A Monograph of the Lichen Genus

*Parmelia* Acharius

sensu stricto (Ascomycotina: Parmeliaceae)

*Mason E. Hale, Jr.*
Hale, Mason E., Jr. A Monograph of the Lichen Genus Parmelia Acharius sensu stricto (Ascomycotina: Parmeliaceae). Smithsonian Contributions to Botany, number 66, 55 pages, 25 figures, 1987.—The 38 species of Parmelia Acharius sensu stricto are revised at the world level. The genus is characterized by punctate or effigurate pseudocyphellae, a black lower surface with simple, fuscate or squarrose rhizines, simple hyaline spores, and cylindrical to weakly bifusiform conidia. The most frequent secondary metabolites are salazinic acid and protocetraric acid. Parmelia is an extremely conservative genus, most common in temperate-boreal and austral regions, with a low level of vegetative morph formation and speciation. The greatest concentrations of species are found in Japan and New Zealand. Seven new species are described: P. neodiscordans Hale, P. norcrambidiocarpa Hale, P. novae-zelandiae Hale, P. queenslandensis Hale, P. salcrambidiocarpa Hale, P. skultii Hale, and P. subtestacea Hale.
## Contents

<table>
<thead>
<tr>
<th>Section</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>Introduction</td>
<td>1</td>
</tr>
<tr>
<td>Acknowledgments</td>
<td>2</td>
</tr>
<tr>
<td>Cortical and Internal Structure</td>
<td>2</td>
</tr>
<tr>
<td>Vegetative Structures</td>
<td>2</td>
</tr>
<tr>
<td>Reproductive Structures</td>
<td>12</td>
</tr>
<tr>
<td>Chemistry</td>
<td>14</td>
</tr>
<tr>
<td>Chemotypes</td>
<td>14</td>
</tr>
<tr>
<td>Phytogeography</td>
<td>16</td>
</tr>
<tr>
<td>Key to the Species of Parmelia</td>
<td>16</td>
</tr>
<tr>
<td>Taxonomic Treatment</td>
<td>18</td>
</tr>
<tr>
<td>Literature Cited</td>
<td>52</td>
</tr>
<tr>
<td>Index</td>
<td>55</td>
</tr>
</tbody>
</table>
A Monograph of the Lichen Genus

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sensu stricte (Ascomycotina: Parmeliaceae)

Mason E. Hale, Jr.

Introduction

The genus *Parmelia* was proposed by Acharius in 1803. His circumscription was very broad and encompassed a large number of foliose species with lecanorine apothecia, species now recognized in such diverse genera as *Cetraria*, *Heterodermia*, *Hypogymnia*, *Lobaria*, *Pannaria*, *Parmelia* sensu lato, *Parmeliella*, *Parmeliopsis*, *Physcia*, *Physconia*, and *Xanthoria*. Early 19th century authors continued to use the name in this broad sense for almost any lichen with a thalline apothecial rim, from *Lecanora* to *Usnea*.

By the end of the 19th century *Parmelia* had begun to assume its more modern and familiar circumscription as a foliose rhizinate genus with laminal apothecia and simple spores (Fries, 1871–1874). At the same time, recognizing clear morphological discontinuities, lichenologists began to describe a number of segregate genera. Early ones, with their dates of publication, included *Menegazzia* Massalongo (1854), *Parmotrema* Massalongo (1860), *Anzia* Stizenberger (1861), *Parmeliopsis* (Nylander) Nylander (1896), *Hypogymnia* (Nylander) Nylander (1896), *Pseudevernia* Zopf (1903), *Pannoparmelia* (Müller Argoviensis) Darbishire (1912), and *Pseudoparmelia* Lynge (1914). Of these genera only *Anzia* and *Parmeliopsis* were ultimately adopted by Zahlbruckner in his catalogue (1929), the others being synonymized under *Parmelia*. However, since 1950, many workers have adopted *Hypogymnia*, *Menegazzia*, *Pannoparmelia*, and *Pseudevernia*.


A second group consists of the pseudocyphellate species of *Parmelia* (Hale, 1975, 1976a, 1981). This group has been further subdivided into *Flavopunctelia* (Krog) Hale (the *P. flaventior* group) (Hale, 1980, 1984), *Melanelia* Esslinger (the brown *Parmeliae*) (Esslinger, 1978), and *Punctelia* Krog (Krog, 1982) (the *P. borreri* group), now leaving in *Parmelia* a small, apparently irreducible assemblage of 38 species typified by *P. saxatilis*.

The following characters may be used to delimit *Parmelia*: adnate, sublinear to subirregular lobes without cilia; upper surface effigurate-pseudo-cyphellate, less commonly punctate-pseudocyphellate (in three Asian species); lower surface black, rhizinate, the rhizines simple, furcate, or squarrosely branched; microconidia cylindrical or weakly bifusiform, less than 8.0 μm long; spores simple, 8 per ascus. Chemically it is distinguished by the presence of atranorin and chloroatranorin and lack of usnic acid in the cortex. The closest relative in the family is *Punctelia*, which Krog (1982) characterizes by punctate pseudocyphellae and cylindrical, filiform, or unciniform microconidia. I am excluding from *Punctelia* and *Parmelia* the unique usnic acid-containing American endemic *P. sphaerosporella* Müller Argoviensis, now recognized as the monotypic genus *Ahtiana* Goward (Goward, 1985), closer to *Cetraria* Acharius than to *Parmelia*.

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ACKNOWLEDGMENTS.—I am indebted to Dr. Ove Almborn for reviewing the nomenclature and providing valuable notes on citations and literature. I have also benefited from discussions with Trevor Goward, Dr. J.A. Elix, and Dr. H. Skult. Lastly I must give thanks to the curators of the museums and institutions who sent loans of types and other specimens.

Cortical and Internal Structure

*Parmelia* has a typical paraplectenchymatous cortex (Hale, 1973, 1981). It consists of densely packed cells forming a layer 4–6 cells thick (20–30 μm). Anglesea et al. (1982) recently discovered a technique of digesting the intracellular polysaccharides, giving new insights into cortical organization. The cortical layer consists of densely packed hyphae that branch in a coralloid pattern, forming 3–5 short branches lying in the same plane. The lower cortex is thinner, less than 20 μm thick. The algal layer and the medulla occupy 100–200 μm of the total thallus thickness.

The upper cortex of *Parmelia* species is perforated by pseudocyphellae. These pores originate as the cortex disintegrates to form a narrow tube about 10 μm in diameter, which enlarges and becomes filled with medullary hyphae (Figure 1a) (Hale, 1981). This structure is quite different from the epicortex, which is a pored polysaccharide sheet overlaying a more or less loosely packed, continuous palisade parenchymatous layer (Hale, 1973, 1981). These two structures differ considerably in size: pseudocyphellae are essentially macroscopic and visible with low power magnification (0.1–2 mm long), but the pores in the epicortex can be seen only with SEM, being of the order of 15–40 μm in diameter.

Each species of *Parmelia* has a characteristic orientation of pseudocyphellae as illustrated in Figures 2–8. The most frequent type appears as an irregular effigurate white marking under low power. These so-called maculate markings are marginal and laminal and often fuse into a loose reticulate network as they grow beyond 1 mm in length (Figure 1c). At maturity the cortex tends to crack open along the pseudocyphellae, which may then serve as points of origin for isidia and soredia.

Under SEM the maculate appearance can be explained as a thin persistent, densely pored polysaccharide layer acting as a roof over the disintegrating pore area below. This layer is part of the polysaccharide layer covering the rest of the surface. This roof may persist (Figure 1d) or soon disintegrate, leaving an open pore (Figure 1b) (see Hale (1981) for additional figures).

Pseudocyphellae may also originate exclusively along the lobe margins, just back from the edge. In these cases they form a continuous white line, a rim around the lobes, as in *P. neodiscordans, P. nitiakana* (Figure 1e), *P. pseudoshinanoana, P. sectilis, P. shinanoana, P. ricasolioides*, and in part *P. cochleata, P. crambidiocarpa, P. norcrambidiocarpa, P. salcrambidiocarpa, P. subestacea, and P. testacea*, and some narrow-lobed forms of *P. discordans* and *P. omphalodes*, and in *P. skultii*.

Two Asian species, *P. meiophora* and *P. submutata*, are distinctive in having very small effigurate pseudocyphellae not much more than 0.1–0.2 mm in size (Figure 1b), so small that neither Hue, Nylander, nor Zahlbruckner noticed them when describing the species involved. As far as I can tell, they are identical in origin with the larger pseudocyphellae described above.

A third type of pseudocyphellae is characteristic of a small group of three Asian species, *P. istidoiclada, P. laevior, and P. pseudolaevior*. The pores form along the lobe edge as round, widely spaced, and rather inconspicuous white spots (Figure 1f). These pores do not have the persistent roof of other pseudocyphellae in the genus and in fact appear to be identical with the punctiform pores of *Punctelia*. The lobe surface itself is continuous and has neither pseudocyphellae nor reticulated markings. These species are placed more appropriately in *Parmelia* rather than *Punctelia*, because of the presence of salazinic acid and the furcate to squarrosely branched rhizines.

Vegetative Structures

Most *Parmelia* species have rather narrow, sublinear, adnate lobes. They grow on rocks and trees in forested areas and on rocks and humus or mosses in arctic-alpine areas, forming adnate colonies 4–20 cm broad (up to 60 cm in *P. tenuirima*). All of the species are whitish or greenish mineral gray but some, such as *P. discordans, P. omphalodes, P. signifera, and P. skultii*, have a tendency to turn brown to nearly black in exposed habitats.

SURFACE FEATURES.—The surface features of several *Parmelia* species have been studied by Hale (1973) using the scanning electron microscope (SEM). The genus is characterized by a smooth and featureless or nodular surface, typical of lichens with a paraplectenchymatous cortex (Figure 9a).

Many species have a hoary white pruina on the surface. Under SEM this pruina is revealed as masses of crystals. I have not investigated the chemical composition of these crystals, but they are reported to consist of oxalates (Wilson et al., 1980), often weddelite (calcium oxalate tetragonal dihydrate) (CaC₂O₄(2+x).H₂O), and less commonly whewellite (calcium oxalate monohydrate, CaC₂O₄·H₂O) (Jackson, 1981; Wadsten and Moberg, 1985).

The crystals fall into three general shapes: bi-pyramidal weddelite (*P. cochleata, P. cunninghamii, P. fraudans* (Figure 9c), *P. kerguelensis, P. meliophora, P. omphalodes, P. pseudoshinanoana, P. saxatilis, P. sulcata, P. squarrosa, P. testacea* (Figure 9b)); cubic or parallelepipeds shapes, also probably weddelite (*P. cunninghamii, P. hygrophila* (Figure 9d), *P. protosulcata, and P. sulcata* (Figure 9f)); and flat hexagons of whewellite (*P. dauguescens, P. discordans, P. erumpens, P. fraudans* (Figure 9e), *P. isidioclada, P. kerguelensis, P. novae-zelandiae, P. pseudoshinanoana, P. saxatilis, P. tenuirima*). There seems to be little if any
Figure 1.—Pseudocyphellae in Parmelia: a, pore in upper cortex of *P. adnugescens* (Lai 7809); b, pseudocyphellae of *P. submutata* (Poelt L-142); c, pseudocyphellae of *P. marmariza* (Kurokawa 63056); d, pseudocyphellae of *P. marmariza* to show pored “roof” (Kurokawa 63056); e, submarginal pseudocyphellae of *P. nitakana* (Hsu 1374); f, marginal pseudocyphellae of *P. laevior* (Kurokawa 58255).
Figure 2.—Orientation of pseudocyphellae in Parmelia species: a, P. adaugescens (Asahina s.n.); b, P. cochleata (isolate type in US); c, P. crambidiocarpa (Hale, 65541); d, P. cunninghamii (Santesson 6792); e, P. discordans (Issin s.n.); f, P. erumpens (Hale 43876). (All ×8.5.)
FIGURE 3.—Orientation of pseudocyphellae in Parmelia species: a, P. fertilis (Tagawa s.n.); b, P. fraudans (Hale 49870); c, P. kyrophila (Noble 6448); d, P. isidioclada (Kurokawa 58010); e, P. kerguelensis (Harris 5670); f, P. laevior (Cutberson 11104). (All ×8.5.)
Figure 4.—Orientation of pseudocyphellae in Parmelia species: a, *P. marmoriza* (Kurokawa 58062); b, *P. meiophora* (Poelt L-151); c, *P. neodiscordans* (holotype in US); d, *P. niitakana* (Hsu 1374); e, *P. norcrambiocarpa* (holotype in US); f, *P. novae-zelandiae* (Hale 66232). (All x8.5.)
FIGURE 5.—Orientation of pseudocyphellae in Parmelia species: a, P. omphalodes (Santesson 12918); b, P. protosulcata (Santesson 2953); c, P. pseudolaevior (Kurokawa 59205); d, P. pseudoshinanoana (Kurokawa 59206); e, P. pseudoimmaculata (Hale 58276); f, P. queenslandensis (holotype in US). (All ×8.5.)
Figure 6.—Orientation of pseudocyphellae in Parmelia species: a, *P. ricasolioides* (isotype of *P. daliensis* in US); b, *P. salcbambidiocarpa* (holotype in US); c, *P. saxatilsis* (Hale 48453); d, *P. sectilis* (holotype in US); e, *P. shinanoana* (isolectotype in US); f, *P. signifera* (Hale 66435). (All ×8.5.)
Figure 7.—Orientation of pseudocyphellae in Parmelia species: 
a. P. skultii (holotype in US); b. P. squarrosa (Hale 18170); c. P. submontana (Vidad 845); d. P. submutata (Poelt L-142); e. P. subtestacea (Hale 58771); 
f. P. sulcata (Kjellman 8s.n.). (All >8.5.)
correlation with taxonomic features. For example, the crystal shapes of two specimens of *P. fraudans* (Figure 9c,e), are significantly different, whereas common *P. sulcata* shows three types among five specimens examined (three flat and one each pyramidal and cubic). It is obvious that many more specimens will have to be examined with SEM before any definite conclusion can be reached on the usefulness of crystal shape in taxonomy.

The lower surface of all species of *Parmelia* is black and more or less continuously vested with rhizines. Broader-lobed species such as *P. tenuirima* may also have a rather conspicuous brown, bare to papillate marginal zone. The rhizines are black and shiny, 0.5-2 mm long, and either simple to sparsely furcate (Figure 10a,b), simple with a few weakly squarrosely branched (Figure 10c), or mostly strongly squarrosely branched (Figure 10d). The following species have simple to furcate rhizines: *P. adaugescens* (Figure 10a), *P. coehleata, P. discordans, P. fraudans, P. hygrophila, P. isidioclada, P. marmariza* (Figure 10b), *P. neodiscordans, P. niiakana, P. omphalodes, P. pseudolaevior, P. saxatilis, P. sectilis, P. shinanoana, P. skultii, and *P. submontana*. The following species have simple rhizines and at least some (often densely) squarrosely branched: *P. cunninghamii, P. erumpens, P. ferilis, P. kerguelensis, P. laevior, P. meiophora, P. norcrambidioicarpa, P. novae-zelandiae, P. protosulcata, P. pseudoshinanoana, P. pseudotenuirima, P. queenslandensis, P. ricasolioides, P. salcrambidioicarpa, P. signifera, P. squarrosa, P. submutata, P. sulcata* (Figure 10c), *P. subtestacea, P. tenuirima* (Figure 10d), and *P. testacea*.

Soredia.—Soredia appear to originate from pseudocryptocallae in most species and become aggregated into orbicular or linear soralia. In *P. cunninghamii* they originate from marginal fissures not associated with pseudocryptocallae, as well as from laminal pseudocryptocallae. They are predominantly marginal in *P. cunninghamii, P. fraudans* (Figure 11a), and *P. protosulcata; laminal and marginal in P. sulcata* (Figure 11b); and mostly laminal in *P. submontana. Parmelia erumpens* is unique in having mostly laminal pustular soralia.

Isidia.—Although isidia are one of the most easily recognized vegetative propagules in lichens, their origin, development, and structure are not well known. The few SEM pictures published to date (see Hale, 1975, 1976b, for *Hypotrachyna* and 1976a for *Parmelina*) show in general a clearly defined radial structure. There is a more or less continuous polysaccharide layer over the surface, a rather loosely organized paraplectenchymatous cortical layer 20-30 μm thick, which is continuous with the thallus cortex at the base. The interior is filled with loose medullary hyphae, the algae occupying the periphery (Figure 11f).

Five species of *Parmelia* have typical shiny, corticate cylindrical isidia: *P. kerguelensis* (Figure 11c,e), *P. novae-zelandiae, P. pseudotenuirima, P. saxatilis,* and *P. squarrosa*. The isidia of *P. meiophora* are rather short and basally constricted (Figure 10d) in comparison with the other isidiate species. In *P. isidioclada* the isidia become densely coralloid branched and subsorediate. In *P. hygrophila* the isidia are initially corticate but appear to break down apically at maturity, becoming scurfy or subsorediate, an appearance that is enhanced by the dense production of pruina on the isidia.

Lobules.—Lobules in *Parmelia* are dorsiventral and usually originate along lobe margins; they are very narrow, suberect, and almost isidia-like in appearance. There are three lobulate species here in a strict definition: *P. pseudolaevior, P. pseudoshinanoana,* and *P. sectilis. Parmelia pseudolaevior* seems to be a well-matched morph of non-lobulate *P. laevior; P. pseudoshinanoana* differs from its presumptive parent *P. shinanoana* in lacking gyrophoric acid in the cortex. *Parmelia sectilis* has no extant parent morph.

