b>	<b>Dull</b>
Lobe tips	<b>Downturned</b>	<b>Downturned</b>	Upturned	Upturned	<b>Upturned</b>
Lobe margins	Even	Even	<b>Even</b>	<b>Crisped to lobulate</b>	Even
<b>Veins</b>					
Relief	Raised	Raised	Low to raised	Raised	Raised to <b>ropy</b>
Surface	<b>Smooth</b>	<b>Erect-tomentose</b>	Smooth	Smooth	<b>Smooth</b>
Interstices	Lenticular to ±polygonal	Lenticular to ±polygonal	Lenticular to oval	Lenticular	Lenticular
<b>Rhizines</b>					
Habit	Simple	±Simple	Simple	±Simple	Simple to flocculent
Growth	Discrete	Discrete	Discrete	Discrete	Discrete
Surface	<b>Smooth</b>	<b>Erect-tomentose</b>	Smooth	Smooth	Smooth
Chemistry	Absent	Absent	Present	Present	Absent
Habitat	Hygic	Mesic to hygic	Mesic to hygic	Hygic	<b>Xeric</b> to mesic

NOTE: Main diagnostic characters are in boldface.

Goward 78-1274; Vancouver Island, Port Hardy, Deer Island, Lee 91; Vancouver Island, Duncan, Mount Prevost, Noble 3116.

*Peltigera didactyla* (With.) Laundon var. *didactyla*,

Lichenologist, 16: 217. 1984

*Lichen didactylus* With., Bot. Arrang. Veget. Gr. Br. 2: 718. 1776

Syn. *Peltigera erumpens* (Tayl. in Hook.) Vain., Etud. Lich. Bresil, 1: 182. 1890

*Peltigera didactyla* is the only local *Peltigera* to produce exclusively laminal soredia (Fig. 14). Two varieties are recognized by Goffinet and Hastings (1994). Variety *didactyla* has small, mostly unilobate and strongly concave thalli with rather discrete rhizines restricted to the central portions of the thallus. By contrast, var. *extenuata* is more appressed,

**Table 6.** Comparison of glabrous, smooth *Peltigera* species containing *Nostoc* as primary photobiont, having broad to indistinct veins, and lacking soredia.

	<i>P. elisabethae</i>	<i>P. horizontalis</i>	<i>P. hymenina</i>	<i>P. neckeri</i>	<i>P. neopolydactyla</i>	<i>P. occidentalis</i>	<i>P. pacifica</i>	<i>P. polydactylon</i>
Lobes								
Width (cm)	1–2(–3)	1–2(–3)	0.4–0.8(–2)	1–1.5(–2)	2–3(–4)	1–1.5(–2)	0.7–1(–1.5)	0.7–1(–1.5)
Thickness	<b>Thick</b>	<b>Thin</b>	Thin	(Thin to) thick	Thin (to thick)	(Thin to) thick	Thin to thick	Thin to thick
Upper surface								
Detail	<b>Dimpled</b>	<b>Dimpled</b>	Plane	Plane	Plane to <b>billowed</b>	Plane to <b>finely corrugate</b>	Plane	Plane
Pruina	<b>Near lobe tip</b>	<b>Absent</b>	Absent	<b>Near lobe tip</b>	<b>Absent</b>	Absent or near lobe tip	Absent	Absent
Stress cracks	<b>±Numerous</b>	<b>Sparse</b>	Sparse	<b>±Numerous</b>	Sparse	Sparse	Sparse	Sparse
Lobe margins	Crisped to <b>lobulate</b>	<b>Even to ±crisped</b>	±Crisped	<b>Even</b>	Even	±Even	Crisped to <b>lobulate</b>	Crisped
Veins								
Width	<b>Indistinct</b>	<b>Broad</b> (to distinct)	Indistinct	Indistinct (to broad)	Broad (to narrow)	±Indistinct	<b>Broad to ±narrow</b>	<b>Broad</b>
Relief	Low	Low	Low	Low	Low to raised	Low	Raised	Low
Inward darkening	Abrupt	<b>Abrupt</b>	Gradual	Abrupt	Gradual	Gradual	Gradual	<b>Gradual</b>
Inward colouring	Blackish	Dark brown	Brown (blackish)	Blackish	Brown	Brown	Brown	Blackish
Interstices	Oval	Oval	Oval to lenticular	Oval to lenticular	Lenticular to oval	Oval to lenticular	Lenticular	Oval
Rhizines								
Length (mm)	1–3(–5)	2–4(–5)	1–2(–3)	2–3(–5)	4–7(–10)	2–3(–5)	2–4	2–4
Habit	Fasciculate	Fasciculate	(Simple to) flocculent	Simple to fasciculate or flocculent	±Simple	±Flocculent	±Simple	Simple to fasciculate
Alignment	<b>Concentric</b> (outer)	<b>Concentric</b> (outer)	Unaligned	Unaligned	Unaligned	Unaligned	Unaligned	Unaligned
Apothecia								
Aspect	<b>Horizontal</b>	<b>Horizontal</b>	Erect	Erect	Erect	Erect	Erect	Erect
Habit	<b>Plane</b>	<b>Plane</b>	Folded	Folded	Folded	Folded	Folded	Folded
Colour	Brown to black	Brown	Brown	<b>Black</b>	Brown	Brown	Brown	Brown
Distribution	Inland	Inland	<b>Coast</b>	Inland	Widespread	<b>Inland</b>	Coast (inland in humid regions)	Inland

NOTE: Main diagnostic characters are in boldface.

multilobate, and has flocculent rhizines more or less throughout (Fig. 13). Chemically, the two varieties can be distinguished by the absence of depsides in var. *didactyla* versus the presence of methyl gyrophorate and often gyrophoric acid (KC+ red) in var. *extenuata*. Variety *didactyla* is also rather xerophytic and is often found in open habitats, whereas var. *extenuata* is mesophytic with an apparent optimum in moist forested sites. Whereas var. *didactyla* occurs throughout British Columbia, var. *extenuata* seems to be absent from coastal localities.

At maturity, var. *didactyla* is frequently fertile, whereas var. *extenuata* only rarely produces apothecia. Fertile specimens usually lack soredia and may then be difficult to distinguish from *P. rufescens*. In some specimens of var. *didactyla*, however, whitish sororial scars are present at the base of the fertile lobes. A small but consistent difference in the size of the apothecia may also be noted: 3–5(–6) mm long in var. *didactyla* versus 4–8 mm long in *P. rufescens*. In var. *didactyla*, moreover, the rhizines tend to be less flocculent and confluent, and the lower surface less abruptly darkened than in *P. rufescens* (check sterile lobes). For further points of distinction see Tables 3 and 4.

Frequent over soil and moss in open sites throughout, except rare in coastal regions; xerophytic; circumpolar.

CHEMISTRY: No lichen substances detected or a few unidentified substances occasionally present in trace amounts.

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Clearwater River Basin, Murtle Lake, Goward 79-1068; Slocan River Basin, Winlaw, Schofield 82184.

*Peltigera didactyla* (With.) Laundon var. *extenuata* (Nyl. ex Vainio) Goffinet & Hastings, Lichenologist, 1994  
*P. canina* var. *extenuata* Nyl. ex Vain., Medd. Soc. Fauna Flora Fenn. 2: 49. 1878

The presence of strictly laminal soredia in *P. didactyla* var. *extenuata* distinguishes this taxon from all other *Peltigera* except var. *didactyla*; see the discussion under that heading.

Frequent over moss or soil in open inland localities; meophytic; incompletely circumpolar.

CHEMISTRY: Methyl gyrophorate and  $\pm$  gyrophoric acid (often in trace amounts; Goffinet and Hastings 1995).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Selwyn Range, Kinbasket Lake, Ptarmigan Creek, Goffinet 1309 (herb. Goffinet); Clearwater River Basin, Clearwater Lake, Goward 83-903; Thompson River Basin, Kamloops, Goward 88-66; Spatsizi River Basin, Spatsizi Park, Pojar 1205.

*Peltigera elisabethae* Gyelnik, Bot. Kozl. 24: 135. 1927

The combination of plane, horizontally oriented apothecia, and stout, concentrically aligned (outermost) rhizines, together with a shiny, glabrous upper surface distinguishes *P. elisabethae* from all other *Peltigerae* except *P. horizontalis*. That species lacks the marginal lobules and numerous stress cracks of *P. elisabethae*, has a thinner medulla, and bears rather distinct veins that are separated by numerous interstices. In *P. elisabethae* the veins are hardly developed at all, and the interstices are usually sparse. See also Table 6 for additional points of separation.

Frequent over soil and mossy (calcium-rich) rock in open inland forests, especially at lower elevations; weakly xerophytic to mesophytic; circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; zeorin and several unidentified triterpenoids (Holtan-Hartwig 1993).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Clearwater River Basin, Murtle Lake, Ahti 13559; Fort Nelson River Basin, Fort Nelson, Goward 82-1065; Liard River Basin, Muncho Lake, Goward 82-1230; Spahats Creek Provincial Park, Spahats Creek, Marsh 1758 (ALTA).

*Peltigera evansiana* Gyelnik Bryologist, 34: 16. 1931

The presence of cylindrical isidia in this species is diagnostic. Most British Columbia specimens of *P. evansiana* contain copious lobulate isidia in addition to the cylindrical isidia typical of the species. This observation led Goward and Ahti (1992) to suggest that the western material may not actually represent *P. evansiana* s.s. Subsequent studies, however, revealed that this variation occurs throughout the range of the species and is therefore unworthy of taxonomic recognition.

Rare over mosses in sheltered inland forests, especially in boreal regions; mesophytic; North America, especially in eastern temperate regions.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Clearwater River Basin, White Horse Bluff, Goward 89-145; Fort Nelson River Basin, Parker Lake, Goward 82-951; Fort Nelson River Basin, Fort Nelson, Goward 82-1043.

*Peltigera horizontalis* (Huds.) Baumg., Flora Lips. 562. 1790

*Lichen horizontalis* Hudson, Flora Angl. 453. 1762

*Peltigera horizontalis* is similar in general distribution to *P. elisabethae* but is less xerophytic. For points of separation with similar species, see the discussion under *P. elisabethae* and Table 6.

Frequent over soil and moss in sheltered inland forests, usually at lower elevations (Fig. 22); mesophytic to weakly hygrophytic; incompletely circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; zeorin and several unidentified triterpenoids (Holtan-Hartwig 1993).

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Clearwater River Basin, Helmcken Falls, Ahti 13851; Kootenay River Basin, Boswell, Goward 81-1663; Fraser River Basin, Prince George, Mount Baldy Hughes, Goward 81-1555.