*Parmelia discordans, P. neodiscordans,* and *P. omphalodes* often produce lobulate morphotypes, although these lobules...
Figure 9.—Surface features in Parmelia: a, surface of *P. squarrosa* (Hale 18922, x425); b, pruina of *P. testacea* (Hale 58741); c, pruina of *P. fraudans* (Hale 36414); d, pruina of *P. hygrophila* (Noble, 6448); e, pruina of *P. fraudans* (Hale, s.n.); f, pruina of *P. sulcata* (Wetmore 38229).
may be better defined as narrow secondary laciniæ. *Parmelia subtestacea* and *P. testacea* often have roundish marginal lobulate secondary lobes. In these cases the lobules should be considered as secondary lobes.

**Reproductive Structures**

**Pycnidia.**—Vobis (1980) discussed the ontogeny and morphology of pycnidia in many different lichens, but he did not include in his study any species of *Parmelia* sensu stricto. However, he studied *Melanelia acetabulum* (Necker) Esslinger, which has *Umbilicaria*-type ontogeny and Type IV conidiophores, characteristic features of the family Parmeliaceae and apparently encompassing *Parmelia*.

Pycnidia are typically immersed and laminal (Figure 4e), 90–110 μm in diameter, with a tendency to group toward the lobe margins in some species. They have been observed in most species but not in *P. hygrophila*, *P. isidioclada*, *P. kerguelensis*, *P. meiophora*, *P. novae-zelandiae*, *P. protosulcata*, *P. pseudolaevior*, *P. pseudoshinanoana*, *P. shinanoana*, and *P. submontana*. Most of these species are isidiate or sorediate and often lack apothecia.

The first lichenologist to examine pycnidia and conidia carefully was Lindsay (1859). By today’s standards his drawings are rather crude and difficult to interpret. Even with better techniques, however, Hillmann (1936), Krog (1982), and other workers who have examined *Parmelia* species have not been able to describe the conidia of the genus with absolute clarity. Vague and often conflicting descriptions range from cylindrical and straight to somewhat bent or subbifusiform to bifusiform.

It is indeed extremely difficult to see lichen conidia clearly.
FIGURE 11.—Soredia and isidia of Parmelia: a, soralia of P. fraudans (Hale 36414); b, soralia of P. sulcata (Hale 14415); c, isidia of P. kerguelensis (Brodo 11506); d, isidia of P. meiophora (Togashi s.n.); e, isidium of P. kerguelensis (Brodo 11506); f, longitudinal cross section of isidium of P. saxatilis (Hale 36387).
with an ordinary light microscope. One should ideally use oil immersion, but even then some of the best photographs are rather fuzzy (Vobis, 1980). Enhancement with Nomarski lenses or phase contrast can improve clarity of images but the results are still far from perfect. In my own studies I have mounted freehand sections of pycnidia in glycerin-water and observed the conidia released under a Nomarski microscope.

The conidia of *Parmelia* fall within a very narrow range of length and shape (Figure 12). They are either uniformly cylindrical, straight to slightly bent, slightly inflated at the center, or slightly bifusiform. The only species with strongly, unmistakably bifusiform conidia is *P. signifera*. Most conidia are between 5 and 7 μm long, and only in *P. adaugescens*, *P. laevior*, *P. marmoriza*, *P. omphalodes*, *P. submutata*, and *P. sulcata* do they reach 8.0 μm. There is no dimorphism such as has been reported for *Punctelia* (Culberson and Culberson, 1980; Krog, 1982).

**APOTHECIA.**—Henssen (1981) includes the Parmeliaceae among families in the Lecanorales with zonaria apothecia. I have not investigated the ontogeny of apothecia in *Parmelia* but assume it follows a pattern similar to that reported by Henssen for *Melanelia exasperata* (De Notaris) Esslinger.

Mature apothecia are usually substipitate and may be rather large, up to 20 mm, as the disc flattens out and splits radially. The amphithecium is well developed, pseudocyphellate, and rugose or even sublobulate with age. The hymenium, which stains deep blue with IKI, is 50–90 μm high. The asci are almost always 8-spored (Krog, 1951), though they may be 10- to 12-spored and vary in size classes with relatively little overlap. One sharply defined dimorphism such as has been reported for *Punctelia* (Culberson and Culberson, 1980; Krog, 1982).

**Chemistry**

When first studied systematically with microcrystal tests (Krog, 1951), *Parmelia* was thought to produce atranorin in the cortex and only two major medullary substances, salazinic acid and protocetraric acid, with accessory lobaric acid and protolichesterinic acid. Although these depsidones do indeed predominate as secondary metabolites, a number of additional products have been identified with thin layer chromatography and more will probably be discovered. The genus has a distinct chemical profile, with predominantly β-orcinol depsidones, there being no representatives of the para- and meta-depsides (barbatic acid and lecanoric acid groups) in the medulla.

The question of "chemical species" arises in *Parmelia* as it does in most Parmelioid groups. Lichenologists have still not agreed on the proper treatment of chemical variation, even though it is a fundamental species character in many other fungal groups. An overview by Hawksworth (1976) is the most recent summary of this topic. An objective solution to
Figure 12.—Conidia of Parmelia species: a, P. cochleata (isolate type in US); b, P. cunninghamii (Santesson 7814); c, P. discordans (Kellman s.n.); d, P. testacea (James 561); e, P. erumpens (Hale 43657); f, P. marmorea (Nakanishi 2011); g, P. omphalodes (Hale 18851); h, P. saxatilis (Hale 49288); i, P. sulcata (Hale 49675a). (Scale in i = 10 μm.)
this controversial problem will probably not be reached until more experiments, such as those begun by C.F. Culberson (Culberson and Ahmadjian, 1980), are completed.

Ultimately some “chemical species” will be found on closer study to have subtle morphological differences, obviating any decision as to their validity. Others will stand as good species, especially when strong correlating geographical or habitat differences are found. Finally some will be rejected as ever more refined analytical tests show them to be artifacts of earlier, imperfect tests, which were incapable of detecting minor metabolities (Elix, 1982). Another obstacle to an orderly solution is that very few “chemical species” have been adequately sampled and studied in the field.

There are several species pairs in Parmelia that may be considered nearly identical except for chemistry and which I am recognizing at the species level in this monograph. The best known pair is *P. omphalodes* (salazinic acid) and *P. discords* (protocetraric acid). Although these are broadly sympatric, Skult (1984) found that *P. discords* is more strongly oceanic in distribution. A second pair is isidiate *P. saxatilis* (protocetraric acid), which is mostly saxicolous and boreal, and *P. kerguelensis* (protocetraric acid), which is corticolous in North America and mainly saxicolous in South Africa. A third pair is *P. norcrambidiocarpa* (echinocarpic acid) and *P. salcrambidiocarpa* (salazinic acid), which are allopatric in Australia and New Zealand. Similar chemical variation is used in part to separate *P. testacea* (salazinic acid and unknown #27) and *P. subtestacea* (echinocarpic acid and unknown #27). On the other hand, I am not recognizing the protocetraric acid chemotype of Australian *P. signifera* (unnamed), because there are too few collections available to make a decision.

**Phytogeography**

*Parmelia* behaves as a typical boreal-temperate genus in North America and Europe. It is a small, well collected group of 9 species familiar to all lichenologists. Africa has a very small *Parmelia* flora with no endemic species. Eastern Asia has been the most important center of evolution for the genus. Japan alone has at least 12 species, and Asia as a whole 17, 10 of them endemics. Three species, *P. meiophora*, *P. ricasolioides*, and *P. submutata*, seem to have originated in the mountains of southern China.

*Parmelia* has also evolved extensively in Australasia, where 14 species have been found. Twelve of these, *P. crambidiocarpa*, *P. cunninghamii* and *P. protosulcata* (both also in austral South America), *P. norcrambidiocarpa*, *P. novae-celandiae*, *P. pseudotenuirima*, *P. queenslandensis*, *P. salcrambidiocarpa*, *P. signifera*, *P. subtestacea*, *P. tenuirima*, and *P. testacea*, occur only in the southern hemisphere. The remaining two, *P. kerguelensis* and *P. sulcata*, occur in both hemispheres.

The 38 species of *Parmelia* are distributed as follows in the major geopolitical units of the world:

**NORTH AMERICA**
- Canada: *P. fertilis*, *P. fraudans*, *P. hygrophiila*, *P. kerguelensis*, *P. omphalodes*, *P. saxatilis*, *P. skultii*, *P. squarrosa*, *P. sulcata*
- USA: *P. discordans*, *P. fraudans*, *P. hygrophiila*, *P. kerguelensis*, *P. neodiscordans*, *P. omphalodes*, *P. saxatilis*, *P. skultii*, *P. squarrosa*, *P. sulcata*

**SOUTH AMERICA**
- Argentina: *P. cunninghamii*, *P. protosulcata*, *P. saxatilis*, *P. sulcata*
- Chile: *P. cunninghamii*, *P. protosulcata*, *P. saxatilis*, *P. sulcata*
- Falkland (Malvinas) Islands: *P. cunninghamii*, *P. saxatilis*, *P. sulcata*

**EUROPE**
- Greenland/Iceland: *P. fraudans*, *P. omphalodes*, *P. saxatilis*, *P. sulcata*
- Europe (including Turkey): *P. discordans*, *P. fraudans*, *P. omphalodes*, *P. saxatilis*, *P. skultii*, *P. submutata*, *P. sulcata*

**AFRICA**
- Tunisia: *P. submutata*
- East Africa (Ethiopia, Kenya): *P. saxatilis*, *P. sulcata*
- South Africa: *P. erumpens*, *P. kerguelensis*

**ASIA**
- Japan: *P. adaugescens*, *P. cockleata*, *P. erumpens*, *P. fertilis*, *P. isidiocladia*, *P. laevior*, *P. marmariza*, *P. pseudolaevis*, *P. pseudoshinanoana*, *P. shinanoana*, *P. squarrosa*, *P. sulcata*
- Korea: *P. cockleata*, *P. fertilis*, *P. squarrosa*
- Mongolia: *P. cockleata*, *P. omphalodes*
- China: *P. fertilis*, *P. laevior*, *P. marmariza*, *P. meiophora*, *P. ricasolioides*, *P. squarrosa*, *P. submutata*, *P. sulcata*
- Himalayan region (northern India, Nepal, Sikkim, Pakistan): *P. adaugescens*, *P. marmariza*, *P. meiophora*, *P. omphalodes*, *P. ricasolioides*, *P. squarrosa*, *P. submutata*, *P. sulcata*
- Southern India: *P. erumpens*

**SOUTHEAST ASIA**
- Taiwan: *P. adaugescens*, *P. erumpens*, *P. fertilis*, *P. laevior*, *P. marmariza*, *P. niitakana*, *P. submutata*
- Philippines: *P. isidiocladia*, *P. sectilia*
- Sabah: *P. erumpens*, *P. sectilia*
- Indonesia: *P. erumpens*

**AUSTRALASIA**
- Australia: *P. cunninghamii*, *P. erumpens*, *P. norcrambidiocarpa*, *P. pseudotenuirima*, *P. queenslandensis*, *P. salcrambidiocarpa*, *P. signifera*, *P. sulcata*, *P. tenuirima*, *P. testacea*
- New Zealand: *P. crambidiocarpa*, *P. cunninghamii*, *P. kerguelensis*, *P. norcrambidiocarpa*, *P. novae-celandiae*, *P. protosulcata*, *P. salcrambidiocarpa*, *P. saxatilis*, *P. signifera*, *P. subtestacea*, *P. sulcata*, *P. tenuirima*, *P. testacea*

**Key to the Species of Parmelia**

1. Thallus with powdery, granular, pubescent or subisidiate soredia (under high magnification the isidia-like soredia of *P. fraudans* and *P. isidiocladia* may be mistaken for true isidia).
2. Pseudocyphellae punctiform, occurring only on lobe edges ......................................................... *P. isidiocladia*
2. Pseudocyphellae predominantly effigurate, on lobe surface and/or margins.

16 **SMITHSONIAN CONTRIBUTIONS TO BOTANY**
3. Soredia pustular, mostly laminal; cortex deeply fissured .............................. \( P. \) erumpens  
3. Soredia powdery, marginal or along ridges on surface; cortex not deeply cracked.  
4. Medulla K- (protocetraric acid) .............................. \( P. \) protosulcata  
4. Medulla K+ yellow turning red (salazinic acid).  
5. Soralia mostly laminal along ridges.  
6. Rhizines strongly squarrosely branched; pantemperate-panboreal ........................ \( P. \) sulcata  
6. Rhizines simple; Mediterranean region .............................. \( P. \) submontana  
5. Soralia mostly marginal.  
7. Soredia yellowish; boreal regions .............................. \( P. \) fraudans  
7. Soredia greenish or whitish gray; austral regions .............................. \( P. \) cunninghamii

1. Thallus lacking soredia.  
8. Thallus with dense suberect, marginal (or in part laminal) dorsiventral lobules or isidiate lobules.  
9. Pseudocyphellae round, punctiform, only on lobe edges .............................. \( P. \) pseudolaevior  
10. Pseudocyphellae conspicuous as a broad white rim; Japan ........................ \( P. \) pseudoshinanoana  
10. Pseudocyphellae inconspicuous; southeastern Asia .............................. \( P. \) sectilis

8. Thallus without conspicuous suberect lobules (\( P. \) discordans, \( P. \) neodiscordans, \( P. \) omphalodes, \( P. \) subtestacea, and \( P. \) testacea may have dense appressed secondary lobules); if isidiate, the isidia mostly laminal.  
11. Thallus isidiate.  
12. Medulla K- (protocetraric acid) .............................. \( P. \) kerguelensis  
12. Medulla K+ yellow turning red (salazinic acid).  
13. Isidia produced only along lobe margins .............................. \( P. \) isidioclada  
13. Isidia produced mostly on lobe surface or along ridges on lobe surface.  
14. Upper surface finely white-maculate pseudocyphellate, the pseudocyphellae less than 0.5 mm long; China and Taiwan .............................. \( P. \) metaphora  
14. Upper surface with larger effigurate pseudocyphellae more than 0.5 mm long.  
15. Isidia dull, decomposing and becoming subsorediate; Pacific Northwest .............................. \( P. \) hygrophiila  
15. Isidia usually shiny, corticate, not becoming sorediate.  
16. Thallus small, 3–5 cm broad, closely attached; isidia very dense; Australia .............................. \( P. \) pseudotenuirima  
16. Thallus larger, 5–20 cm broad, adnate to loosely attached; not occurring in Australia.  
17. Lobes broad and apically rotund, 4–10 mm wide .............................. \( P. \) novae-zelandiae  
17. Lobes narrower, sublinear, 1–5 mm wide.  
18. Rhizines simple to furcate .............................. \( P. \) saxatilis  
18. Rhizines squarrosely branched .............................. \( P. \) saxatilis

11. Thallus lacking isidia.  
19. Medulla K- (fumarprotocetraric acid, protocetraric acid or unknown \#27).  
20. Thallus corticolous; New Zealand.  
21. Lobes subirregular, contiguous; pseudocyphellae mostly marginal ........................ \( P. \) subtestacea (chemotype)  
21. Lobes sublinear, separate; pseudocyphellae mostly laminal .............................. \( P. \) crambiidiocarpa  
20. Thallus saxicolous; Europe and North America.  
22. Fumarprotocetraric acid present; North America .............................. \( P. \) neodiscordans  
22. Protocetraric acid present; Europe .............................. \( P. \) discordans

19. Medulla K+ yellow or yellow turning red (salazinic acid or echinocarpic acid).  
23. Pseudocyphellae punctate, on lobe edges .............................. \( P. \) laevior  
23. Pseudocyphellae effigurate, laminal and/or marginal.  
24. Pseudocyphellae marginal as a white rim around lobes; Japan and East Asia only.  
25. Saxicolous; cortex C+ rose (gyrophoric acid) .............................. \( P. \) shinanoana  
25. Corticulous; cortex C- (atranorin only).  
26. Lobes subirregular, apically rotund; Japan .............................. \( P. \) cochleata  
26. Lobes sublinear, apically obtuse; Taiwan .............................. \( P. \) niitakana  
24. Pseudocyphellae laminal and marginal, not forming a conspicuous marginal rim (except in \( P. \) subtestacea and \( P. \) testacea from New Zealand).  
27. Rhizines squarrosely branched.  
28. Pseudocyphellae less than 0.3 mm long, appearing as fine white maculae; Taiwan and China .............................. \( P. \) submutata
28. Pseudocyphellae distinct, effigurate, up to 1 mm long.
29. Lobes broad and round, to 10 mm wide; pseudocyphellae separate, laminal ... P. tenuirima
29. Lobes sublinear, 1–5 mm wide; pseudocyphellae marginal and/or laminal, often fusing.
30. Lobes subirregular; pseudocyphellae mostly marginal.
  31. Salazinic acid present ....................................... P. testacea
  32. Echinocarpic acid present ...................................... P. subtestacea
30. Lobes sublinear; pseudocyphellae mostly laminal.
  32. Collected in Japan, East Asia and Canada ...................... P. fertilis
32. Collected in Australasia.
  33. Echinocarpic acid present.
  34. Spores more than 16 μm long .................................. P. crambiociarpa
  34. Spores less than 16 μm long ................................. P. norcrambiociarpa
33. Salazinic acid present.
35. Rhizines forming a dense, projecting mat; lobes sublinear, separate; Tasmania and New Zealand ....................... P. salcrambiociarpa
35. Rhizines sparse to moderate, not projecting; lobes sublinear but short and crowded; Queensland and northern N.S.W., Australia .... P. queenslandensis
36. Pseudocyphellae mostly laminal.
  37. Apothecia numerous, to 2 mm in diameter; Himalayan region .......... P. ricasolioides
  37. Apothecia, if present, larger, to 15 mm in diameter; boreal areas or New Zealand.
  38. Thallus greenish mineral gray; Australasia .................... P. signifera
  39. Salazinic acid present ......................................... P. testacea
  40. Echinocarpic acid present ...................................... P. subtestacea
  38. Thallus whitish to brownish gray or blackening; boreal regions.
  40. Salazinic acid present (without norstictic acid) .............. P. omphalodes
  41. Salazinic and norstictic acids present ........................ P. skultii
36. Pseudocyphellae mostly laminal.
  41. Collected on rocks or soil; thallus often turning brownish.
  42. Pseudocyphellae laminal; upper surface becoming fissured; Australasia ... P. signifera
  42. Pseudocyphellae laminal and marginal; upper surface continuous; boreal regions .............................................. P. omphalodes
  41. Collected on trees; thallus greenish or whitish mineral gray.
  43. Pseudocyphellae separate, less than 0.5 mm long ................ P. marmoriza
  43. Pseudocyphellae separate or fusing into a network, to 1 mm long.
  44. Collected in Australasia (see 32).
  44. Collected in Japan and eastern Asia.
  45. Upper surface conspicuously cracked with age; pseudocyphellae mostly laminal .............................................. P. adaugescens
  45. Upper surface not cracking conspicuously; pseudocyphellae marginal, forming a nearly continuous rim.
  46. Spores about 30 μm long; Taiwan ............................. P. niitakana
  46. Spores about 15 μm long; Japan, East Asia .................. P. cochleata

**Taxonomic Treatment**

The 38 species of *Parmelia* are arranged below in alphabetical order. Locations of specimens cited in synonymies and “Specimen Examined” sections are indicated by standard herbarium acronyms.