*Peltigera hymenina* (Ach.) Del. in Duby Bot. Gallica 2: 397. 1830

*Peltidea hymenina* Ach., Meth. Lich.: 284. 1803

*Peltigera lactucifolia* (With.) Laundon, Lichenologist, 16: 221. 1984

*Lichen lactucifolius* With., Bot. Arr. Veg. Gr. Br. 1, 2: 718. 1776

The nomenclature adopted here (using *P. hymenina* instead of *P. lactucifolia*) follows Santesson (1993). The

material does not match typical *P. hymenina* and may represent a separate taxon. It is morphologically and chemically very similar to some forms of *P. occidentalis* (see below) and could perhaps be included in that species. For the purposes of the present discussion, the name *P. hymenina* will be assigned to coastal material, whereas inland specimens are referred to *P. occidentalis*. However, this taxonomy is very preliminary.

Well-developed specimens of *P. hymenina* are rare in British Columbia and may be characterized as having medium-sized lobes (to 2 cm wide) with a shiny, glabrous upper surface, inconspicuous veins and short, sparse, simple to flocculent rhizines. The lower surface varies from pale throughout to medium brown (rarely blackish) toward the thallus centre. The putative coastal distribution of *P. hymenina* is also distinctive. Some forms of *P. neopolydactyla* are close, but in that species the thallus is membranous and the rhizines numerous, long, and more or less simple.

In exposed sites, e.g., mossy seaside headlands, *P. hymenina* is much smaller, its lobes then averaging only to 0.4–0.8(–1) cm wide. Such specimens are unique among the members of the *P. polydactylon* group in producing marginal lobules similar to those of *P. praetextata*. In some specimens, however, these lobules are sparse or absent. See Table 6 for points of separation with similar species.

Infrequent over exposed mossy outcrops in hypermaritime localities at lower elevations; hygrophytic; global distribution unknown. *Peltigera hymenina* is newly reported for British Columbia.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; peltidactylin, dolichorrhizin, zeorin, and traces of unidentified triterpenoids. The material from British Columbia is chemically identical to the European material as regards its major compounds (Holtan-Hartwig 1993).

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Vancouver Island, Ucluelet, Goward 83-208; Vancouver Island, Bamfield, Goward 91-621.

*Peltigera kristinssonii* Vitik., Ann. Bot. Fenn. 22: 291. 1985

In this distinctive species the upper surface is both scabrid and erect-tomentose (check lobe tips), and the lower surface bears broad, low to weakly raised, blackish veins that are strikingly contrastive with the interstices. See Tables 2 and 6 for points of separation with similar species.

Infrequent over soil and moss in sheltered inland forests, usually at lower elevations; mesophytic; incompletely circumpolar (Vitikainen 1985).

CHEMISTRY: No constant lichen substances reported (Vitikainen 1985).

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Homathko River Basin, Twist Lake, Goward 81-1429; Thompson River Basin, Lac du Bois, Goward 83-506; Elk River Basin, Crownnest Pass, Goward 81-1718.

*Peltigera lepidophora* (Nyl. ex Vainio) Bitter, Ber. Dtsch. Bot. Ges. 22: 251. 1904

*P. canina* var. *lepidophora* Nyl. in Vainio, Medd. Soc. Fauna Flora Fenn. 2: 49. 1878

The presence of copious appressed dorsiventral isidia (=lobules) over the upper surface is diagnostic. Local

material of *P. evansiana* frequently produces dorsiventral isidia in addition to the more typical cylindrical isidia, though these are mostly upright, not appressed. *Peltigera evansiana* also has a more mesophytic ecology than *P. lepidophora* and occurs in sheltered sites.

Infrequent over calcium-rich soils and moss in open sites throughout, except apparently rare in coastal regions; xerophytic; probably circumpolar.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Liard River Basin, Toad River, Goward 82-1086; Chilcotin River Basin, Taseko River, Goward 81-1529a; Clearwater River Basin, Helmcken Falls, Goward 80-288; Mt. Robson Provincial Park, Berg Lake Trail, Marsh JE819 (ALTA).

*Peltigera leucophlebia* (Nyl.) Gyelnik (green phototype), Mag. Bot. Lapok, 24: 79. 1926  
*P. aphthosa* var. *leucophlebia* Nyl., Syn. Lich. 1: 323. 1860

For points of distinction with similar species, see Table 1 and notes under *P. aphthosa*.

Frequent over (calcium-rich) soil, moss, and mossy rocks and logs in open forests throughout (Fig. 20); weakly xerophytic to mesophytic. *Peltigera leucophlebia* is similar in ecology to *P. aphthosa* but favours less acidic substrates and is also considerably more common in coastal localities.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; two to four unidentified triterpenoids. The chemistry of our material agrees with that documented from European specimens (Holtan-Hartwig 1993).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Vanderhoof, Fraser Lake, Goffinet 380 (herb. Goffinet); Skeena River Basin, Hazelton, Goward 91-1616; Taku River Basin, Tulsequah River, Goward 82-642; Chilcotin River Basin, Tatla Lake, Goward 81-1435.

*Peltigera leucophlebia* (Nyl.) Gyelnik (blue-green phototype)

This phototype has not previously been reported. The single specimen on which our present record is based (Goward 92-319, UBC) was collected over moss at the base of a conifer in a shady old-growth forest north of Hazelton, at 55°25'N, 127°48'W.

In most regards the specimen is similar in morphology to the blue-green phototypes of *P. aphthosa* and *P. britannica*, though the rhizines appear to be somewhat less branched and more discrete than in those taxa. The upper surface is distinctly maculate and is sparsely covered in erect tomentum, especially near the lobe margins. The lobe margins themselves essentially lack lobules and in this regard are similar to blue-green phototype of *P. aphthosa*.

Chemically, the blue-green phototype of *P. leucophlebia* is similar to its green counterpart, for example in containing two of the major "leucophlebia unknowns." These substances are found also, albeit rarely, in *P. aphthosa*.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; two unknown triterpenoids (in common with the green phototype).

SPECIMEN EXAMINED: See text.



*Peltigera malacea* (Ach.) Funck, Cryptogam. Gewachse, 33: 5. 1817

*Peltidea malacea* Ach., Syn. Meth. Lich.: 240. 1814

*Peltigera malacea* differs from other cyanobacterium-containing *Peltigerae* by its very thick lobes (to 1500  $\mu\text{m}$ ), indistinct veins (Fig. 5), and greenish upper surface bearing erect tomentum (check lobe tips). The blue-green phototypes of *P. aphthosa* and related species are similar but have bluish lobes and conspicuous laminal maculae. See Table 2 for other points of distinction with these and other species.

Frequent over (acid) soil and moss in open, usually dryish inland forests and alpine ridges; xerophytic to weakly mesophytic; probably circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; two to three unidentified triterpenoids. Holtan-Hartwig (1993) also reports dolichorrhizin and zeorin.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Fort Nelson River Basin, Fort Nelson, Annas 27-3; Clearwater River Basin, Spahats Falls, Goward 79-859; Terrace, Williams Creek, Ohlsson 2617 (ALTA).

*Peltigera membranacea* (Ach.) Nyl., Bull. Soc. Linn. Normandie, ser. 4, 1: 74. 1887

*Peltidea canina* var. *membranacea* Ach., Lich. Univ.: 518. 1810

Typical material of *P. membranacea* may be distinguished from all other laminally tomentose species of *Peltigera* by the lower surface, in which the interstices are polygonal, the veins narrow, the rhizines simple, and the veins and rhizines erect-tomentose more or less throughout (Figs. 3, 7, and 10). Poorly developed material may be difficult to separate from *P. praetextata*. In that species, however, the interstices are lenticular, the rhizines typically lack tomentum, and marginal lobules are usually present. See Table 3 for additional points of separation with similar species.

In hypermaritime localities, some specimens of *P. membranacea* lack laminal tomentum. Such specimens may be confused with *P. degenii* or various members of the *P. polydactylon* group, though in those species the veins and rhizines are never erect-tomentose (see also Table 6).

Frequent over soil, moss, and mossy rocks and logs in humid forested localities throughout, except essentially absent from semi-arid and boreal regions; weakly mesophytic to hygrophytic; probably incompletely circumpolar.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Queen Charlotte Islands, Maude Island, Brodo and Shchepanek 11287 (ALTA); Vancouver Island, Port Alberni, Mount Arrow-smith, Goward 91-1890; Kispiox River Basin, Kispiox, Date Creek, Goward 91-997; Kitsumkalum River Basin, Glacier Creek, Goward 91-1171.

*Peltigera neckeri* Hepp ex Müll. Arg., Mem. Soc. Phys. Geneve, 16, 2: 370. 1862

*Peltigera neckeri* is highly variable, but typical material may be distinguished by the glossy, bluish upper surface, erect black apothecia, marginal pruina (not always present), unaligned rhizines, and abruptly darkening lower surface. Nontomentose forms of blue-green *P. aphthosa* are similar

but are usually distinctly maculate and bear at least some green lobes.

Poorly developed specimens of *P. neckeri* can also be confused with several members of the *P. polydactylon* group. For additional points of distinction, see Table 6.

Infrequent over soil, mossy rocks and decaying logs in inland localities at lower elevations, especially in humid forest sites, but also rare in steppe communities; mesophytic; probably incompletely circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; dolichorrhizin, zeorin and three or more unidentified triterpenoids.

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Fort Nelson River Basin, Fort Nelson, Goward 82-1066; Moyie River Basin, Moyie Lake, Goward 81-1588; Clearwater River Basin, Clearwater, Schofield 75464.

*Peltigera neopolydactyla* (Gyelnik) Gyelnik Rev. Bryol. Lichenol. 5: 171. 1932

*P. polydactyla* var. *neopolydactyla* Gyelnik, Mag. Bot. Lapok, 31: 46. 1932

Syn. *Peltigera polydactylon* (Necker) Hoffm. var. *dolichorhiza* Nyl. sensu Thomson (1950)

Typical *P. neopolydactyla* may be distinguished from other glabrous *Peltigera* by its long, simple rhizines, broad, nonlobulate lobes, billowed upper surface, and weakly raised veins. Less robust forms are similar to *P. polydactylon*, but that species has shorter rhizines, crisped lobe margins, more rounded interstices, and (typically) flatter, broader veins. *Peltigera pacifica* has lobulate margins, while *P. degenii* and glabrous forms of *P. membranacea* both have distinctly raised, narrow veins. For points of separation with other similar species, see Table 6.

Even with the segregation of *P. hymenina* and *P. occidentalis*, *P. neopolydactyla* remains heterogeneous. Ahti and Vitikainen (1977) have already called attention to the existence of "bluish-grey" and "greenish" colour forms of this species in Newfoundland. In British Columbia, at least three colour forms may be recognized: olive green, milky blue, and dark slate blue. Where such forms correlate with chemistry or venation, taxonomic recognition may be indicated. Our present delimitation may thus include at least two additional taxa, i.e., an olivaceous taxon having a more or less yellowish medulla and pale, raised veins, and a milky blue taxon with low, broad veins that darken toward the thallus centre. Alternatively, this variation could be attributed to a single mycobiont associating with different species of *Nostoc* (Hawksworth 1988). Similar specimens have been seen from China, Japan, and New Zealand.