*Parmelia*

*Parmelia* Acharius, 1803:153 [nomen conservandum].

*Lichen* L., 1753:1140. [Lectotype species: *Lichen saxatilis* L.]

*Aspidelia* Stirton, 1900:81. [Lectotype species *Aspidelia hecketii* Stirton (= *Parmelia tenuirima*, see Culberson, 1966).]

**Description.**—Thallus foliose, 4–60 cm broad, greenish to whitish mineral gray; lobes sublinear to more rarely subirregular, 1.5–10 mm wide; upper surface plane to foveolate, isidiate, sorediate, or lacking soredia and isidia, pseudocyphellate; the pseudocyphellae usually effigurate, rarely punctiform; lower surface black, moderately to densely rhizinate, the rhizines simple, furcate or squarrosely branched. Pycnidia common, immersed, laminal; conidia cylindrical to slightly...
bifusiform, straight or slightly bent, 5.5–8.0 μm long. Apothecia adnate to substipitate, 1–20 mm in diameter, the disc pale brown, the amphithecium usually pseudocyphellate; spores 8/ascus, simple, colorless, 3–18 × 6–33 μm long, the episporium 1–4 μm thick.

**Chemistry.**—Atranorin and chloroatranorin (rarely gyrophoric acid) in the cortex: salazinic acid, consalazinic acid, protocetraric acid, fumarprotocetraric acid, echinocarpic acid, or unidentified substances and as accessory or trace substances conechinocarpic acid, galbinic acid, lobaric acid, norstictic acid, protolichesterinic or related fatty acids, or stictic acid in the medulla.

**Parmelia adaugescens**

*Figures 2a, 13a*

*Parmelia adaugescens* Nylander, 1890:28. [Type collection: Ichigome, Japan, Almqvist (H, NyL herb. no. 34876, lectotype).]

*Parmelia pseudomarmariza* Awasthi, 1976:186. [Type collection: Mervakhola Valley, Nepal, Awasthi 2305 (AWAS).]

**Description.**—Thallus adnate on bark, rather firm, 8–15 cm broad, greenish to whitish mineral gray (brownish in the herbarium); lobes sublinear, long, contiguous, 2–5 mm wide; upper surface shiny, plane, rugose-foveolate with age, transversely cracked in older parts, pseudocyphellae effigurate, conspicuous, 0.5–1.5 mm long, marginal and laminal, mostly separate or forming a loose network; lower surface black, densely rhizinate, the rhizines simple to furcate or dichotomously branched, 1–2 mm long. Pycnidia common but poorly developed; conidia cylindrical, straight, 7–8 μm long. Apothecia common, substipitate, urceolate and inrolled when young, 4–8 mm in diameter, the amphitheicum rugose, pseudocyphellate; hymenium 65–70 μm; spores 13–15 × 21–27 μm, the episporium distinct, 2–3 μm thick.

**Chemistry.**—Atranorin and salazinic acid (Asahina, 1951b) and consalazinic acid.

**Remarks.**—This widespread Asian species is characterized by the large spores and large, uniformly dispersed pseudocyphellae. It is most common in Japan and Taiwan but extends as far west as Pakistan in Asia. It seems rather isolated from other large-spired species such as *P. isidioclada* and *P. sectilis*, which have different orientation of the pseudocyphellae. There is some intergradation with *P. cochleata*, which has small spores, as well as with *P. fertilis*, which also has small spores and richly branched rhizines.

*Parmelia pseudomarmariza*, described from Nepal, has similarly large spores and slightly smaller but comparable pseudocyphellae. It does not seem sufficiently different from *P. adaugescens* to be kept as a distinct species.

**Specimens Examined**

Pakistan: Iqbal 742 (US). Sikkim: Hara et al. s.n. (TNS, US). India: West Bengal, Hara et al. s.n. (TNS, US). China: Prov. Heilong, Takahashi 2928 (TNS). Japan: Prov. Awa, Fujikawa (TNS); Prov. Inaba, Nakamichi 24 (TNS); Prov. Ishikari, Asahina s.n. (TNS); Prov. Iwayama, Kurokawa 58169 (TNS, US); Prov. Iyo, Nakatsiki 56 (US); Prov. Kii, Numajiri s.n. (TNS); Prov. Kozu, Asahina s.n. (TNS); Prov. Musashi, Asahina s.n. (TNS); Prov. Mutsu, Hale 29301, 29302, 29306, 29312, 29355 (US); Prov. Shimotsuke, Kurokawa 56530A (TNS); Prov. Tosa, Fujikawa s.n. (TNS); Taiwan: Kurokawa 1209 (TNS, US); Misoli County, Lat 6874, 7795, 7809, 7813 (US); Nantou County, Suzuki 1001 (US); Taichung County, Lat 6874, 6875 (US).

**Parmelia cochleata**

*Figures 2b, 13b*

*Parmelia cochleata* Zahlbruckner, 1927b:350. [Type collection: Mt. Fuji, Japan, Asahina 27 (W, holotype; TNS, US, isotypes).]

*Parmelia marmariza* var. *physcioides* Zahlbruckner, 1927b:352. [Type collection: Mt. Buko, Musashi, Japan, Asahina 24 (W, holotype, TNS, isotype).]

*Parmelia pseudosaxatifilis* Asahina, 1951b:354. [Type collection: based on *P. marmariza* var. *physcioides* Zahlbruckner.]

**Description.**—Thallus loosely adnate on bark, firm, greenish mineral gray, 6–20 cm broad; lobes sublinear to subirregular, crowded, 1–5 mm wide, the margins lobulate, lobules round, 1–2 mm wide, more or less concave or hood-shaped, becoming suberect; upper surface plane to very weakly foveolate, continuous, shiny, becoming pruinose at the lobe tips, pseudocyphellae marginal, forming a nearly continuous narrow white rim, only sparsely developed on the lobe surface, separate; lower surface black, moderately to densely rhizinate, the rhizines simple to furcate, 1–2 mm long. Pycnidia numerous; conidia (Figure 12a) cylindrical to weakly bifusiform, slightly bent, 5.5–7.0 μm long. Apothecia numerous, substipitate, 3–8 mm in diameter, the rim somewhat inrolled, finely crenate, the amphitheicum sparsely pseudocyphellate; hymenium 60–70 μm; spores poorly developed, about 6 × 10 μm, the episporium 1 μm thick (Asahina reports 6–8 × 12–13 μm in type description).

**Chemistry.**—Atranorin and salazinic acid (consalazinic acid lacking). Protolichesterinic acid also reported by Kurokawa and Nakaniishi (1971) in 2 of 5 specimens tested.

**Remarks.**—*Parmelia cochleata* is widespread but not especially common in Japan. In the typical form it has strongly cochleate lobes but at other times the lobes are quite flat and appressed and the species lacks other distinguishing features except the generally marginal pseudocyphellae, similar to those in *P. rudior* and *P. testacea* from New Zealand.

**Specimens Examined**

Korea: Kimura s.n. (TNS). Japan: Prov. Buzen, Kurokawa 62481 (TNS); Prov. Inaba, Ikoma 2179 (TNS); Nakaniishi 12167 (KOBE); Prov. Iyo, Ogiya 159 (TNS); Prov. Kii, Kurokawa 60235, Numajiri 24 (TNS); Prov. Musashi, Kurokawa 64288 (TNS); Prov. Shinano, Hiratsuka s.n. (TNS); Prov. Sunaga, Asahina 27 (TNS); Prov. Tottori, Nakaniishi 51 (TNS). Golubkova (1981) reports the species from Mongolia.
Figure 13.—Species of Parmelia: a, P. adaugescens (lectotype in H); b, P. cochleata (type of P. marmoriza var. physcioides Zahlbruckner in W); c, P. crambidiocarpa (lectotype in W); d, P. cunninghamii (Santesson 6790); e, P. discordans (Laurila in Lichenes Fennici Exsiccati 195); f, P. erwnpens (Hale 59471). (Scales in mm.)
Parmelia crambidiocarpa

DESCRIPTION.—Thallus adnate to loosely adnate on bark, firm, whitish or pale greenish gray, 6–15 cm broad; lobes sublinear, often little branched, subdivaricate, browning at the tips, 1–4 mm wide; upper surface shiny, continuous or cracking transversely with age, plane, pseudocyphellae forming an irregular but nearly continuous rim around the lobe margins, tips, 14 mm wide; upper surface shiny, continuous or cracking transversely with age, plane, pseudocyphellae forming an irregular but nearly continuous rim around the lobe margins, tips, 14 mm wide; upper surface shiny, continuous or cracking transversely with age, plane, pseudocyphellae forming an irregular but nearly continuous rim around the lobe margins.

Chemistry.—Atranorin, chloroatranorin, and protocetraric acid or echinocarpic acid (and associated unknowns) or protocetraric and echinocarpic acids together in nearly equal concentration.

REMARKS.—Parmelia crambidiocarpa is a member of the P. testacea complex, closely related to P. norcrambidiocarpa and P. salcrambidiocarpa. Although Galloway and Elix (1983) synonymized it with P. testacea, I have concluded from my own field studies in New Zealand that it is a distinct species, separated by a series of highly correlated morphological and chemical characters.

The morphological characters are quite distinctive. The thallus is typically loosely adnate, rather large, and with narrow, sublinear lobes. The pseudocyphellae are both marginal and laminal and usually fissure with age. The rhizines form a dense mat below and often project out from the margins. The apothecia tend to be strongly stipitate and nearly urceolate, although very large apothecia become flattened and radially split. Disc color ranges from very pale tan (11% of 37 fertile specimens examined) to light brown (59%) or very dark brown (30%).

The spores of P. crambidiocarpa are consistently large. The average maximum length is 18.4 μm (range 15–21 μm) and width 11.4 μm (9–12 μm) (29 measurements). The episporium is about 2 μm thick. For the other two externally similar species in this group, P. norcrambidiocarpa and P. salcrambidiocarpa, spores do not exceed 15 μm in length and the episporium is only 1–1.5 μm thick.

The chemistry is also distinctive. The type specimen from the Dawson Falls area at Mt. Egmont contains a mixture of echinocarpic and protocetraric acids. I visited this locality and made a random sample of 69 specimens in the subalpine scrub zone at 1000–1200 m elevation. The sample consisted of 39% with echinocarpic and protocetraric acids, 45% with echinocarpic acid (and associated unknowns)—although traces of protocetraric acid might have been missed on the TLC plates—and 16% with protocetraric acid alone. Unknown #27, so typical of the P. testacea group, was not detected in any specimens.

Taking the whole range of P. crambidiocarpa, one finds a complex pattern for combinations of the acids. At Tongariro National Park, another isolated volcanic peak about 150 km east of Mt. Egmont, specimens with protocetraric acid alone made up an overwhelming 98% of the population (54 specimens tested), the remainder containing both echinocarpic and protocetraric acids. A similar proportion appears to hold for the Urewera area farther to the east although the sample size (5) is too small to be sure. On the South Island, where the species is far less abundant and largely replaced by P. norcrambidiocarpa, all specimens (21 tested) contained protocetraric acid except for one collection in beech forest near Tuatapere and one (sterile) from Lewis Pass with both echinocarpic and protocetraric acids present.

Parmelia crambidiocarpa has strong ecological requirements. On North Island of New Zealand it is abundantly developed—and in fact the only member of the P. testacea group except for rare P. salcrambidiocarpa—at 1000–1300 m elevation in the subalpine zone on a variety of trees and shrubs (Nothofagus, Dracophyllum, Nothopanax, Pseudopanax, etc.). I did not collect it below 600 m elevation. On South Island it occurs above 600 m in the highest passes but also grows near sea level at high latitudes in the extreme south, where it occurs with P. norcrambidiocarpa (Figure 14). In random samples made at 71 localities in New Zealand, I collected 149 specimens (23%) of P. crambidiocarpa out of a total of 715 collections in the P. testacea complex. A similar percentage (17% or 14 of 88 collections) was found in the herbarium collections at CHR.

Representative Specimens Examined
(protocetraric acid)

New Zealand: North Island, Elix 8195, 8208 (ANUC), Hale 65108, 65527, 65572 (US), Hayward H1112.70 (US), South Island, Elix 7702 (ANUC), 8527 (CHR), Hale 65146, 65236, 65497, 65782 (US), Imshaug 47879, 55985 (MSC), Molloy CHR266952 (CHR).

Representative Specimens Examined
(echinocarpic acid)

New Zealand: North Island, Davey CHR160226 (CHR), Hale 65296, 65533 (US).
Figure 14.—Distribution of Parmelia crambidiocarpa in New Zealand.
Representative Specimens Examined (echinocarpic and protocetraric acids)

New Zealand: North Island, Hale 65279, 65537, 65783 (US); South Island, Eliz 7507 (CHR), Hale 65779 (US).

Parmelia cunninghamii

Figs. 2d, 13d

Parmelia cunninghamii Cbrontie, 1876:228. [Type collection: Island Harbou, Falkland Islands, 18 April 1868, Cunningham (BM, lectotype; H, isotype).]

Description. — Thallus adnate on bark, more rarely on rocks, very firm, pale greenish to brownish mineral gray, 8–12 cm broad; lobes subirregular, apically subrotund, contiguous, usually turning up at the margins, 3–7 mm wide; upper surface shiny, becoming white pruinose at the tips, plane to rugose-foveolate with age, reticulately fissured only in older parts, sorediate, the soralia linear along the margins, orbicular when laminar, pseudocyphellate effigurate, 0.3–1 mm long, rather sparsely developed to well developed, marginal and laminar, separate, sinuous; lower surface black, moderately to densely rhizinate, the rhizines simple to squarely branched, 1–2 mm long. Pycnidia rare, marginal; conidia (Figure 12b) cylindrical, straight to slightly bent, 5.5–7.0 μm long. Apothecia rare, substipitate, 4–15 mm in diameter, the amphitheicum arugose, pseudocyphellate, the disc brown; hymenium 65–70 μm; spores 8–9 × 10–12 μm, the episporium 1 μm thick.

Chemistry. — Atranorin and chloroauanorin, salazinic acid (Galloway and Elix, 1983), consalazinic acid, and accessory lobaric acid.

Remarks. — This widespread austral species can be recognized by the firm, shiny thallus and well-developed marginal soralia. It differs from closely related P. sulcata, with which it occurs in austral regions, in several respects. For example, the surface is not strongly foveolate-ridged, the soralia are chiefly marginal, and the rhizines are not so densely squarely branched. Parmelia protosulcata, a narrow-lobed species with protocetraric acid, has sparser, often orbicular soralia. When these are better developed they become linear and approach P. cunninghamii very closely.

Parmelia cunninghamii is preeminently a species of the moist forests of austral South America and New Zealand. Farther west in Australia it occurs in temperate rain forest.