Many specimens from coastal localities are variously scabrid and may be confused with *P. scabrosa*. That species, however, appears to have a strictly inland distribution in British Columbia. As circumscribed here, *P. scabrosa* may be recognized by its more evenly scabrid upper surface and its short, fasciculate rhizines that are dark even at the thallus margins; in *P. neopolydactyla*, the outermost rhizines are typically simple and pale. See Table 4 for a comparison with other scabrid taxa.

Frequent over soil, moss, mossy rocks, and mossy logs in humid localities throughout; mesophytic to hygrophytic; probably circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid;  $\pm$  peltidactylin,  $\pm$  dolichorrhizin,  $\pm$  zeorin, and various unidentified triterpenoids. The variation observed is similar to that reported from Norwegian material (Holtan-Hartwig 1993). One specimen (Goward 81-2086, UBC) lacked major triterpenoids but showed unusually high amounts of gyrophoric acid.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA Vancouver Island, Sayward, Schoen Lake, Goward 91-752; Kispiox River Basin, Kispiox, Date Creek, Goward 91-998a; Clearwater River Basin, Spahats Falls, Goward 79-1408; Queen Charlotte Islands, Graham Island, Horton 1755 (ALTA).

*Peltigera occidentalis* (E. Dahl) H. Krist. Bryologist, 71: 38. 1968

*Peltigera canina* var. *occidentalis* Dahl, Medd. Gronl. 150: 68. 1950

Among the glabrous *Peltigerae*, *P. occidentalis* is the only species combining a distinctly thickened thallus, minutely corrugate upper surface (Fig. 2), indistinct veins, and short, unaligned rhizines. It is usually included in *P. neopolydactyla* but may be distinguished by the thicker lobes, much shorter (usually fasciculate or tapered) rhizines and less hygrophytic ecology. It is also a much more difficult species to collect intact and usually consists of broken fragments in the herbarium packet. For points of distinction with *P. neckeri*, see Table 6; see also the discussion under *P. hymenina*.

Infrequent over moss in bogs and at the margins of alpine tarns; mesophytic; global distribution unknown.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid;  $\pm$  peltidactylin, dolichorrhizin, zeorin, and one or two unidentified triterpenoids. The chemistry is similar to that reported for the type specimen (Vitikainen 1985).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Monashee Mountains, Malton Range, Kinbasket Lake, Goffinet 1521 (ALTA); Fort Nelson River Basin, Fort Nelson, Parker Lake, Goward 82-970; Fraser River Basin, Yale, Goward 83-401; Liard River Basin, Toad River, Goward 82-1117; Clearwater River Basin, Trophy Mountains, Goward 79-1145.

*Peltigera pacifica* Vitik. Ann. Bot. Fenn. 22: 294. 1985

Among the local species, the only other glabrous *Peltigera* combining a shiny upper surface with typically crisped or lobulate lobe margins (Fig. 17) are *P. elisabethae* and *P. polydactylon*. In those species, however, the veins are low and darken abruptly toward the thallus centre, whereas in *P. pacifica* the veins are distinctly raised and darken gradually. See also Tables 5 and 6.

Infrequent over soil, moss, and mossy logs in sheltered to shady forests in coastal localities at lower elevations, also rare in humid old-growth inland forests; hygrophytic; western North America (Vitikainen 1985).

CHEMISTRY: Tenuiorin, methyl gyrophorate, gyrophoric acid; peltidactylin, dolichorrhizin, and zeorin (Vitikainen 1985).

SELECTED SPECIMENS EXAMINED (all UBC): CANADA:

BRITISH COLUMBIA: Skeena River Basin, Lakelse Lake, Goward 91-1173; Burrard Inlet, Lighthouse Park, Goward 86-1; Kispiox River Basin, Kispiox, Date Creek, Goward 91-972.

*Peltigera polydactylon* (Necker) Hoffm. Descr. Pl. Cl.

Crypt. 1: 19. 1790

*Lichen polydactylon* Necker, Meth. Muscor.: 85. 1771

Syn. *Peltigera polydactyla* (Necker) Hoffm. (Vitikainen 1994)

*Peltigera polydactylon* is a glabrous species in which the lobes are small, the lobe margins crisped, the veins low and broad, the interstices oval (Fig. 6), and the rhizines unaligned. Though often confused with *P. neopolydactyla*, that species has broader noncrisped lobes, broadly raised veins, and typically lenticular interstices. For points of separation with other similar species, see Table 6.

Infrequent over soil, moss, and mossy rocks and logs in open but humid inland forests; mesophytic to weakly hygrophytic; circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; peltidactylin, dolichorrhizin, and zeorin.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Maltin Range, Kinbasket Lake, Goffinet 1537 (herb. Goffinet); Clearwater River Basin, Murtle Lake, Goward 83-824; Columbia River Basin, Revelstoke, Goward 81-1353; Similkameen River Basin, Manning Park, Mount Frosty, Goward 83-979.

*Peltigera ponojensis* Gyelnik Medd. Soc. Fauna Flora Fenn. 7: 143. 1931

Syn. *Peltigera plittii* Gyelnik, Nytt Mag. Naturvidensk. 68: 270. 1930

*Peltigera plittii* Gyelnik is an older name for *P. ponojensis* and should therefore technically have priority over it. We prefer, however, to refrain from reinstating *P. plittii* until *P. ponojensis* has been submitted for possible conservation (O. Vitikainen, unpublished proposal).

*Peltigera ponojensis* is a small, xerophytic species in which the lobe tips are upturned and the upper surface is usually densely tomentose (but see below). It has traditionally been included within *P. rufescens* (Thomson 1950) but differs from that species in having simple, typically discrete rhizines, and thicker, more ropy veins (Fig. 8) that darken only gradually, if at all, toward the thallus centre. In *P. rufescens*, the rhizines are usually confluent and mat-forming, and the veins darken abruptly. *Peltigera praetextata* is also similar but has lobulate lobe margins (check central portions of thallus), low to raised veins, and a more mesophytic ecology. For points of distinction with similar species, see Tables 3 and 4.

The upper surface in *P. ponojensis* varies in British Columbia from densely tomentose to entirely glabrous, with many specimens intermediate between these two extremes. The glabrous form has been treated by Goffinet and Hastings (1994) as a distinct species, *P. sp. 1*. Such glabrous specimens might be confused with *P. degenii* or *P. pacifica*, but in those species the lobes are membranous, the upper surface is distinctly shiny, and the ecology is hygrophytic. See also Table 6.

Frequent over soil or moss in open inland localities, especially in dry to semi-arid regions, also infrequent in exposed coastal sites in mediterranean climates; xerophytic to weakly mesophytic; circumpolar.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Thompson River Basin, Lac Le Jeune, Mount Chuwhels, Goward 81-1289b; Skagit River Basin, Manning Park, Rhododendron Flats, Goward 82-272; Kootenay River Basin, Kokanee Creek, Goward 81-1641.

*Peltigera praetextata* (Flörke ex Sommerf.) Zopf Ann. Chem. 364: 299. 1909

*Peltidea ulorrhiza* var. *praetextata* Florke ex Sommerf., Suppl. Fl. Lappon. 123. 1826

*Peltigera praetextata* has been poorly understood in North America and is often confused with other members of the *P. canina* group. No other species, however, combines upturned lobe tips with simple rhizines and marginal lobules (Fig. 16). The marginal lobules are typically sparse in the British Columbia material and are confined to the older, central portions of the thallus. Occasional specimens having erect tomentum over the rhizines or veins might be mistaken for *P. membranacea*, but this species has broader lobes, downturned lobe tips and more or less polygonal interstices. For further points of distinction, see Table 3.

Infrequent over soil, moss, and mossy rocks and logs in open or sheltered forests in humid regions at lower elevations throughout; mesophytic; circumpolar.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Selwyn Range, Kinbasket Lake, Goffinet 1272 (herb. Goffinet); Chilliwack River Basin, Chilliwack Lake, Goward 91-2159; Clearwater River Basin, Spahats Falls, Goward 91-90; Similkameen River Basin, Manning Park, Strawberry Flats, Goward 83-972.

*Peltigera retifoveata* Vitik. Ann. Bot. Fenn. 22: 296. 1985

The appressed-tomentose upper surface and broad, spongy, erect-tomentose veins are diagnostic. *Peltigera membranacea* also has erect-tomentose veins (and rhizines), but in that species the veins are distinctly narrow. See Table 3 for points of separation with other species.

Though *P. retifoveata* occurs south to northern Washington State (Goffinet 1992), this is essentially a boreal species; in the southern portion of its range it appears to be restricted to cool spruce forests at montane elevations.

Infrequent over thick moss in somewhat sheltered inland forests, especially in boreal regions at lower elevations; mesophytic; incompletely circumpolar (Vitikainen 1985; Goffinet 1992).

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid; peltidactylin, dolichorrhizin, zeorin, and one unidentified triterpenoid (trace amounts).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Fraser River Basin, Quesnel, Nazko Road, Goward 81-1533; Similkameen River Basin, Allison Lake, Goward 83-514; Nicola

River Basin, Logan Lake, Goward 84-93; Fort St. John, Horton 90 (ALTA).

*Peltigera rufescens* (Weis) Humb. Flora Friburg, 2. 1793  
*Lichen caninus* var. *rufescens* Weis, Plant Cryptogam. Flora Goett. 79. 1770

Among *Peltigera* having a tomentose upper surface, only *P. rufescens* has upturned lobe tips, confluent rhizines, and veins that darken abruptly toward the thallus centre. *Peltigera ponojensis* is similar but has discrete rhizines and roopy veins that darken only gradually, if at all, toward the thallus centre.

Included in our present circumscription of *P. rufescens* are several specimens having widely spaced veins and simple, more or less discrete rhizines. Such material may warrant separate taxonomic recognition. Further studies are in progress.

Frequent over soil (especially calcium-rich soil), moss or mossy rock in open, often somewhat exposed sites throughout; xerophytic; circumpolar.

CHEMISTRY: No lichen substances detected.

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Kootenay National Park, Fairbarns 2137 (ALTA); Clearwater River Basin, Clearwater Lake, Goward 78-210; Peace River Basin, Hudson Hope, Otto 6253; Kettle River Basin, McRae Creek, Paulson, Otto 6373.

*Peltigera scabrosa* Th. Fr., Lich. Arct. 45. 1860

*Peltigera scabrosa* can be characterized as a thick, glabrous, strongly scabrid species with an indistinctly veined lower surface, and short, fasciculate rhizines (Fig. 11) that are invariably dark. Scabrid forms of *P. neopolydactyla* are readily distinguished by the more defined veins and the simple rhizines. An earlier report of *P. scabrosa* from coastal British Columbia and Alaska (Ohlsson 1973) should be referred to *P. neopolydactyla*. For points of distinction with other scabrid species see Table 4.