Specimens Examined

Argentina: Prov. Chubut, Lamb 5860 (US); Cerro Mayo, James 1644 (BM); SW Patagonia, James 579 (BM); Tierra del Fuego, Saniesson 1145 (S, US). Falkland Islands: Imhaug 40162 (US). Chile: Prov. Chiloé, Redon 03575 (US); Prov. Malleco, Ejerdam 10860 (CLO, US), Mahu 2537 (US); Terr. Magallanes, Imhaug 44566 (MSC), Saniesson 7814 (US), 8012, 8188 (S); Tierra del Fuego, Saniesson 5910, 6003, 6792, 7385, 7396 (S, US), 5812, 6005, 7497 (S); Valdivia, Mahu 1699 (US). New Zealand: Antipodes Island, Du Rietz 2598 (US); South Island Fiord District, Du Rietz 1856a (US, US); South Island—Eastern Botany District, Du Rietz 1462 (US, US); Otago, James 611/2 (BM), Martin 1116 (BM), Murray 1273 (BM), James 1623 (BM, US), Thomson 2136 (CHR), Canterbury, Elix 8570 (CHR), Galloway s. n. (CHR), Tihell 9223, 9439, 9682 (US); Auckland Islands, Imhaug 56283 (MSC), James 1345 (BM), 1378 (FH, US). Australia: New South Wales, Hale 66605 (US), South Australia, Elix 4901 (ANUC); Tasmania, Elix 5593 (ANUC); Victoria, Bastow (US), Elix 57 (ANUC), James Au2136, Au2138 (BM); Marion Island, Huntley 971 (US).
**Parmelia discordans** appears to be a relatively rare species in Europe, at least in comparison with *P. omphalodes*. Degelius (1931, 1944), however, found it to be more common on the basis of a KOH test in Ångermanland and Gotland, Sweden, and in Westland, Norway (1934). Skult (1984) collected it intensively in Finland, where it behaves as an oceanic species in the southwestern part of the country.

**Specimens Examined**

Europe. Great Britain: Scotland, Denison 251, Dixon, s.n. (US). Finland: Satakunta, Lauria in Lichenes Fenniae Exsiccati 195 (US); Sweden: Bohuslän, Magnusson in Lichenes Selecti Exsiccati 106 (FLAS) and Kryptogamae Exsiccatae 2571 (US); Småland, Zetterstedt s.n. (US); Västmanland, Kjellmert s.n. (US); Västergötland, Magnusson, in Lichenes Selecti Exsiccati 106 (US). Belgium: Prov. Luxembourg, Lamberon in Vézda, Lichenes Selecti Exsiccati 916 (US); France: Sarthe, Mouguillon in des Abbayes, Lichenes Gallici s.n. (US); Spain: Asturias, Vasquez s.n. (US).

**Parmelia erumpens**

**Figures 2f, 15f, 15**

*Parmelia erumpens* Kurokawa, 1969, no. 74. [Based on *Parmelia tenuirima* f. corallina Müller Argoviensis.]

*Parmelia tenuirima* f. corallina Müller Argoviensis, 1883:46. [Type collection: Oppland, Austria, Stirling s.n. (G, lectotype; UPS, US, isotype).]

**Description.**—Thallus adnate to loosely adnate on rocks and trees, fairly firm, pale greenish to whitish mineral gray, 8–20 cm broad; lobes short, subirregular to apically rounded, imbricate, 2–8 mm wide; upper surface shiny, plane, soon becoming conspicuously reticulately cracked, pseudocyphellae effigurate, 0.2–1 mm long, somewhat raised, dense, fusing into a reticulate network over the whole surface, sorediate, the soredia coarse and isidioid, often bursting apically, forming dense marginal and laminal soralia; lower surface black, densely rhizinate, the rhizines simple or squarrosely branched at maturity, 1–2 mm long. Pycnidia rather rare; conidia (Figure 12e) cylindrical to weakly bifusiform, straight, 5.5–7.0 μm long. Apothecia rare, stipitate, the rim inrolled but the disc flattening and splitting radially at maturity, 4–15 mm in diameter, the amphitheciurn reticulately cracked, pseudocyphellate, sorediate; hymenium 65–70 μm; spores 6–8 × 10–12 μm, the episporium 1 μm thick.

**Chemistry.**—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983), and consalazinic acid.

**Remarks.**—This is one of the more widespread Asian-African species (Figure 15), easily recognized by the deeply reticulately fissured cortex and abundant coarse pustular isidia. In Australia it is collected most commonly on sandstone outcrops in sclerophyll forests but in other areas it is usually corticolous. In India, for example, it occurs at 1400–2200 m elevation in open montane forests. In New Zealand it grows in mature, moist Nothofagus forests, and in South Africa it is found in the wet coastal forests in the Tsitsikama area. It seems to lack any recognizable parent morph, although *P. signifera* would have to be considered very closely related. *Parmelia signifera* has larger spores (13–15 μm) and greater chemical variation. Another parent morph proposed by Galloway and Elix (1983), *P. tenuirima*, is a much larger lichen with separate pseudocyphellae and larger spores (12–15 μm long).

**Specimens Examined**

Australia: Lord Howe Island, Watts (US); Australian Capital Territory, Streinmann 4452, 7893 (US); New South Wales, Cheel and Borman 1045 (BM, US), Craigie L1692 (NSW), Degelius A-77 (US), Du Rietz 60a, 546th (UPS, US), Flockton 725 (US), Hale 38450, 58835, 59011, 59257, 59262, 59471 (US), Kurokawa 5151, 6542 (TNS, US), Sayer L1720 (NSW), Streinmann 9518 (US), Weber and McVean L47307, L49615, L49912 (US); Victoria, Hale 58254, 28258 (US), Streinmann 2355 (US); Western Australia, Weber L50111 (COLO, US). New Zealand: North Island, Galloway s.n. (CHR), Hale 59503, 59499 (US), James 111 (BM, US), Tibe! 13203 (UPS); South Island, Hale 66234 (US). South Africa: Cape Province, Hale 72001, 72002 (US). India: Tamil Nadu, Hale 40245, 40250, 45378, 45657, 43813, 43815, 43876 (US), Sabah: Hale 29017 (US). Kurokawa (1969) has published additional records from Japan, Taiwan, and Indonesia.

**Parmelia fertilis**

**Figures 3a, 16a**

*Parmelia fertilis* Müller Argoviensis, 1887:316. [Type collection: Siberia, USSR, comm. Lahm, no. 7 (G, lectotype).]

*Parmelia subdivaricata* Asahina, 1951b:356. [Type collection: Mt. Aisan, Nimandaira, Taiwan, Asahina F:71 (TNS, lectotype).]

**Description.**—Thallus adnate on bark, firm, pale greenish to whitish mineral gray, 6–12 cm broad; lobes sublinear, fairly long and divaricate to contiguous (shorter and more adnate in Canadian specimens), 1.5–5 mm wide; upper surface plane to weakly foveolate, transversely cracked with age, pseudocyphellae effigurate, conspicuous, 0.5–1 mm long, marginal and laminal, sometimes forming a discontinuous white rim, fusing with age to form a coarse reticulate network; lower surface black, densely rhizinate, the rhizines simple or densely squarrosely branched, 0.5–2 mm long. Pycnidia common; conidia cylindrical to weakly bifusiform, straight to slightly bent, 5.5–6.5 μm long. Apothecia common, substipitate, the rim inrolled, 2–7 mm in diameter, the disc dark brown, the amphitheciurn finely reticulate-pseudocyphellate; hymenium 55–60 μm; spores usually lacking or very poorly developed, 6–8 × 12–14 μm, the episporium 1 μm thick.

**Chemistry.**—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983), and consalazinic acid.

**Remarks.**—Asahina (1951b) described this as a new species, *P. subdivaricata*, unaware that Müller Argoviensis had earlier published *P. fertilis* on the basis of a single rather poor specimen from Siberia. He noted the squarrosely branched rhizines, an important diagnostic character for the species. Asahina found bifusiform conidia, but material that I have examined has mostly cylindrical ones.

*Parmelia fertilis* is very common in Japan on maples, oaks, and other trees in open forests along with its probable isidiate morphotype *P. squarrosa*. The probable sorediate morphotype...
is *P. sulcata*, a very rare species in the range of *P. fertilis*, which differs in having larger microconidia (6–8 μm long).

Sharon Gowan and colleagues recently discovered the species in New Brunswick and Nova Scotia, where it is rare. The specimens are more crowded and adnate than the Japanese material but spore size and rhizine branching are identical.

**Specimens Examined**

Canada: New Brunswick, Gowan 3332-4 (CAN, US). Korea: Chosen, Asahina s.n. (TNS), Fujikawa (TNS). Japan: Prov. Awa, Fujikawa (TNS); Prov. Bingo, Sato 60 (TNS); Prov. Bungo, Kurokawa 62356 (TNS), 63194 in *Lichenes Critici et Selecti* 27 (US); Prov. Buzen, Asahina s.n. (TNS); Prov. Etchu, Nishijima 18 (TNS); Prov. Hoki, Asahina s.n. (TNS); Prov. Inaba, Nakanishi 12076 (KOBE); Prov. Ishikawa, Endo 216 (TNS); Prov. Kurokawa 56183 (TNS), 78009 in *Lichenes Selecti et Critici* 426 (US); Prov. Iyo, Nakanishi 90 (KOBE), Yanagisawa 1484 (TNS), Kurokawa 60050 in *Lichenes Rariores Critici Exsiccati* 85 (as *P. subdivaricata*) (US); Prov. Kii, Numajiri s.n. (TNS); Prov. Mutsu, Asahina 46 (TNS), Hale 29333, 29342 (US), Kurokawa 56218 (TNS); Prov. Nihon, Nakanishi B92 (KOBE), Prov. Sagami, Kurokawa 58050 (US); Prov. Shimosuki, Hale 63138 (US), Ogata 1815 (TNS); Saghalin, Asahina s.n. (TNS); Prov. Yamato, Tagawa s.n. (US). Taiwan: Chia-yi County, Kopenen 17314 (US); Taichung County, Lai 6866 (US); Taitung, Kurokawa 2586 (US). Zhao et al. (1982) reported it from Anhui, Chekiang, and Kiangsi provinces in China (as *P. subdivaricata*).

**Parmelia fraudans**

**Figures 36, 16b**

*Parmelia saxatilis* (L.) Acharius *fraudans* Nylander, 1861:100. [Type collection: Savolaxia, Finland, Nylander (II, Nyl. Herb. no. 34869, lectotype. A syntype (Malmgren: Kajana) was not located at II.]

*Parmelia fraudans* (Nylander) Nylander, 1890:28.

**Description.**—Thallus adnate on rock, rather brittle, greenish to brownish mineral gray with a yellowish cast, 8–16 cm broad; lobes sublinear, short, contiguous to imbricate, 1–4 mm wide; upper surface shiny or dull and white pruinose, plane to rugose-foveolate, transversely cracked with age, pseudocyphellae effigurate, small, to 0.5 mm long, mostly marginal and soon becoming densely sorediate, the soralia sinuous along lobe margins with a few isolated orbicular laminal soralia, the soredia coarse to almost subisidiose at maturity; lower surface dark brown and shiny at the margin, black at the center, densely rhizinate, the rhizines simple to furcate, 1–1.5 mm long. Pycnidia rather rare and often poorly developed; conidia oicylindrical to weakly bitusiform, straight to slightly bent, 5.5–6.5 μm long. Apothecia rare, adnate, 2–3 mm in diameter; hymenium 45 μm; spores 5–6 × 10–12 μm, the episporium 1 μm thick.
FIGURE 16.—Species of Parmelia: a, P. fertilis (Hale 29333); b, P. fraudans (Hale 49870); c, P. hygrophiola (Noble 6448); d, P. usidioclada (Kurokawa 58010); e, P. kerguelensis (lectotype in BM); f, P. kerguelensis (Brodo 11506). (Scales in mm.)
Parmelia hygrophila

**Figures 3c, 16c**

*Parmelia hygrophila* Goward and Ahl, 1983:9. [Type collections: 17 km E of Nelson, Kokanee Creek Park, BC, Canada, Goward 81-1601 (UBC, holotype; US, isotype).]

**Description.**—Thallus adnate on bark, whitish gray, often becoming densely pruinose, 4–10 cm in diameter; lobes sublinear, 3–5 mm wide; surface plane to weakly ridged, pseudocyphellae effigurate, 0.1–0.3 mm long, forming a network in the marginal area, erupting at maturity with the formation of coarse, granular, subsorediate isidia, the isidia very weakly corticate with pale tips, densely clumped and growing along the length of the lobes, to 1 mm high, apically crumbling and subsorediate with age; upper surface plane, shiny, continuous; lower surface brown to whitish in a narrow marginal zone, black at the center, densely rhizinate, the rhizines simple to sparsely fertile, 1–1.5 mm long. Pycnidia not seen. Apothecia rare, substipitate, less than 5 mm wide; hymenium about 60 μm high; spores 13–16 × 23–30 μm (from description of *P. psoromoides*).

**Chemistry.**—Atranorin and salazinic acid (Asahina, 1951a; Krog, 1968). This rare, montane-tropical, temperate species appears to be related too *P. laevior* because of the lateral punctate pseudocyphellae. It is unusual, however, in having very large spores, as well as marginal granular isidia.

**Specimens Examined**


Parmelia isidioclada

**Figures 3d, 16d**

*Parmelia isidioclada* Vainio, 1921:48. [Type collection: Prov. Mimasaka, Japan, Yasuda 210 (TUR, lectotype).]

**Description.**—Thallus loosely adnate on bark or rock, rather firm, greenish mineral gray (turning brownish in the herbarium), 8–12 cm broad; lobes sublinear, elongate, contiguous, 2–4 mm wide, the margins rolled upward, punctate-pseudocyphellate along the edges, the pseudocyphellae soon becoming granular and giving rise to dense, branched, cylindrical to somewhat lobulate, eventually coralloid-isidioid growths along the length of the lobes, to 1 mm high, apically crumbling and subsorediate with age; upper surface plane, shiny, continuous; lower surface brown to whitish in a narrow marginal zone, black at the center, densely rhizinate, the rhizines simple to fertile, 1–1.5 mm long. Pycnidia not seen. Apothecia rare, substipitate, less than 5 mm wide; hymenium about 60 μm high; spores 13–16 × 23–30 μm (from description of *P. psoromoides*).

**Chemistry.**—Atranorin and salazinic acid (Asahina, 1951a; Krog, 1968) and consalazinic acid.

**Remarks.**—This rare, montane-tropical, temperate species appears to be related too *P. laevior* because of the lateral punctate pseudocyphellae. It is unusual, however, in having very large spores, as well as marginal granular isidia.

**Specimens Examined**


Parmelia kerguelensis

**Figures 3e, 16e-f**

*Parmelia kerguelensis* Wilson, 1900:87. [Type collection: Royal Sound, Kerguelen Island, Robert Hall s.n. (MEL, lectotype).]

**Description.**—Thallus adnate to loosely adnate on bark or rock, fairly firm, greenish to light brownish mineral gray, 6–10 cm broad; lobes sublinear, contiguous, sometimes short and more crowded, 1–2.5 mm wide, brownish towards the tips, at times white pruinose; upper surface dull, plane to weakly foveolate, continuous but becoming fissured with age, pseudocyphellae irregularly effigurate, 0.2–0.5 mm long, sparse and inconspicuous to fairly well developed, marginal and laminal, isidiate, the isidia developing mostly on the surface, scattered initially but at maturity clumped along faint ridges, cylindrical, little branched, 0.04–0.06 × 0.1–0.3 mm; lower surface black, moderately rhizinate, the rhizines simple...
Parmelia laevior

Parmelia

Parmelia onfakensir

Parmelia laevior

Parmelia laevior

Parmelia long. Pycnidia not seen. Apothecia rare, substipitate, 10-15 mm in diameter, flat with a radially split disc at maturity; hymenium 65-70 μm; spores 9-12 × 14-18 μm, the episporium 1-2 μm wide.

Chemistry.—Atranorin, protocetraric acid, and lobaric acid.

Remarks.—Parmelia kerguelensis has the same northern hemisphere-southern hemisphere distribution pattern as P. saxatilis and P. sulcata but is much less common. It is the only Parmelia species in South Africa. In the northern hemisphere it is known only from the moist coastal forests of the Pacific Northwest, where it was first recognized as P. pseudosulcata by Geylriik. Although the specific epithet implies a close relationship with sorediate Parmelia, this species is actually very close to P. saxatilis, as both have mostly simple rhizines and isidia. Without careful examination, in fact, P. kerguelensis would be identified as P. saxatilis. Aside from the clear chemical distinction (K- in the medulla), it lacks the conspicuous reticulate network of pseudocyphellae on the lobe surfaces and has a tendency for squarrose rhizines. In Canada at least P. kerguelensis is found on tree bark, P. saxatilis on rocks, a basic habitat difference. In South Africa, however, where trees are rare, it is found on sheltered sandstone outcrops as well as on trees in forested areas.

Specimens Examined


**Parmelia laevior**

**FIGURES 3f, 17a**

*Parmelia laevior* Nylander, 1890:28. [Type collection: Ichigome, Japan, Ainaqist s.n. (H, Nyl. herb. no. 34857, lectotype; S, isotype).]

*Parmelia laevior f. denigrata* Hue, 1839:166. [Type collection: Onikobe, Japan, Faurie 305 (PC, lectotype).]

*Parmelia petrophila* Vainio, 1921:48. [Type collection: Prov. Kii, Japan, Yasuda 193 (TUR, Vain. herb. no. 2933, isotype).]

*Parmelia hakonensis* Zahlbruckner, 1927b:348. [Type collection: Hakone, Prov. Sagami, Japan, Yamashita 13 (TNS, isotype).]


*Parmelia ontakensis* Asahina, 1954:323. [Type collection: Mt. Ontake, Hidaguchi 6-gome, Prov. Hida, Japan, Asahina 54819 (TNS, lectotype; US, isotype).]

Description.—Thallus loosely adnate on bark, firm, pule greenish to brownish mineral gray, 6-15 cm broad; lobes subirregular to sublinear, rather short, contiguous, 2-8 mm wide; upper surface shiny, plane to weakly foveolate, continuous, black-rimmed, coarsely lobulate with age, pseudocyphellae effigurate, raised, small, 0.2-0.5 mm long, numerous and conspicuous, marginal and laminal, in part fusing into a weak reticulate network; lower surface black, densely rhizinate, the rhizines simple to fuscate, 1-2 mm long. Pycnidia common; conidia cylindrical, straight to slightly bent, 6-8 μm long. Apothecia common stipitate and urceolate, flaring at maturity with an open, radially split disc, 5-10 mm in diameter, the rim and paraphyses warty pseudocyphellate; hymenium 60-65 μm; spores 8-9 × 14-16 μm, the episporium distinct, about 1 μm thick.

Chemistry.—Atranorin, salazinic acid (Asahina, 1951a), and consalazinic acid.

Remarks.—The most important feature of this Asian species...
FIGURE 17.—Species of Parmelia: a, P. laevior (Hale 29357); b, P. marmariza (lectotype in H); c, P. meiophora (Poelt L-151); d, P. neodiscordans (holotype in US); e, P. niitakana (Hsu 1374); f, P. norcrambidio-carpa (holotype in US). (Scales in mm.)
is the distinct and numerous but comparatively small and crowded pseudocyphellae. This is in contrast to the larger, less numerous pseudocyphellae of \textit{P. adaugelescens}, another common Asian species, with mostly simple rhizines but much larger spores.

Asahina described \textit{P. submarmariza} to accommodate some specimens with smaller spores (8–11 \(\mu\)m long)—in my opinion not significantly smaller—and a less strongly rugose amphitheicum.

**Specimens Examined**

Japan: Prov. Awa, \textit{Fujikawa} s.n. (TNS); Prov. Higo, \textit{Kurokawa} 63120 (TNS); Hiroshima Pref., \textit{M. Nakanishi} 2811 (US); Prov. Hitzen, \textit{Kurokawa} 62597 (TNS); Prov. Inaba, \textit{Nakanishi} 12157 (KOB); Prov. Iyo, \textit{Ogata}, s.n. (TNS), \textit{Nakanishi} 72 (KOB); \textit{Yoshimura} 1675 (US); Prov. Izu, \textit{Asahina} 30825 (TNS), \textit{Kurokawa} 57038 (US); Prov. Ki, \textit{Kurokawa} 71099 in \textit{Lichenes Critici Selecti Exsiccati} 234 (US); Prov. Kozuke, \textit{Kurokawa} 55480 (US); Prov. Ohsumi, \textit{Kurokawa} 63056 in \textit{Lichenes Critici Selecti Exsiccati} 29 (TNS, US); Prov. Sagami, \textit{Kurokawa} 58062 (US); Prov. SuPruga, \textit{Asahina} 538 (US); \textit{Yakushima, Fujikawa} s.n. (TNS); Prov. Yamato, \textit{Nakanishi} 50 (KOBE).


**Parmelia meiophora**

**FIGURES 4b, 17c**

\textit{Parmelia meiophora} Nylander, 1889:45. [Type collection: Song-pin, Yunnan, China, \textit{Delavay} s.n. (I, \textit{Nyl. Herb. no. 35201, lectotype; US, W, isoleto-types.}]

\textit{Parmelia meiophora} var. \textit{iudicata} \textit{Chao} [\textit{Zhao}], 1964:156. [Type collection: Yunnan, China, \textit{Chao} 1002 (not seen).]

**DESCRIPTION.**—Thallus loosely adnate on bark, firm, greenish mineral gray (turning brownish in the herbarium), 8–15 cm broad; lobes subirregular, contiguous to imbricate, 3–5 mm wide; upper surface shiny, plane, continuously and finely cracked with age, pseudocyphellae numerous and small, 0.2–0.3 mm long, separate, isidiate, the isidia bulbate, short, about 0.1 mm thick and 0.1–0.2 mm high, unbranched, the tips often darkening; lower surface black, densely rhizinate, the rhizines richly squamously branched, 1–2 mm long. Pycnidia not found. Apothecia rare, adnate, 3–5 mm in diameter; hymenium 55–60 \(\mu\)m; spores 5–6 \(\times\) 7–8 \(\mu\)m, the episporium 1 \(\mu\)m thick.

**CHEMISTRY.**—Atranorin and salazinic acid (Misra et al., 1976) and consalazinic acid.

**REMARKS.**—\textit{Parmelia meiophora} is unquestionably the isidiate morphotype of \textit{P. submutata}. Together they make up an anomalous element in the genus, because of the numerous small pseudocyphellae, too small to be seen with the naked eye. In his original description Nylander did not mention the presence of pseudocyphellae at all.

Very little is known of the habitat and ecology of the species, except to note that it occurs at high elevation (3000–4000 m) in conifer-Rhododendron cloud forests.
Philippine species *Pseudocyphellae*. It is also characterized by the large spores

Taiwan: Hattsukan, Kurokawa 1211 (US).

Mountains above 3000 m high.

It occurs at high elevations in Taiwan, probably on most major

amphithecium rugose-sublobulate with pseudocyphellae on the

well depicted by Asahina. It is most closely related to the

CmmsmY.-Atranorin and salazinic acid (Asahina, 1951a) and consalazinic acid.

REMrws.-This Taiwan endemic has lobes with a conspic-

uous white marginal rim formed by the continuous linear pseudocyphellae. It is also characterized by the large spores and the curiously sublobulate ridging on the amphithecium so well depicted by Asahina. It is most closely related to the Philippine species *P. sectilis* because of the very large spores. It occurs at high elevations in Taiwan, probably on most major mountains above 3000 m high.

Specimens Examined

Taiwan: Hattsukan, Suzuki s.n. (TNS), Chiayi County, Hsu 1374 (US), Mt. Nan-Fu-Ta-San, Kurokawa 1211 (US).

**Parmelia norcrambidiocarpa** Hale, new species

**DESCRIPTION.**—Thallus ut in *P. crambidiocarpa* sed sporis parvis (6–8 × 11–13 um) differt.

Thallus adnate to loosely attached on bark, fairly firm, whitish gray, 6–12 cm broad; lobes subirregular to sublinear, little branched, becoming divaricate, browning at the tips, 1–4 mm wide; upper surface shiny, continuous to transversely cracked with age, plane, pseudocyphellae forming a very narrow, nearly continuous marginal rim, 0.1–0.2 mm wide, also laminal and effigurate, 0.2–0.6 mm long, separate, fissuring with age; lower surface densely rhizinate, the rhizines simple to strongly squarrosely branched, 0.5–2 mm long, usually projecting as a mat around the lobe margins. Pycnidia common, 90–110 μm in diameter; conidia cylindrical, rod-shaped, 5.5–6.0 μm long. Apothecia common, stipitate and cupuliform, splitting radially with age, to 20 mm in diameter, the disc brown to dark brown, the amphithecium rugose, effigurate-pseudocyphellate; hymenium 60–70 μm high; spores 7–10 × 10–15 μm, the episporium 1 μm thick.

**CHEMISTRY.**—Atranorin and chloroatranorin, and echinocarpic acid (and associated unknowns).

**HOLOTYPE.**—St. James Walkway, Tarn Nature Trail, Lewis Pass road, South Island, New Zealand, elev. 850 m, M.E. Hale 65352 (US; isotypes in ANUC, BM, CHR, UPS).

**REMARKS.**—This new species is a member of the *P. testacea* complex. It is closely related to *P. crambidiocarpa* and *P. salcrambidiocarpa*, the thallus of these three species being essentially identical with sublinear lobes, marginal and laminal pseudocyphellae splitting open with age, and a dense mat of rhizines below. However, there are significant differences in chemistry, distribution, and, in part, spores.

The apothecia of *P. norcrambidiocarpa* are typical for the group except that the disc is even darker than in *P. crambidiocarpa*. Of 34 specimens examined, none had a pale tan disc, 56% were light to medium brown, and 44% were dark brown. Spore differences are more significant: average maximum length is 13.4 μm (25 measurements) with a range of 12–15 μm, and average width 8.8 μm (range 7–10 μm). There is no overlap with the larger spores of *P. crambidiocarpa* and in fact a highly statistically significant value of P = .005 was calculated for spore length differences between the two species. *Parmelia salcrambidiocarpa* has identical small spores.

Chemistry is extremely uniform: atranorin and echinocarpic acid and associated unknowns. Some specimens of *P. crambidiocarpa* on North Island only contain echinocarpic acid (and were identified by spore size); the only two from South Island with echinocarpic acid also contained protocetraric acid. *Parmelia salcrambidiocarpa* contains only salazinic acid.

**Parmelia norcrambidiocarpa** is by far the most common foliose lichen in the subalpine scrub zone on the major mountain chains running the length of the South Island (Figure 18). I collected 161 specimens at 32 localities, the bulk (85%) between 300 m and 910 m elevation. It comprised 23% of the 715 specimens I collected at random in New Zealand and 30% of the 88 collections in CHR. It has yet to be collected on North Island or in Tasmania.

Representative Specimens Examined

New Zealand: South Island, Allan CHR160255 (CHR), Child 1556 (CHR), Elix 8675 (ANUC), Hale 65118, 65325, 65391, 65472, 65659, 65670, 65719, 65789, 65841 (US).

**Parmelia novae-zelandiae** Hale, new species

**FIGURES 4f, 17f, 18**

**DESCRIPTION.**—Thallus ut in *P. tenuirima* sed isidiis munitis differt.

Thallus loosely adnate on bark, rather fragile, pale greenish straw colored, 6–15 cm broad, lobes broad and rounded, 4–10 mm wide; upper surface plane, the pseudocyphellae mostly laminal, uniformly dispersed, angular, 0.3–1.0 mm long, simple or branched, splitting open with the formation of coarse isidia, the isidia somewhat inflated, branching with age; lower surface black and shiny, the rhizines coarse, sparsely developed, 1–2 mm long. Pycnidia and apothecia not seen.

**CHEMISTRY.**—Atranorin and salazinic acid.

**HOLOTYPE.**—5 Mile stream trail, Rimutaka State Forest, E of Lower Hutt, North Island, New Zealand, M.E. Hale 58809 (US).

**REMARKS.**—This New Zealand endemic was identified as *P. pseudo-tenuirima* by Galloway and Elix (1983), although they subsequently recognized the variation in the New Zealand collections (Galloway and Elix, 1984). It is amply distinct because of the much larger thallus, large separate pseudocyphellae (as in *P. tenuirima*), and coarse, irregularly inflated
Figure 18.—Distribution of Parmelia norcrambidioarpa in New Zealand.
FIGURE 19.—Species of Parmelia: a, P. novae-zelandiae (holotype in US); b, P. omphalodes (Santesson 23706); c, P. omphalodes (pinatifida form) (Vézda in Lichenès Selecti Exsiccati 1735); d, P. protosulcata (holotype in US); e, P. pseudolaevior (Kurokawa 59205); f, P. pseudoshinanoana (Nakanishi 5172). (Scales in mm.)
isidia. Parmelia pseudotenuirima can therefore be considered as a strict Australian endemic and P. novae-zelandiae a New Zealand one, although, of course, it may yet be found in Tasmania. In New Zealand it occurs rather rarely in moist Nothofagus forests or even on large trees in pastures at low elevation.

Specimens Examined

New Zealand: North Island, Hale 58809 (US); South Island, Hale 65443, 66232 (US). Three additional records are listed under P. tenuirima in Galloway and Elix (1983), of which I have checked Bartlett s.n. from Pandora.

Parmelia omphalodes

FÜGÈRE 5a, 19b,c

Parmelia omphalodes (L.) Achasius, 1803:204.

Lichen omphalodes var., 1753:114. [Type collection: specimens and Dilleniens, 1742, pl. 24: fig. 80a (OXF, lectotype).]

Parmelia omphalodes β. panniformis Achasius, 1803:204. [Type collection: Helvetia, Schleicher 257 (H-Ach, lectotype).]

Parmelia omphalodes var. panniformis f. subconcentrica Crombie, 1872:306. [Type collection: Braemar, Marrone, Aberdeen, Great Britain, Crombie s.n. (BM, lectotype).]

Parmelia sulcata var. laevis f. hirsuta Crombie, 1875:140. [Type collection: Ben Lawers, Perth, Great Britain, Crombie s.n. (BM, lectotype).]

Parmelia omphalodes var. hirsutcra Tavares, 1945:120. [Type collection: Sierra da Estrela, Tavares s.n. (LISU) (not seen).]

Parmelia pinnatifida Kurokawa, 1976:378. [Based on Parmelia omphalodes β. panniformis Achasius.]

Parmelia omphalodes subsp. pinnatifida (Kurokawa) Skult, 1984:138. [Additional varieties and forms, which I consider to be synonyms, will be found in Hillmann (1936) and Skult (1984).]

Description.—Thallus adnate to loosely adnate on rocks, firm to somewhat brittle, extremely variable in color, whitish mineral gray to dark chestnut brown or even black, 6-20 cm broad; lobes sublinear, short, becoming crowded and imbricate, often becoming laciniate with dense marginal secondary lobes, 1-4 mm wide; upper surface shiny, plane to weakly foveolate, continuous or becoming cracked along older pseudocyphellae, pseudocyphellae effigurate, variable, to 0.5 mm long, mostly marginal as a nearly continuous rim (especially in P. pinnatifida), becoming more numerous on the lobe surface with age and forming a distinct network; lower surface black or dark brown, 1-1.5 mm long. Pycnidia common; conidia cylindrical, straight or a few bent or very weakly bifusiform, 5.5-6.5 μm long (Figure 12g) (Hillmann (1936) reports 1 x 5-6 μm). Apothecia not common, stipitate and urceolate but at maturity open, 7-10 μm long, the episporium 1-2 μm thick.

Chemistry.—Atranorin, lobaric acid (lacking in “P. pinnatifida”), salazinic acid (Culberson, 1970; Krog, 1968; Kurokawa, 1976; Thomson, 1979), consalazinic acid, protocetraric acid, fumarprotocetraric acid, or protocetraric acid (Skult, 1984) and several unidentified fatty acids (Dey, 1978; Kurokawa, 1976; Skult, 1984).

Remarks.—The Swedish specimen (Flora Suecica 947) cited by Linnaeus is not in the Linnean Herbarium. I have selected the Dillenian sheet at OXF as the lectotype (see Crombie, 1880).

As might be expected for a widespread boreal-arctic lichen, P. omphalodes exhibits a great range of variation in thallus color (from whitish mineral gray to blackish brown), development of pseudocyphellae (from sparse and marginal to well developed as a laminar network) and secondary lobation (some specimens without secondary lobes, others heavily lobulate), in large part variations that are modified by the harsh, exposed habitats it frequently occupies. Poelt (1974) does not recognize any of the numerous varieties and forms based on habitat modifications described from Europe.

Skult (1984) has made an especially thorough study of the species in Finland, recognizing three taxa: P. omphalodes subsp. discordans, P. omphalodes subsp. omphalodes, and P. omphalodes subsp. pinnatifida. Subspecies discordans was separated by the presence of protocetraric acid and subsp. pinnatifida by the absence of lobaric acid in salazinic acid-containing specimens. All specimens with lobaric and salazinic acids were called subsp. omphalodes. Relatively few intermediates were found in Fennoscandia.

Parmelia pinnatifida, long recognized by European lichenologists as P. omphalodes var. panniformis, is also differentiated from typical P. omphalodes by a number of subtle, intergrading morphological characters. Kurokawa (1976) emphasized the predominance of marginal pseudocyphellae. It also has somewhat narrower lobes (Skult, 1984), which are repeatedly branched, and a congested, nearly pulvinate thallus.

The populations of P. omphalodes in North America, however, although almost always lacking lobaric acid (96% of 84 specimens tested), are not like the European ones. Their morphology is much closer to typical P. omphalodes and, after studying a small sample Skult (1984) considered them to be intermediate between his subsp. omphalodes and subsp. pinnatifida. I am inclined not to make any taxonomic divisions in the group at this time.

An unnamed chemotype first recognized by Skult is distinguished by several subtle morphological characters and by the presence of norstictic acid in equal concentration with salazinic acid. I am calling this a new species, P. skultii (see below).

In the United States Parmelia omphalodes is locally common on rocks at the highest elevations in the Appalachian Mountains (Dey, 1978; Hale 1959) but is very rare in the western states. Imshaug (1957:249) found it only on Mt. Rainier in Washington in his intensive study of alpine lichens, and I have collected it only in Montana. It is, however, a very common tundra lichen in the arctic-boreal regions of Canada, Alaska (Krog, 1968), and Europe (see map in Thomson, 1984:308).
Representative Specimens Examined
(salazinic acid with or without lobaric acid).


**Parmelia prosoluta**

*Figures 5b, 19d*

_Parmelia prosoluta_ Hale, 1982:162. [Type collection: Lago Fagnano, Tierra del Fuego, Argentina, Santesson 7955 (S, holotype; US, isotype).]

**Description.**—Thallus adnate to loosely adnate on bark, pale greenish to brownish mineral gray, 2–6 cm broad; lobes sublinear, short, contiguous, 2–3 mm wide; upper surface plane to weakly foveolate, becoming white pruinose at the tips, deeply reticulately fissured in older parts, pseudocyphellae effigurate, small and rather sparsely developed, mostly on the lobe tips or margins, sorediate, the soralia developing on lobe tips and margins, usually orbicular but fusing and becoming linear or densely aggregated with age, the soredia coarse; lower surface black, moderately rhizinate, the rhizines simple to sparsely fuscate or squarrosely branched, 0.5–1 mm long. Pycnidia not seen. Apothecia rare, substipitate, 4–5 mm in diameter, the amphithecium rugose, pseudocyphellae; hymenium 60–65 μm; spores 7–9 × 11–13 μm (spore data from Imshaug and Ohlsson 45613).