In the course of our study, we identified a specimen of *P. scabrosella* Holt.-Hartw. from the Yukon (Trout Lake, south shore, north facing, alt. 500 ft, 68°30'N, 138°40'W, June 29, 1964, Lambert, UBC). This species has not previously been reported for North America. It resembles *P. scabrosa* in most details but has a pale lower surface and pale outermost rhizines (Holtan-Hartwig 1988). *Peltigera scabrosella* is expected to occur also in northern British Columbia. The chemistry of the North American specimen is identical to that reported from Europe, i.e., tenuiorin, methyl gyrophorate, gyrophoric acid, dolichorrhizin, zeorin, and two unidentified terpenoids (Holtan-Hartwig 1993).

Infrequent over moss, mossy logs, and mossy rock in somewhat open inland localities at lower elevations; mesophytic; circumpolar.

CHEMISTRY: Tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid, peltidactylin, and two unidentified triterpenoids. The material from British Columbia differs from both known European chemotypes in lacking dolichorrhizin and zeorin (Holtan-Hartwig 1993).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Clearwater River

Basin, Murtle Lake, Ahti 14342; Monashee Mountains, Malton Range, Kinbasket Lake, Goffinet 1616 (herb. Goffinet); Fort Nelson River Basin, Fort Nelson, Clark Lake, Goward 82-1057; Kicking Horse River Basin, Yoho Park, Lake O'Hara, Scotter 60065.

*Peltigera venosa* (L.) Hoffm. Descr. Adumbr. Plant Cryptogam. Lich. 1: 31. 1794

*Lichen venosus* L., Sp. Pl.: 1148. 1753

*Peltigera venosa* is a small, green, peltate lichen with highly contrastive veins. It is highly distinctive and is unlikely to be confused with any other species.

In *P. venosa*, cephalodia are located on the veins of the lower surface; under humid conditions they may become detached and develop into tiny, dark, almost black, homiomorous lobules (Ott 1988). Such lobules are frequently found growing at the base of this species in the British Columbia material; their close resemblance to *Leptogium* is interesting in light of the fact that the blue-green phototypes of other *Peltigera* species are distinctly Peltigeroid. This degree of intrageneric dimorphism in blue-green phototypes has previously been reported only in *Sticta* (see James and Henssen 1976).

Frequent over calcium-rich soil, especially cut banks, in open or somewhat sheltered sites throughout; mesophytic to hygrophytic; circumpolar.

CHEMISTRY: Green phototype: tenuiorin, methyl gyrophorate,  $\pm$  gyrophoric acid, phlebic acid B, and three to five unidentified triterpenoids. Blue-green phototype: no lichen substances detected (Tønberg and Holtan-Hartwig 1983; Goffinet and Hastings 1994).

SELECTED SPECIMENS EXAMINED (UBC unless otherwise indicated): CANADA: BRITISH COLUMBIA: Thompson River Basin, Clearwater, Brodo 27261; Clearwater River Basin, Trophy Mountains, Goward 79-1134; Top of the World Provincial Park, Home Base Campground, Vitt 31168 (ALTA).

*Peltigera* sp. 1.

Syn. *Peltigera apthosa* s.l.

The British Columbia material conforms in many regards with *P. sp. 1* of Holtan-Hartwig (1993) but differs in having continuously corticate apothecial lower surfaces and in lacking hairs over the inner portions of the upper surface. Given that three specimens of *P. sp. 1* sensu Holtan-Hartwig have been reported from Alaska (Holtan-Hartwig 1993), we prefer to leave open for the moment whether the British Columbia material may, notwithstanding the above differences, be conspecific with it.

*Peltigera* sp. 1 is a member of the *P. apthosa* group. It can be distinguished from similar species on the combined basis of the lower surface of the apothecia, which is continuously corticate, and its veins, which darken only gradually toward the thallus centre (see Fig. 18, in Goffinet and Hastings 1994). In general aspect, *P. sp. 1* is closest to *P. apthosa* s.s., but in that species the lower surface darkens abruptly toward the thallus centre.

This species is tolerant of prolonged snow cover. In inland regions it is in fact essentially restricted to localities in which snow persists for more than half the year, though along the coast it may also occur in districts that receive very

little snow. This is the only member of the *P. apthosa* group for which a blue-green phototype has not yet been reported.

Frequent over moss and mossy rocks and logs in sheltered forests, usually at higher elevations, but also rarely in seaside forests; hygrophytic; possibly western North America, eastern North America, western Eurasia.

CHEMISTRY: Tenuiorin, methyl gyrophorate, phlebic acid B, and unidentified triterpenoids.

SELECTED SPECIMENS EXAMINED (all UBC): CANADA: BRITISH COLUMBIA: Clearwater River Basin, Upper Azure River, Goward 84-1026; Cheakamus River Basin, Garibaldi Lake, Ohlsson 557; Columbia River Basin, Mount Revelstoke, Otto 3253.