**Chemistry.**—Atranorin, chloroatranorin, protocetraric acid, accessory lobaric acid, echinocaric acid, and conchehlicaric acid (Galloway and Elix, 1984) or rarely fumarprotocetraric acid.

**Remarks.**—This austral species occurs in South America and on some of the subantarctic islands, as well as in Australia and New Zealand (Galloway and Elix, 1984). It may be accompanied by _P. sulcata_, which would be distinguished by the different chemistry, a more foveolate surface, laminal soralia, large fissurine pseudocyphellae, and densely squarrosely branched rhizines. It is most closely related to another austral species, _P. cunninghamii_, which has broader lobes, linear soralia, and salazinic acid.

**Specimens Examined**


**Parmelia pseudoaeolior**

*Figures 5c, 19e*

_Parmelia pseudoaeolior_ Asahina, 1951a:331. [Type collection: Sengenjuna, Prov. Suruga, Japan, Asahina s.n. (US, lectotype; US, isotype).]

**Description.**—Thallus adnate on bark or rock, rather brittle, pale greenish to brownish mineral gray, 8–12 cm broad; lobes sublinear, contiguous to imbricate, 1–3 mm wide, the margins becoming densely lobulate, the lobules suberect to erect, 0.1–0.3 mm wide, 1–2 mm long, the lower surface whitish; upper surface shiny, plane to weakly rugose-foveolate, continuous, pseudocyphellae punctate, round, lateral on lobe edges, rarely submarginal, 0.1–0.2 mm long; lower surface black, shiny moderately rhizinate, the rhizines simple to sparsely fuscate, 0.5–1 mm long. Pycnidia not seen. Apothecia rare, substipitate, 2–10 mm in diameter, at first urceolate, then expanded, flat and radially split, the amphithecium sparingly punctate-pseudocyphellate; hymenium 60–65 μm; spores 6–9 × 10–15 μm, the episporium 1 μm thick.

**Chemistry.**—Atranorin, salazinic acid (Asahina, 1951a), and consalazinic acid.

**Remarks.**—_Parmelia pseudoaeolior_ is clearly the lobulate morphotype of _P. laevior_, both having lateral punctate pseudocyphellae. It is rather common in Japan and apparently restricted there. A synonym cited by Asahina, _P. laevior_ f. microphyllina Hue, is actually better identified with _P. pseudoshinanoana._

**Specimens Examined**

Japan: Prov. Aki, Hale 29363, 29377, 29505 (US); Prov. Bungo, Kurokawa 63193 (TNS); Prov. Im, Asahina, s.n. (TNS); Prov. Kii, Kurokawa 56061, 57281 (US), 60262 (TNS); Prov. Ishikari, Yoshimura 12235b in Lichenes Japonici Exsiccati 41 (US); Prov. Rikutyu, Kurokawa 92777 (US); Prov. Shimotutsu, Hale 63127 (US); Prov. Shinano, Kurokawa 59205 in Lichenes Selecti Exsiccati 33 (US); Prov. Suruga, Asahina 92 (TNS).

**Parmelia pseudoshinanoana**

*Figures 5d, 19f*

_Parmelia pseudoshinanoana_ Asahina, 1951a:334. [Type collection: Omiya-guchi, 2-gome, Mt. Fuji, Prov. Suruga, Japan, Asahina 52 (TNS, lectotype; US, isotype).]
Parmelia laevior f. microphyllina Hue, 1899:166. [Type collection: Japan, Faurie 518 (PC, lectotype).]

Description.—Thallus adnate on bark, fragile, pale greenish to brownish mineral gray, 6–12 cm broad; lobes sublinear, contiguous, 1.5–3 mm wide, the margins becoming densely lobulate, the lobules 0.2–0.3 mm wide, 1–2 mm long, suberect; upper surface plane, shiny, white pruinose at the tips, continuous, pseudocyphellae marginal, appearing as a more or less continuous white rim 0.5–1 mm wide; lower surface black, densely rhizinate, the rhizines shiny, becoming densely squarrosely branched, 1–3 mm long. Pycnidia not seen. Apothecia not common, substipitate, 2–4 mm in diameter, the rim finely crenate, pseudocyphellate; hymenium 55–60 μm; spores 6 x 10–12 μm, the episporium 1 μm thick.

Chemistry.—Atranorin and chloroatranorin, lobaric acid and salazinic acid (Galloway and Elix, 1983).

Remarks.—This small lichen is known only from Australia (see distribution map in Galloway and Elix, 1983:403). It is not related to any other species in the genus. Literature reports of P. saxatilis from Australia probably represent this species. New Zealand records cited by Galloway and Elix (1983) are all P. novae-zelandiae. A typical habitat is the base and lower trunks of Callitris endlicheri and Casuarina in open eucalypt forest and especially on old burned stumps.

Specimens Examined

Australia: New South Wales, Hale 59276, Weber 365 in Lichenes Ersiccati (US); Weber and McVean L-49416, L-50060 (US); Victoria, James Au2139, Streimann HSS2223 (US). Filsøn (1982:555) gives additional records for Australian Capital Territory and South Australia.


dermia pseudotenuirima

FIGURES 5e, 20a

Parmelia pseudotenuirima Gyelnik, 1931:289. [Type collection: based on P. tenuirima f. isidiosa Müller Argoviensis.]

Parmelia tenuirima f. isidiosa Müller Argoviensis, 1896:90. [Type collection: Victoria, Australia, Wilson 83 (G, lectotype). Collector on the label is Knight.]

Description.—Thallus closely adnate on bark, firm, pale greenish to whitish mineral gray (brownish in the herbarium), 3–5 cm broad; lobes sublinear to subirregular, short, contiguous, 1–2 mm wide; upper surface shiny, finely foveolate, reticulately cracked with age, pseudocyphellae small, 0.2–0.3 mm long, effigurate in outline, numerous, mostly laminal, isidiate, the isidia cylindrical, 0.05–0.07 x 0.1–0.3 mm, simple to branched, very dense on older parts of the thallus and obscuring the lobes; lower surface black, moderately rhizinate, the rhizines simple to squarrosely branched, 0.5–1 mm long. Pycnidia rare, about 100 μm in diameter; conidia cylindrical, rod-shaped, 5.5–6.0 μm long. Apothecia very rare, substipitate, 3–6 mm in diameter, the amphitheicum warty, isidiate, the disc brown; hymenium 45–55 μm; spores poorly developed, 7–9 x 11–13 μm, the episporium 1 μm thick.

Chemistry.—Atranorin and chloroatranorin, lobaric acid and salazinic acid (Galloway and Elix, 1983).

Remarks.—I first identified this lichen as P. signifera in spite of the unusual substrate, canopy branches in rain forest. Parmelia queenslandensis is strictly corticolous, persistently whitish or greenish gray and occurs at elevations of 400 to 1100 m from extreme northern New South Wales to the Atherton Tablelands in northern Queensland, well north of the range of P. signifera. Parmelia signifera is almost always saxicolous in rather exposed habitats and usually turns pale to dark brown. In Australia it occurs from northern New South Wales to Tasmania with no reports yet from Queensland (Galloway and Elix, 1983). Spore differences, which I have not tested statistically, are minor but consistent; 11–12 μm
Figure 20.—Species of Parmelia: a, P. pseudotenuirina (Hale 58276); b, P. queenslandensis (holotype in US); c, P. ricasolioides lectotype in H); d, P. salcrambidiocarpa (holotype in US); e, P. saxatilis (Arnold in Lichenes Universalis 9); f, P. sectilia (Hale 26536). (Scales in mm.)
long in *P. queenslandensis* and 13–15 μm in *P. signifera*. Another related corticolous species, *P. tenuirima*, also has larger spores (12–15 μm long), brown round lobes (4–10 mm wide), and rather small, separate pseudocyphellae. It is common in New Zealand, much less so in Australia and represented by only one record as far north as Queensland.

Specimens Examined
Australia: Queensland, Hale 59480, 64001, 64128, 65971, 65972 (US); New South Wales, Hale 66686 (US).

*Parmelia ricasolioides*

**Figures 6a, 20c**

*Parmelia ricasolioides* Nylander, 1887:135. [Type collection: Yunnan, China, s. c. (H, Nyl. Herb. no. 35283, lectotype; PC, TUR, isolectotypes).]


*Parmelia daliensis f. tardiva* Zahlbruckner, 1930:184. [Type collection: Muli, Yunnan, China, Handel-Mazzetti 7368 (W, lectotype; WU, isolectotype).]

**Description.**—Thallus adnate to loosely adnate on bark, brittle, brownish mineral gray in the herbarium, 6–8 cm broad; lobes subirregular, short and crowded, contiguous, 2–3 mm wide; upper surface shiny, plane to weakly rugose, continuous, pseudocyphellae inconspicuous, entire margin, elongate; lower surface black, densely rhizinate, the rhizines simple to furcate, 0.5–1 mm long. Pycnidia common; conidia cylindrical, straight 5–6 μm long (Nylander, 1887). Apothecia numerous, stipitate, 1–2 mm in diameter, the rim inrolled, crenate; hymenium 55 μm; spores 9–13 × 20–24 μm, the episporium about 2 μm thick.

**Chemistry.**—Atranorin and salazinic acid.

**Remarks.**—This species occupies an isolated position in the genus. Nylander likened it to both *P. perlata* and *P. tenuirima*. The pseudocyphellae are very weakly developed along the lobe margins and the surface is continuous. It occurs at high elevations (to 3700 m), probably in *Rhododendron* forests.

Specimens Examined

*Parmelia salcrambidiocarpa* Hale, new species

**Figures 6b, 20d, 21**

**Description.**—Similis *P. crambidiocarpa* sed sporis parvis (7–10 × 12–15 μm) et thallo acidum salazinicum continenti differt.

Thallus corticolous, adnate to loosely attached, nearly pulvinate with age, firm, whitish mineral gray, 4–12 cm broad; lobes sublinear, little branched, becoming divaricately branched, 1.5–4 mm wide; upper surface shiny, plane, smooth to rugose, continuous or transversely cracked with age, the pseudocyphellae forming a nearly continuous narrow rim around the margins, 0.1–0.2 mm wide, also laminal and effigurate, 0.2–1 mm long, separate, fissuring with age; lower surface moderately to densely rhizinate, the rhizines simple to moderately squarrosely branched, 1–3 mm long, usually projecting as a mat around the lobe margins. Pycnidia numerous, 90–110 μm in diameter; conidia cylindrical to weakly bifusiform, 5–6 μm long. Apothecia common, stipitate, 5–18 mm in diameter, the disc sometimes flat and radially splitting, light to dark brown; hymenium 55–65 μm; spores 7–10 × 12–15 μm, the episporium 1.0–1.5 μm thick.

**Chemistry.**—Atranorin, chloroatranorin, and salazinic acid with or without consalazinic acid (one collection, Kanvilas and James 633/81, also contains lobaric acid).

**Holotype.**—Whakapapanui Walk Trail Head near the Chateau, Tongariro National Park, North Island, New Zealand, elev. 1180 m, M.E. Hale 65558 (US).

**Remarks.**—This species is in the *P. testacea* complex, closely related to both *P. crambidiocarpa* and *P. norcrambidiocarpa* (see discussions under these species). It is easily distinguished from *P. crambidiocarpa* by the smaller spores and chemistry. The average maximum spore size, 8.9 × 13.4 μm (range 7–10 × 12–15 μm for 17 collections), is the same as in *P. norcrambidiocarpa*. As in *P. crambidiocarpa* the apothecial disc ranges from very pale brown (29%) to brown (23%) or dark brown (47%) (17 collections examined).

*Parmelia salcrambidiocarpa* differs from morphologically identical *P. norcrambidiocarpa* in containing salazinic acid rather than echinocarpic acid. In addition the two species are allopatric, *P. salcrambidiocarpa* occurring in Tasmania and the Tongariro-Urewera region of North Island of New Zealand (Figure 21). *Parmelia norcrambidiocarpa* occurs only on South Island of New Zealand. I collected *P. salcrambidiocarpa* at 8 localities in Tasmania, a total of 28 specimens out of 186, the remainder being *P. testacea*.

Ecologically *P. salcrambidiocarpa* behaves much as the other species in this group. It is usually collected on *Nothofagus cunninghamii* in Tasmania at 600–1200 m elevation and in New Zealand on *Dracophyllum* and other subalpine shrubs up to 1300 m elevation.

Specimens Examined

*Parmelia saxatilis*

**Figures 6c, 20e**

Figure 21.—Distribution of Parmelia salicrpmidiocarpa in New Zealand.
 Parmelia saxatilis var. leavis Nylander, 1860:389. [Type collection: Pyrenees central, Nylander s.n. (H, Nyl. herb. no. 34863, lectotype).]
 Parmelia saxatilis f. rubricosta Steiner, 1904:399. [Type collection: Cumbre Nueva, La Palma, Canary Islands, Bornmüller 3256 (WU, lectotype).]
 Parmelia acervata Hue, 1915:43. [Type collection: Cape Tuxen, Graham Land s.c. 190 (PC, lectotype; see Lamb, 1948:241).]
 Parmelia saxatilis f. squamigera Geylinski, 1931a:152. [Type collection: Helsinki, Finland, Geylinski s.n. (BP, lectotype).]
 Parmelia saxatilis f. corallina Geylinski, 1931a:152. [Type collection: Donos, Mt. Vadallokovik, Pest, Hungary, Geylinski s.n. (BP, lectotype).]
 Parmelia saxatilis f. prima Geylinski, 1931b:284. [Type collection: Magas Tatra, Koprova Valley, Hungary, Timko s.n. (BP, lectotype).]
 Parmelia saxatilis var. imbricatoides Geylinski, 1932:450. [Type collection: Artukainen, Finland, Linkola s.n. (BP, lectotype).]
 Parmelia saxatilis var. pseudoviridis Geylinski, 1932:448. [Type collection: St. Gilgen, Austria, Geylinski s.n. (BP, lectotype).]
 Parmelia saxatilis f. acervata (Hue) Lamb, 1948:241.
 [See Hillmann (1936) for additional subspecific taxa, all of which appear to be synonyms of P. saxatilis.]

DESCRIPTION.—Thallus adnate to loosely adnate on rock, more rarely on bark, fairly firm, greenish mineral gray, turning brownish in exposed habitats, sometimes whitish with varying amounts of pruina, 8–20 cm broad; lobes sublinear, contiguous to crowded, 2–4 mm wide; upper surface shiny, continuous or cracking with age along the pseudocyphellae, reticulate-foveolate, the pseudocyphellae effigurate, large, 0.3–1.0 mm long, marginal and laminal, often fusing into a reticulate network and soon becoming isidiate, the isidia cylindrical, simple to sparsely branched, darkening at the apexes, 0.06–0.15 mm in diameter, up to 0.5 mm high, becoming very dense on older lobes; lower surface black, densely rhizinate, the rhizines simple to fuscate or rarely subquarrosely branched, 1–2 mm long. Pycnidia uncommon, about 100 μm in diameter; conidia cylindrical, straight to slightly bent, 6–7 μm long (Hillmann (1936) reported 1 × 5–7 μm). Apothecia occasional, substipitate, 2–8 mm in diameter, cupuliform, the amphitheicum and rim coarsely rugulose, isidiate; hymenium 80–100 μm; spores 9–11 × 16–18 μm, the episporeum 2–3 μm thick.

CHEMISTRY.—Atranorin, chloroatranorin, and salazinic acid (Galloway and Elix, 1983), accessory lobaric acid (Krog, 1951) with or without protolichesterinic acid (Kurokawa and Nakanishi, 1971) or unidentified fatty acids (Dey, 1978).

REMARKS.—This is the most widespread species in the genus, occurring in both hemispheres and known to all lichenologists. For such a common species it has very little morphological and chemical variation. The presence or absence of the accessory substance lobaric acid is loosely correlated with geography. In Europe about a third of the collections (50 tested) have only salazinic acid, the rest having salazinic and lobaric acids. In Alaska and Canada (see map in Thomson, 1984:310) these two chemotypes are nearly equally common, but in western United States and South America most specimens contain only salazinic acid (91% of 75 tested). All specimens in the Appalachian region of eastern North America, where the species occurs on rocks at the highest elevations, seem to have lobaric acid constantly (Dey, 1978). Parmelia kerguelensis appears to be a protolichesteric acid-containing chemotype.

Most corticolous specimens from Japan, eastern North America, and the west coast of North America, usually identified as P. saxatilis in herbaria, have proved to be P. squarrosa, a closely related species with densely squarrosely branched rhizines. This probably includes the reports of Zhao et al. (1982) for P. saxatilis in China.

Representative Specimens Examined


Parmelia sectilla

FIGURES 64, 26

Parmelia sectilla Hale, 1968:326. [Type collection: summit of Mt. Data, Mountain Prov., Philippines, Hale 26536 (US, holotype; TNS, isotype).]

DESCRIPTION.—Thallus adnate to closely adnate on bark, brittle, light greenish mineral gray, 8–12 cm broad; lobes sublinear, contiguous, 1.5–2 mm wide, marginally dissected and densely isidiate-lobulate, the lobules erect, branched, 0.1–0.5 mm wide, to 1 mm long, the tips cylindrical; upper surface shiny, plane to weakly rugose, continuous, pseudocyphellae effigurate, elongate, mostly marginal, forming an
interrupted white rim around the lobes; lower surface black, densely rhizinate, the rhizines simple to furcate, 1–1.5 mm long. Pycnidia rare; conidia cylindrical, straight, 5–6 μm long. Apothecia not common, subtipitate, 2–4 mm in diameter, the rim and amphitheciun deeply rugose with numerous lobules or isidia-like projections, the disc brown; hymenium 90–100 μm high; spores 15–18 × 28–33 μm, the episporium distinct, 3–4 μm.