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## References

- Ahti, T., and Vitikainen, O. 1977. Notes on the lichens of Newfoundland. 5. Peltigeraceae. *Ann. Bot. Fenn.* **14**: 89–94.
- Brodo, I.M., and Richardson, D.H.S. 1978. Chimeroid associations in the genus *Peltigera*. *Lichenologist*, **10**: 150–170.
- Culberson, C.F. 1972. Improved conditions and new data for the identification of lichen products by a standardized thin-layer chromatography method. *J. Chromatogr.* **72**: 113–125.
- Culberson, C.F., and Kristinsson, H. 1970. A standardized method for the identification of lichen products. *J. Chromatogr.* **46**: 85–93.
- Demarchi, D.A., Marsh, R.D., Harcombe, A.P., and Lea, E.C. 1990. The environment. In *The birds of British Columbia 1. Edited by R.W. Campbell, N.K. Dawe, I. McTaggart Cowan, J.M. Cooper, G.W. Kaiser, and M.C.E. McNall.* Royal British Columbia Museum, Victoria, B.C. pp. 55–144.
- Egan, R.S. 1987. A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. *Bryologist*, **90**: 77–173.
- Egan, R.S. 1991. Changes to the "Fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada." 3rd ed. *Bryologist*, **94**: 396–400.
- Galloway, D.J. 1991. Chemical evolution in the order Peltigerales: triterpenoids. *Symbiosis*, **11**: 327–344.
- Goffinet, B. 1992. The North American distribution of *Peltigera retifoveata* Vitik. *Evansia*, **9**: 49–51.
- Goffinet, B., and Hastings, R. 1994. The lichen genus *Peltigera* (L.) Willd. in Alberta. Provincial Museum of Alberta, Natural History. Occas. Pap. No. 21, pp. i–vi, 1–54.

- Goffinet, B., and Hastings, R. 1995. Two new sorediate taxa in *Peltigera* (Lichenized Ascomycetes). *Lichenologist*. In press.
- Goward, T., and Ahti, T. 1992. Macrolichens and their zonal distribution in Wells Gray Provincial Park and its vicinity, British Columbia, Canada. *Acta Bot. Fenn.* **147**: 1–60.
- Gyelnik, V. 1927. *Peltigera*-tanulmányok. *Peltigera-Studien*. *Bot. Kozl.* **24**: 122–140.
- Hawksworth, D.L. 1988. The variety of fungal–algal symbioses, their evolutionary significance, and the nature of lichens. *Bot. J. Linn. Soc.* **96**: 3–20.
- Holtan-Hartwig, J. 1988. Two new species of *Peltigera*. *Lichenologist*, **20**: 11–17.
- Holtan-Hartwig, J. 1993. The lichen genus *Peltigera*, exclusive of the *P. canina* group, in Norway. *Sommerfeltia*, **15**: 1–77.
- Jahns, H.M., and Frey, P. 1982. Thallus growth and development of the fruit bodies of *Peltigera canina*. *Beih. Nova Hedwigia*, **36**: 485–498.
- James, P.W., and Henssen, A. 1976. The morphological and taxonomic significance of cephalodia. In *Lichenology: progress and problems*. Edited by D.H. Brown, D.L. Hawksworth, and R.H. Bailey. Academic Press, London. pp. 27–77.
- Nicholson, D.H., and Greuter, W. 1994. Guidelines for proposals to conserve or reject names. *Taxon*, **43**: 109–112.
- Ohlsson, K. 1973. New and interesting macrolichens of British Columbia. *Bryologist*, **76**: 366–387.
- Ott, S. 1988. Photosymbiodemes and their development in *Peltigera venosa*. *Lichenologist*, **20**: 361–368.
- Poelt, J. 1972. Die taxonomische Behandlung von Artenpaaren bei den Flechten. *Bot. Not.* **125**: 77–81.
- Santesson, R. 1993. The lichens and lichenicolous fungi of Sweden and Norway. SBT-forlaget, Lund.
- Sjödín, A. 1954. Gyelnik's new lichen names. *Acta Horti Gotob.* **19**: 113–156.
- Thomson, J.W. 1948. Experiments upon the regeneration of certain species of *Peltigera*, and their relationship to the taxonomy of this genus. *Bull. Torrey Bot. Club*, **75**: 486–491.
- Thomson, J.W. 1950. The species of *Peltigera* of North America north of Mexico. *Am. Midl. Nat.* **44**: 1–68.
- Tønberg, T., and Holtan-Hartwig, J. 1983. Phycotype pairs in *Nephroma*, *Peltigera* and *Lobaria* in Norway. *Nord. J. Bot.* **3**: 681–688.
- Tuhkanen, S. 1984. A circumboreal system of climatic-phytogeographical regions. *Acta Bot. Fenn.* **127**: 1–50.
- Vitikainen, O. 1981. *Peltigera* Willd., nom.cons. In *Bestimmungsschlüssel europäischer Flechten*. Ergänzungsheft 2. Edited by J. Poelt and A. Vězda. *Bibl. Lichenol.* **16**: 236–242.
- Vitikainen, O. 1985. Three new species of *Peltigera* (lichenized Ascomycetes). *Ann. Bot. Fenn.* **22**: 291–298.
- Vitikainen, O. 1987. Distribution patterns of European *Peltigera*. *Bibl. Lichenol.* **25**: 423–426.
- Vitikainen, O. 1994. Taxonomic revision of *Peltigera* (lichenized Ascomycotina) in Europe. *Acta Bot. Fenn.* **152**: 1–96.
- Walker, F.J., and James, P.W. 1980. A revised guide to microchemical techniques for the identification of lichen products. *Bull. Br. Lichen Soc.* **46**(Suppl.): 13–49.
- Wetmore, C.M. 1960. The lichen genus *Nephroma* in North and Middle America. *Mich. State Univ. Publ. Mus. Biol. Ser.* **1**: 373–452.