**Chemistry.**—Atranorin, salazinic acid, and consalazinic acid.

**Remarks.**—*Parmelia sectilis* occurs at higher elevations (1600–2300 m) in the pine forests of the Philippines and in oak forests in Sabah. It is the only species of *Parmelia* that seems to have evolved and remained in the tropics. It is distantly related to *P. niitakana*, *P. pseudoshinanoana*, and *P. shinanoana*, which have similar though more strongly developed rim-forming pseudocyphellae. It has the largest spores in the genus.

**Specimens Examined**


*Parmelia shinanoana*

**Figures 6e, 22a**


**Description.**—Thallus adnate on rock, fragile, pale greenish to distinctly brownish mineral gray, 8–20 cm broad; lobes sublinear, contiguous, 1.5–3 mm wide, sparsely lobulate in older parts; upper surface shiny, plane, continuous, pseudocyphellae marginal, linear, forming a conspicuous white rim about 2 mm wide around the lobes; lower surface black, sparsely to moderately rhizinate, the rhizines simple to furcate, 1–2 mm long. Pycnidia not seen. Apothecia rare, adnate and inconspicuous, 1–2 mm in diameter, the rim crenate, pseudocyphellae; hymenium 60–65 μm; spores poorly developed, 5–6 × 9–11 μm, the episporium 1 μm thick (after *Asahina*, 1952:114).

**Chemistry.**—Atranorin, gyrophoric acid, and 4-O-methylgyrophoric acid in the cortex, salazinic acid in the medulla (*Kurokawa* and *Takahashi*, 1970).

**Remarks.**—*Parmelia shinanoana* has very conspicuous rim-forming pseudocyphellae, similar to *P. niitakana* and *P. pseudoshinanoana* and, as the main chemical feature, the production of gyrophoric acid in the cortex, unique in the entire family Parmeliaceae. It is known only from Japan, where it is not commonly collected.

**Specimens Examined**


*Parmelia signifera*

**Figures 6f, 22b**

*Parmelia signifera* Nylander, 1888:25. [Type collection: New Zealand, Knight s.n. (H, Nyl. Herb. no. 34828, lectotype; BM, isolectotype).]

**Parmelia saxatilis var. signifera** (Nylander) Müller Argoviensis, 1892:30.

**Description.**—Thallus adnate to loosely adnate on rock (rarely on bark), sometimes forming dense, pulvinate mats, rather firm to brittle, darkish green to brownish mineral gray, the tips usually distinctly brownish, 8–20 cm or more broad; lobes sublinear, crowded and imbricate, 2–8 mm wide, more or less lobulate with age in the center, the lobules marginal, suberect; upper surface shiny, plane to rugose or foveolate, extensively fissured with age along pseudocyphellae, the pseudocyphellae effigurate, 0.3–1 mm long, separate or in part fusing into a loose white network, appearing raised; lower surface black, the margin shiny and dark brown, densely rhizinate, the rhizines rather dense, about 1 mm long, simple to sparsely squarrosely branched. Pycnidia common; conidia bifusiform, 5.0–56.5 μm long. Apothecia common, adnate to subtipitate, 6–12 mm in diameter, the disc brown, flattened, often radially split, the amphitheciun heavily effigurate-pseudocyphellate; hymenium 55–60 μm; spores 6–8 × 13–15 μm, the episporium distinct, about 1 μm thick.

**Chemistry.**—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983) and consalazinic acid, and accessory lobaric acid; or rarely atranorin and protocetraric acid.

**Remarks.**—This is by far the most commonly collected saxicolous *Parmelia* in Australia and New Zealand (see distribution map in Galloway and Elix, 1983:408). In Australia, in particular, it forms large, pulvinate, exfoliating colonies on granite and sandstone outcrops in open sclerophyll forests. In New Zealand the typical habitat is more exposed ridges in open mountainous areas. In a sense it is the austral counterpart of *P. omphalodes*, which has much less conspicuous pseudocyphellae and is, of course, a northern arctic-alpine lichen. A few specimens (*Hale* 58374, *Melville* 2009) containing protocetraric acid instead of salazinic acid are morphologically indistinguishable.

When corticolous, there is rarely confusion with *P. tenuirima*, a large greenish mineral gray lichen that has less dense, separate pseudocyphellae and cylindrical to vaguely bifusiform conidia. However, a few narrow-lobed, usually corticolous specimens may be difficult to name as *P. signifera* or *P. tenuirima* (see also Hillmann, 1939). Filson (1982:565) feels that the two species may prove to be identical, but both morphological and conidial differences seem to preclude this unlikely possibility.
FIGURE 22.—Species of Parmelia: a, *P. shinanoana* (Kurokawa 58588); b, *P. signifera* (Hale 58289); c, *P. skullii* (holotype in US); d, *P. squarrosa* (holotype in US); e, *P. submollana* (lectotype of *P. contorta* Bory in PC); f, *P. submutata* (Poelt L-142). (Scales in mm.)
Specimens Examined

Australia: New South Wales, Du Rietz 704, 792a (UPS, US), Fleckton 1443 (US), Hale 58289, 58301, 58927, 59106, 59286, 59296, 59443, 66122, 66399 (US), Streimann 2496, 4017, 7414, 7473, 9138, 9286 (US), Verdon 1364, 1428, 1513, 1587, 1832, 7415 (US); Australian Capital Territory, Hoogland 7775, 7779 (US), Weber 251 (US); Victoria, Hale 58256, 58330, 58326, 58374, 58474, 58977, 59159, 59414, 59541 (US), Melville 2009 (BM, US), Streimann 2820, 3267, 3410, 3414 (US); Macquarie Island, Isaid s.n. (US). New Zealand: South Island, Du Rietz 1802a (UPS, US), Hale 66177, 66455 (US), James 482, 1419, 1471 (BM, US), Galloway s.n. (CHR), Marin s.n. (BM, US), Mason 134 (BM).

Parmelia skultii Hale, new species

![Figure 7a, 22c](image)

*Parmelia omphalodes* subsp. *glacialis* Skult., 1985:201. [Type collection: Mould Bay, Prince Patrick Island, NWT, Canada, MacDonald s.n. (CANL, holotype).]

**Description.**—Subsimilis *Parmelia omphalodi* sed thallo acidum salazinicum continenti differt.

Thallus usually growing on soil among mosses or on rocks, fragile, brown to nearly black at maturity (or whitish with pruina), 6–10 cm broad; lobes sublinear, rather short, 2–4 mm wide, crowded and imbricate with secondary laciniae; upper surface plane, smooth to minutely rugulose, often becoming white pruinose with age, the margins pseudocyphellate, the pseudocyphellae more or less continuous, narrow and inconspicuous, laminal pseudocyphellae rarely seen; lower surface black and shiny, sparsely to moderately rhizinate, the rhizines simple to fucate, 0.5–2 mm long. Pycnidia rare, 90–110 µm in diameter; conidia cylindrical, rod-shaped, 6–8 µm long. Apothecia not seen.

**Chemistry.**—Atrnorin, salazinic acid, norstictic acid (equal or exceeding the concentration of salazinic acid), consalazinic acid (±), protolichesterinic acid (±), fumarprotocetraric acid (±), stictic acid (±), and several unknowns (Skult, 1984).

**Holotype.**—West wall of pass, on soil over rocks, Anaktuvuk Pass, 151°52'W, 68°20'N, Alaska, USA, G.A. Llano 299a (US).

**Remarks.**—Skult (1984) first pointed out the existence of a norstictic acid-containing population of *P. omphalodes* in his broader study of the *P. omphalodes* complex in eastern Fennoscandia. He noted the rather broad, marginally pseudocyphellate lobes and frequent occurrence of pruina, the two most important morphological features that separate it from typical *P. omphalodes*. I believe this combination of characters to recognize it as a distinct species. It appears to be restricted to high latitudes, especially near the ocean, from the Aleutian Islands to Novaya Zemlya.

**Representative Specimens Examined**

Canada: Nova Scotia, Maas 73 (US); Quebec, Fabius 7836, Gallo 3095 (US); Ontario, Hale 33556, 34818, 34945, 36556, 49836 (US), Sharp 440 (US); British Columbia, Brodo 14257 (US). USA: Maine, Egan 5833, Hale 37534, Merrill in Lichenes Exsiccati 35 (US); New Hampshire, Tucker in Reliquiae Tuckermanianae 72; Massachusetts, Hermann 14087, Willey s.n. (US); Connecticut, Hale 33, 14915, 15406 (US); New York, Brodo 1213, Hale 16661 (US); New Jersey, Hale 15288 (US); Pennsylvania, Hale 16046, 17217.
Parmelia submontana, new name

**Parmelia conforfa** Bory, 1832:305. [Type collection: Atlas Cedres, Tagygeta 1420 (PC, lectotype). Not *Parmelia conforfa* (Hoffmann) Sprengel, 1827:298 (= *Aspicilia conforfa* (Hoffmann) Kremphuber.)

*Parmelia saxatilis var. conforfa* (Bory) Zahlbruckner, 1907:68.

*Parmelia sulcata f. conforfoides* Zahlbruckner, 1927a:97. [Type collection: Hohenberg, Brennulpe, Austria, Suzuki s.n. and Neuwaldc, St. Agid, Austria, Suzuki s.n. (W, synonyms; not seen.).]

*Parmelia bohemia Nadvornik, 1951:244.[Type collection: Planavv, Illinsko, Bohemia, Nadvornik s.n. in 1931 (PRM, lectotype; US, isolyecotypes). Not *Parmelia bohemia* Gyelnik, 1932a:218 (= *Xanthoparmelia conspersa* (Acharius) Hale.).]

*Parmelia bohemia f. conforfoides* (Zahlbruckner) Nadvornik, 1951:244.

*Parmelia submontana* Nadvornik, 1957:72. [Nomen illeg. Basionym not cited in description. Type collection: Based on *P. bohemia* Nadvornik.]

**Description.**—Thallus loosely attached to bark, trailing in well-developed specimens, firm, greenish mineral gray, 10–15 cm broad; lobes elongate, linear, up to 30 mm long, little branched, divaricate, sometimes weakly canaliculate, 2–5 mm wide; upper surface shiny, plane to rugulose, continuous, pseudocyphellae small, round to effigurate, laminal and marginal, 0.3–1 mm long, soon becoming sorediate, the soralia orbicular to linear with an eroded center with age, the soredia cracked, pseudocyphellae numerous and small, 0.1–0.2 mm long, laminal; lower surface black, densely rhizinate, the rhizines simple to densely squarrosely branched, 1–1.5 mm long. Apothecia and pyecnidia not seen.

**Chemistry.**—Atranorin, salazinic acid, and consalazinic acid with or without norstictic acid.

**Remarks.**—This is the parent morph of *P. meiophora*. In his descriptions Zahlbruckner recognized the dendroid branched rhizines but not the fine reticulations on the surface representing pseudocyphellae. It is more widespread than *P. meiophora* but seems to occur in similar habitats, high elevation pine-Rhododendron forests. About a third of the specimens tested from Taiwan have relatively high concentrations of norstictic acid.

**Representative Specimens Examined**

Taiwan: Prov. Ilan, Kurokawa 929, 931, 1038 in *Lichenes Crifici Selecti Exsiccati* 38 (US); Mt. Chien-San, Kurokawa 932 (US); Mt. Arissan, Ogata s.n. (TNS); Taichung County, Han s.n. (US). China: Yunnan, Delavay s.n. (PC). It has also been reported by Kurokawa (1966:410) from Nepal.
Parmelia subtestacea Hale, new species

**Figure 23.**—Species of Parmelia: a, P. subtestacea (holotype in US); b, P. sulcata (Kjellmeri s.n.); c, P. tenuirima (James 488 pp.); d, P. rudior (type of P. erimos in H). (Scales in mm.)

**Description.**—Similis P. testacea sed thallo acidum echinocarpicum continenti differt.

Thallus adnate on bark, usually thin and rather brittle, pale greenish mineral gray, 5–12 cm broad; lobes sublinear to mostly subirregular, short, imbricate, 1–5 mm wide, usually with marginal secondary lobes 1–2 mm wide, flaring to rounded, developing with age; upper surface shiny, plane to distinctly rugose-foveolate, continuous, pseudocyphellae forming a nearly continuous white rim 0.1–0.2 mm wide around the main and secondary lobes, also laminal on the main or older lobes, separate, sparse, 0.2–0.4 mm long, usually not fissuring with age; lower surface black, sparsely to moderately rhizinate but with a distinct bare to papillate brown zone around the margins, the rhizines simple to furcate to sparsely squarrosely branched, 0.5–1.5 mm long. Pycnidia numerous, 90–100 μm in diameter; conidia cylindrical, rod-shaped to weakly bifusiform, 5.5–6.5 μm long. Apothecia common, substipitate, generally remaining flat but sometimes cupuliform, 4–20 mm in diameter, the disc very pale brown, rarely darkening, splitting radially at maturity, the amphithecium rugose and effigurate-pseudocyphellate; hymenium 60–65 μm; spores 7–10 × 11–15 μm, the episporium 1.0–1.5 μm thick.

**Chemistry.**—Atranorin, chloroatranorin, echinocarpic acid (and associated unknowns), with or without unknown #27 or rarely with unknown #27 alone. A fatty acid near protolichesterinic acid was detected in several specimens tested by Dr. C.F. Culberson.

**Holotype.**—Silver beech forest with understory grazing, near entrance to Mt. Aspiring National Park, Routeburn Road,
Figure 24.—Distribution of Parmelia subtestacea in New Zealand. (Circles = unknown #27 chemotype; solid dots = echinocarpic acid and unknown #27 chemotype.)
The Parmelia testacea complex, corticolous lichens especially common in New Zealand and Tasmania. They concluded from a study of herbarium specimens that this complex represented a single variable species, P. testacea, but also stressed the need for more detailed field studies.

Hoping to elucidate this species more fully myself for this monograph, I conducted field studies of several weeks duration in New Zealand and Tasmania in 1984 and 1985, randomly collecting 902 specimens at 86 localities. All of the material was chromatographed and examined for spores and morphology. I concluded that the P. testacea complex can be divided into two distinct major groups, the P. crambidiocarpa group (P. crambidiocarpa, P. norcrambidiocarpa and P. salcrambidiocarpa) and the P. testacea group (P. subtestacea and P. testacea).

In terms of gross morphology, the P. testacea group is distinguished by the adnate to closely adnate thallus, irregularly lobed thallus with frequent production of roundish to flaring marginal secondary lobes, by the relatively sparse, mostly marginal pseudocyphellae, and by sparse to moderate rhizines. In contrast the P. crambidiocarpa group has sublinear lobes, infrequent production of secondary lobes, marginal and laminal pseudocyphellae, and dense rhizines (see P. crambidiocarpa for fuller discussions of the differences).

The Parmelia testacea group has three different lichen substances produced in four different combinations: echinocarpic acid–unknown #27, salazinic acid, salazinic acid–unknown #27, and unknown #27 alone. Of 381 random collections on North and South islands of New Zealand, the echinocarpic acid–unknown #27 chemotype made up 56% (215 specimens) with salazinic acid (salazinic acid–unknown #27 in 99 specimens). It does not occur on North Island at all but predominates on South Island (Figure 24), where it makes up 71% of the group (215 of 302 collections). It is virtually the only member of the echinocarpic group occurs.

The chemotype unknown #27 alone is considered to be the “acid-free” chemotype of P. subtestacea. It is rare and I collected only 27 specimens out of 241 in this group. It occurred with the echinocarpic acid–unknown #27 chemotype at 4 localities, intermixed on the same trees, and alone at 4 other localities. On North Island, where the echinocarpic acid–unknown #27 chemotype is lacking, I collected 13 specimens with unknown #27 at just two localities, 12 of them in a mass sample of a fallen tree near the Tongariro National Park headquarters on Okahune road. No specimens have been collected at the same sites as P. testacea, and this is the main justification for recognizing this chemotype as the acid-free chemotype of P. subtestacea.
Parmelia rosiformis f. pomazesia Gyelnik, 1931b:289. [Type collection: near Pomáž, Pest, Hungary, Gyelnik s.n. (BP, lectotype).]

Parmelia rosiformis f. rufescensirodiosa Gyelnik, 1931b:290. [Type collection: Mt. Paulmauer, St. Aegyd, Austria, Susa s.n. (BP, lectotype).]

Parmelia rosiformis f. subnobilisorediosa Gyelnik, 1931b:290. [Type collection: near Subnýsafurd, Turos, Hungary, Gysgiat s.n. (BP, lectotype).]

Parmelia rosiformis f. viridisorediosa Gyelnik, 1931b:289. [Type collection: Nagyszenas Mountains near Budapest, Hungary, Gyelnik s.n. (BP, lectotype).]

Parmelia rosiformis var. fagicola Gyelnik, 1932b:448. [Type collection: St. Gilgen, Austria, Gyelnik s.n. (BP, lectotype).]

Parmelia rosiformis f. fagicola Gyelnik, 1932b:450. [Type collection: near Kudisir, Hungary, Gyelnik s.n. (BP, lectotype).]

[See Hillmann (1936) for additional subspecific epithets that I consider to be synonyms.]

Description.—Thallus adnate to loosely adnate on bark and rock, rather firm, greenish to whitish mineral gray, 8-20 cm broad; lobes sublinear but rather short, crowded to imbricate, 2-5 mm wide; upper surface shiny, becoming strongly foveolate, continuous to irregularly cracked with age, pseudocyphellae effigurate, 0.3-1 mm long, laminal and marginal, separate, soon becoming sorediate, the soralia marginal and laminal along the ridges; lower surface black, densely rhizinate, the rhizines becoming densely squarrosely branched. Pycnidia poorly developed; conidia (Figure 12i) cylindrical, straight to slightly bent, 6-8 µm long (Hillmann 1939) reports 5-8 µm.

Apothecia rare, substipitate, 2-6 mm in diameter, the hymenium smooth, the rim sorediate, disc dark brown; hymenium 55-60 µm; spores usually poorly developed, 6-8 × 11-14 µm, the episporium 1 µm thick.

Chemistry.—Atranorin and chloroatranorin, salazinic acid (Galloway and Elix, 1983), and consalazinic acid. Dey (1978) also reports accessory lobaric acid.

Remarks.—Parmelia sulcata is easily typified by material in the Taylor herbarium. Gyelnik (1930) chose the name "rosaeformis" because it is older (but of a different rank!) than sulcata. Although Magnusson (1933) disapproved of this name change for such a long-established species, he need not have worried, because this epithet was never actually used in species rank. Zahlbruckner’s (1929:216) reference to "P. rosaeformis Röhll.” is erroneous. Röhling merely cited “P. rosaeformis” as a variety of P. saxatilis.

The most important diagnostic characters of P. sulcata are the well-developed laminal soralia and the richly squarrosely branched rhizines. Morphological variation in lobe configuration is slight. Most of the numerous varieties and forms have been described on the basis of soredial characters, such as coarseness and color. The chemistry is very uniform. No accessory substances were detected among approximately 100 specimens tested with thin layer chromatography, although Dey (1978) reported specimens from the Appalachian Mountains with lobaric acid.

Parmelia sulcata is very closely related to P. fertilis, its probable parent morph, which is less foveolate and has less dense pseudocyphellae and slightly smaller conidia. The two species are largely allopatric. The companion isidiate morph, P. squarrosa, is more closely related to P. fertilis.

This is a very widespread, even weedy species (see map of the American arctic distribution in Thomson, 1984:318, and of the Australasian distribution in Galloway and Eliz, 1983:412), which is more common than P. saxatilis in temperate and subalpine regions. The rarity of the species in Japan, however, is remarkable (Kurokawa, 1968). In Austral regions it has been collected as far south as Georgia (59°S), where it may in fact have been introduced from whaling ships (Lindsay, 1973a).

Representative Specimens Examined

Canada: Newfoundland, Waghorne 116 (US); Quebec, Bigelow s.n., Fabius 696, 7830 (US); Ontario, Cain 26889 (TRT, US), Hale 34806, 34912 (US); Alberta, Hale 38944, Turner 10174 (US); British Columbia, Macoun 150 (US); Northwest Territories, Hale 329 (US); Maine, Hale 37626, Harris and Bailey 5855 (US); Vermont, Drumel 10581 (US); Massachusetts, Gaines 2244, Smith 12368 (US); Connecticut, Hale 158, 14768 (US), New York, Hale 16664, Hermann 14441, Ogden 54109 (US); New Jersey, Hale 15315, Leonard 6428 (US); Pennsylvania, Hale 16058, 10170, Oidly 356 (US); Maryland, Hale 14488, 14506, Norden 36 (US); West Virginia, Allard 1058, Hale 12608, 16647 (US); Michigan, Hale 11081 (US), Imhoff 25423 (MSC, US); Minnesota, Fink 57, Hale 23148 (US), Weimor 21759, 22774 (MIN, US); North Dakota, Trana and Disrud 71038 (US); South Dakota, Hale 49373 (US), Weimor 10532 (MIN, US); Montana, Hale 48612, 49201 (US); Idaho, Hale 49374 (US); Wyoming, Hale 49178 (US); Colorado, Weber and Shushan 29132, Shushan 5205 (COLO, US); New Mexico, Hale 48924, Imhoff 10008, Standley 13985 (US); Arizona, Darrow 1853 (US); Washington, Ireland 5997 (US); Oregon, Hale 21562, 48498 (US); California, Brown 737, Hale 51762, Herre 450, Lindsay 258, Tucker 6219 (US). Argentina: Tierra del Fuego, Imhoff 54304, 54445 (MSC), Santesson 452 (S, US), 410, 611, 1098, 7787 (S); Chile: Magallanes, Imhoff 38699, 39310 (MSC), Santesson 1844, 6384, 7999, 8189 (S). Greenland: Hansen in Lichenes Groenlandici Exsiccati 12 (US). Ireland: W. Mayo, Wustum s.n. (BM). Great Britain: Cumberland, Johnzon 69 (BM). Finland: Fagerstrom in Lichenotheca Fennica 685 (US), Lai 10594 (US); Sweden; Almborn and Hale 33485, Kjelmers s.n. (US). Denmark; Christiansen s.n. (US). Germany; Ericsson 159 (US). France: Croazat s.n. (US). Hungary; Förs in Lichenotheca Hungarica 527. Spain: Vasquez and Rico s.n. (US). Portugal: Sampaio in Lichenes de Portugal 258, Tavares in Lichenes Lisboanae Selecti Exsiccati 169 (US). USSR: Eljas et al. L-67970 (COLO, US). Kenya: Hedger 1846b (UPS, US). Nepal: Khambu, Poel 124, 137, 201 (M). India: Kashmir, Awasthi 2628, 993 (AWAS). New Zealand: South Island, Du Rietz 17137 (UPS, US), Hale 65095, 66429 (US), Marin 5373 (BM, US). Australia: New South Wales, Eliz s.n. (ANUC).

Parmelia tenuircypha

FIGURES 8a, 23c

Parmelia tenuirnima Hooker and Taylor, 1844:645. [Type collection: Tasmania, "van Diemens Land," Gwnn s.n. (FH-Tayl. herb. sheet 1131, lectotype; BM, isotype).]


Aspidelia beckettii Burton, 1900:81. [Type collection: New Zealand, Beckett
Parmelia tenuirima var. platyna Zahlbruckner, 1941:108. [Type collection: Mt. Cargill, Dunedin, New Zealand, Thomson ZA56 (W, lectotype).]

DESCRIPTION.—Thallus adnate to loosely adnate on bark, rather firm, pale to dark greenish mineral gray, 8–60 cm broad; lobes broad and subirregular, 4–10 mm wide, often clearly black rimmed; upper surface shiny, sometimes coarsely white maculate, plane to foveolate in older parts, continuous but to moderately rhizinate, the rhizines simple to thickly cracking along old pseudocyphellae, the pseudocyphellae effigurate, fairly small but conspicuous, 0.5–1 mm long, marginal and laminal, uniformly scattered, separate; lower surface black except for a brown marginal bare zone, sparsely to moderately rhizinate, the rhizines simple to thickly squarrosely branched, 1–1.5 mm long. Pycnidia common; conidia cylindrical to slightly bent, a few vaguely bifusiform, 5.5–7.0 µm long. Apothecia common, stipitate, 5–15 mm in diameter, the amphithecium rugose, pseudocyphellate, the disc brown, radially split and sometimes perforate with age; hymenium 60–65 µm; spores 8–10 × 12–15 µm, the episporium about 1 µm thick.

CHEMISTRY.—Atranorin and chloroatranorin, salazinic acid (Culberson, 1966; Galloway and Elix, 1983), and consalazinic acid.

REMARKS.—This distinctive species has the broadest lobes of any in the genus, with conspicuous, separate pseudocyphellae. It often has a faintly greenish cast. Closely related P. signifera, largely a saxicolous species, has denser, net-forming pseudocyphellae and a brownish cast. Parmelia tenuirima is common at higher (and wetter) elevations in southeastern mainland Australia, but reaches its best development at higher latitudes in New Zealand and Tasmania (see distribution map in Galloway and Elix, 1983:415), occurring most often on lower trunks of large Nothofagus trees in open mossy forests, where colonies attain enormous size.

Hillmann (1939) examined this species rather carefully and disposed of most of the published subspecific names. He regarded f. corylina Müller Argoviensis as a probable distinct species, at least a variety (it is now recognized as P. erumpens Kurokawa). A f. sorediata Müller Argoviensis (1894:258), based on a Holst specimen from Usambara, is Parmotrema reticulatum (Taylor) Choisy. A variety described by Wilson (1893), var. multifida, was not found by Hillmann or me. Finally, f. isidiosa Müller Argoviensis had already been raised to species level by Gyelnik as P. pseudotenuirima over Hillmann's objections (“Von der Anschauung ausgehend, dass jede 'planta isidiosa' eine eigene Species darstellt hat Gyelnik die f. isidiosa Müller. Arg. ... zur Art erhoben”).

Specimens Examined

New Zealand: North Island, Hale 58886, 66468 (US); South Island, Du Rietz 17601, 1851:b (UPS, US), Galloway s.n. (CHR), Hale 65086, 65755 (US), James 488, 1531 (BM, US), Martin 357 (BM), Thomson T522 (CHR), Wade 96 (BM). Australia: Australian Capital Territory, Hale 59395 (US); New South Wales, Hale 59357, 59370 (US), Weber and McVean L-49328 (US); Tasmania, Brown s.n. (BM), James Au2112, Au2116 (BM), Oldfield s.n. (US), Pearson

Parmelia testacea

FIGURES 8h, 23d, 25

Parmelia testacea Stilton, 1877–1878:203. [Type collection: near Wellington, North Island, New Zealand, Buchanan s.n. (BM, lectotype).]

Parmelia tenuirima *P. rudior* Nylander, 1888:25. [Type collection: New Zealand, Knight 27 (H, Nyl. herb. no. 35289, lectotype).]

Parmelia tenuirima Hooker and Taylor var. erimis Nylander, 1888:25. [Type collection: New Zealand, Knight 55 (H, Nyl. herb. no. 35286, lectotype).]

Parmelia rudior (Nylander) Zahlbruckner, 1929:198.


Parmelia signifera f. pallidior Zahlbruckner, 1941:107. [Type collection: Dunedin, South Island, New Zealand, Thomson ZA249 (W, lectotype). The syntype (Otago Heads, Thomson ZA211 in W) is Parmotrema reticulatum (Taylor) Choisy.]

DESCRIPTION.—Thallus adnate to closely adnate on bark, thin and rather brittle, pale greenish gray, 5–15 cm broad; lobes sublinear to mostly subirregular, short and imbricate, 1–5 mm wide, usually with marginal secondary lobules 1–2 mm wide, flaring to rounded, becoming dense with age; upper surface shiny, plane to rugose-foveolate, continuous, the pseudocyphellae forming a nearly continuous white rim 0.1–0.2 mm wide around the main and secondary lobes, also sparsely laminal on the main or older lobes, separate, 0.2–0.4 mm long, usually not fissuring with age; lower surface black, sparsely to moderately rhizinate but with a distinct narrow bare to papillate brown zone around the margins, the rhizines simple to fuscate to sparsely squarrosely branched, 0.5–1.5 mm long. Pycnidia numerous, 90–100 µm in diameter; conidia cylindrical, rod-shaped to weakly bifusiform, 5.5–6.5 µm long (Hillmann (1939) reported them as bifusiform, 6.0–6.5 µm long for the type of *P. erimis*). Apothecia common, adnate to substipitate, generally remaining flat but sometimes cupuliform, 4–20 mm in diameter, the disc very pale tan (sometimes concolorous with the thallus) to medium brown, rarely darkening, splitting radially at maturity, the amphithecium rugose and effigurate-pseudocyphellate; hymenium 60–65 µm; spores 7–10 × 11–15 µm, the episporium 1–1.5 µm thick.

CHEMISTRY.—Atranorin, chloroatranorin, salazinic acid, and usually consalazinic acid, with or without unknown #27 (all types contain unknown #27).

REMARKS.—Parmelia testacea (see under *P. subtestacea* for additional discussions of the *P. testacea* complex) is characterized by the adnate, irregularly lobed, marginally pseudocyphellate thallus with sparse to moderate rhizines, small spores, and the presence of salazinic acid. Externally it is indistinguishable from *P. subtestacea*. Adnation and lobe configuration are the same, as are apothecial characters. The apothecia have an average maximum diameter of 8.4 mm and a range of 4–20 mm (29 specimens examined). The disc tends to be pale tan and rarely darkens to brown. Of 29 specimens scored for color, 52% were classified as pale tan, 45% as light.
Figure 25.—Distribution of Parmelia testacea in New Zealand. (Circles = salazinic acid and unknown #27 chemotype; solid dots = salazinic acid chemotype.)
brown, and only 3% as dark brown. Spores are small, the average dimensions being 8.5 × 12.7 μm (range: 7–10 × 11–15 μm for 21 specimens examined), virtually identical with those of *P. subtestacea*.

*Parmelia testacea* is not chemically uniform. Although the main component is salazinic acid, most specimens (71% or 99 of 140 randomly collected specimens) also contain unknown #27. Specimens containing salazinic acid–unknown #27 were collected at 6 localities, specimens with only salazinic acid at 3 localities, and specimens of both chemotypes at 8 localities, often intermixed on the same trees. In Tasmania, where *P. testacea* was the commonest member of the *P. testacea* complex, all specimens (156 tested) contained salazinic acid and unknown #27.

*Parmelia testacea* occupies habitats very similar to those of *P. subtestacea*, although the two species are almost completely allopatric, occurring together at only three localities (Tuatapere, Mt. Cook, and Tongariro) (Figure 25). It grows very frequently on *Nothofagus* species in New Zealand and Tasmania, especially on trunks of trees along highways or river banks. In dense forest it grows on canopy branches and is difficult to collect.

Representative Specimens Examined
(salazinic acid)
New Zealand: North Island, Allan CHR160212 (CHR), Elk 8030 (ANUC), Hale 58837, 65194, 65763 (US); South Island, Elk 7807 (ANUC, CHR), 8171 (ANUC), Galloway CHR348312 (CHR), Hale 65302, 65377, 65839 (US).

Representative Specimens Examined
(salazinic acid and unknown #27)
New Zealand: North Island, Barton CHR342984 (CHR), Elk 8003 (ANUC), Hale 65112, 65196, 65385, 65740, 65775 (US); South Island, Elk 6677, 7716 (ANUC), Galloway CHR240705 (CHR), Hale 65304, 65335, 65769 (US), Taylor 8a (CHR). Australia: Tasmania, Kantvilas 125/82 (ANUC), Hale 68613, 68636-642, 68671, 68688 (US).
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Index
(Synonyms in italics)

Aspidelia
beckettii, 18, 48
Lichen
omphalodes, 34
saxatilis, 18, 38
Parmelia
acervata, 40
adaugescens, 19
bohemica f. contortoides, 44
bohemica, 44
brownii, 23
cochleata, 19
cruenta, 41
cunninghamii, 23
daliensis f. tardiva, 38
doliensis, 38
discordans, 23
erimis, 49
erumpens, 24
fertilis, 24
fraudans, 25
hakonensis, 28
hygrophiha, 27
insensitiva, 23
isidioclada, 27
kerguelensis, 27
laevior, 28
laevior f. denigrata, 28
laevior f. hakonensis, 28
laevior f. microphyllina, 36
leucoarodes, 44
marmariza, 28
marmariza f. angustifolia, 28
marmariza var. physcioides, 19
metiophora, 30
meiophora var. isidiata, 30
neodiscordans, 30
niitakana, 30
norcrambidiocarpa, 31

Aspidelia
beckettii, 18, 48
Lichen
omphalodes, 34
saxatilis, 18, 38
Parmelia
acervata, 40
adaugescens, 19
bohemica f. contortoides, 44
bohemica, 44
brownii, 23
cochleata, 19
cruenta, 41
cunninghamii, 23
daliensis f. tardiva, 38
doliensis, 38
discordans, 23
erimis, 49
erumpens, 24
fertilis, 24
fraudans, 25
hakonensis, 28
hygrophiha, 27
insensitiva, 23
isidioclada, 27
kerguelensis, 27
laevior, 28
laevior f. denigrata, 28
laevior f. hakonensis, 28
laevior f. microphyllina, 36
leucoarodes, 44
marmariza, 28
marmariza f. angustifolia, 28
marmariza var. physcioides, 19
metiophora, 30
meiophora var. isidiata, 30
neodiscordans, 30
niitakana, 30
norcrambidiocarpa, 31

saxatilis *fraudans, 25
saxatilis f. acervata, 40
saxatilis f. corallicola, 40
saxatilis f. prima, 40
saxatilis f. rubricosa, 40
saxatilis f. squamigera, 40
saxatilis var. contorta, 44
saxatilis var. dimorpha, 36
saxatilis var. imbricatoides, 40
saxatilis var. laevis, 40
saxatilis var. pseudoviridis, 40
saxatilis var. rosiformis, 47
saxatilis var. signifera, 41
saxatilis var. sulcata, 47
sectilla, 40
shinanoana, 41
shinanoana f. calvescens, 30
signifera, 41
signifera f. pallidior, 49
skullii, 43
squarrosa, 43
subdivaricata, 24
submarmariza, 28
submontana, 44
submutata, 44
subtestacea, 45
sulcata, 47
sulcata f. aberrans, 47
sulcata f. contortoides, 44
sulcata var. laevis f. hirsuta, 34
tenuirima, 48
tenuirima *rudior, 49
tenuirima f. corallina, 24
tenuirima f. isidiata, 36
tenuirima var. erimis, 49
tenuirima var. platyna, 49
tenuiscypha, 48
testacea, 49
yasudaæ, 27