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The Lichen Genus *Porpidia* (Porpidiaceae) in North America

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Abstract. *Porpidia* is a saxicolous segregate of the large classical crustose genus *Lecidea*, distinguished from other segregate genera and families mainly by a tall hymenium, a particular excipulum structure, and large, nonseptate, halonate spores. In this, the first revisionary study of North American herbarium materials, both chemical and morphological data were found to be useful taxonomically. The thallus characters—thickness, color, texture, and presence of soredia—could be used in some cases; however, useful apothecial characters were more numerous: pruinina on the disks, size, shape and pigmentation of excipular cells, hymenium height, relative hymenium and subhymenium heights, and spore size. Presence of certain β-orcinol depsidones and long-sidechain orcinol depsides were also meaningful. Among the 21 species accepted, seven were new: P. calcarea, P. carlottiana, P. grisea, P. herteliana, P. lowiana, P. tahawasiana, and P. thomsonii. A lectotype was chosen for *P. cinereoatra*, and two new combinations were made: *P. diversa* and *P. flavicunda*. Four phenetic groups could be discerned among the North American species. They were given informal names: the albocaerulescens complex, with narrow excipular cells and heavily pruinose apothelial disks; the macrocarpa complex, with thin thallus, nonpruinose or very rarely pruinose disks, and blue subhypothecial pigment; the speirea complex, with carbonaceous exciple, small spores, generally a low hymenium, and a short hymenium-to-subhymenium ratio; and the superba complex, with tall hymenium and usually an HCl+ substrate. The genus occurs from arctic to temperate regions. Although most species follow well known distribution patterns, a few morphological types were found disjunctively in climatically different regions.

This paper documents the phenotypic variation and geographic distributions of North American species of *Porpidia*. Among the growing number of taxonomic segregates of *Lecidea*, *Porpidia* is one of the most thoroughly studied: European species by Hertel (1967, 1975), Hertel and Knoph (1984), Knoph (1984), and Schwab (1986); Asian species by Hertel (1977) and Inoue (1976, 1982, 1983a,b,c); and subantarctic species by Hertel (1984). Although 11 species have been reported from North America (Egan 1987), there has been no previous systematic study of all the North American species. This study therefore fills a conspicuous geographic gap in the knowledge of the genus in the northern hemisphere.

The classical family Lecideaceae and classical genus *Lecidea* (Zahlbruckner 1926) are firmly recognized as unnatural taxa (Hafellner 1984; Hertel 1984). When the genus now called *Porpidia* was segregated from *Lecidea* it was first given the name *Huilia* (Hertel 1975), and the older synonym *Porpidia* was only recently resurrected (Hertel 1984). A general understanding of the genus and its history can be gleaned from Hertel (1967, 1975, 1977, 1984).

The 11 genera of the Porpidiaceae were also just recently segregated from the Lecideaceae (Hafellner 1984). They are distinguished among the old Lecideaceae by the following suite of characters (see below for a more complete description of the genus): A green algal photobiont (*Trebbouxia* in *P. albocaerulescens*; Ahmadjian 1980), sometimes also with a cyanobacterium in cephalodia (*Gloeocapsa* and *Stigonema*); crustose thallus; black (to brownish black) apothecia sunken into or sessile on the thallus; lecenteine or rudimentary exciple; octosporous asci surrounded by a thin, amyloid, gelatinous layer, and a weakly amyloid tholus containing a more strongly amyloid cylinder (illustration: Hafellner 1984); weakly to strongly anastomosed paraphyses that are usually branched in the upper 10–20 μm; and halonate, hyaline, simple, ellipsoid spores. None of these characters is unique to the Porpidiaceae. The porpidiaceous tholus would be unique if it were not also found in the Koerberiellaceae (Hafellner 1984).

Despite the recent work on the Porpidiaceae, the taxonomic limits of *Porpidia* are still unsettled. A close relationship has been documented between *Porpidia* and *Amygdalaria*, resulting in the transfer of three species, including the type of *Huilia*, to *Amygdalaria* (Brodo & Hertel 1987). Brodo and Hertel separate *Amygdalaria* on the basis of cephalodia, tall hymenia, large spores, and a compact epispore, but *Amygdalaria* and *Porpidia* intergrade phenotypically so that some species belonging to
the different genera are quite similar. Several porpidiaceous genera have also been described as a result of work in the subantarctic (Hertel 1984). The relationships between these genera and *Porpidia* are likewise unclear.

*Porpidia* is presently considered the group of 19 species (Hertel 1984; Schwab 1986) with distinct exciples and dark hypothecia, but without any of a number of unique features that distinguish related genera (description of 11 related genera: Brodo & Hertel 1987; Hertel 1984). Each of these other porpidiaceous genera consists of fewer than five species (mostly one or two: Hertel 1984), except *Amygdalaria*, which consists of eight (Brodo & Hertel 1987). The absence of unique and likely synapomorphic traits for *Porpidia* suggests that the genus is paraphyletic, with other genera having evolved from it. The phylogeny of the family is the subject of a paper in preparation. The present study deals with delimitation of North American species.

**Materials and Methods**

The study was based on 1,351 specimens of *Porpidia* and 61 of related species collected in North America (CANT, COLO, DUKE, H, M, MICH, MIN, NY, UC, US, WISC).

Thallus and apothecial morphologies were examined with a dissecting stereoscope. Microscopic characters were studied from handmade wet mounts and occasionally microtome sections (13–15 μm) with high-dry magnification. Hymenium and subhymenial heights were estimated to the nearest 5 μm, and spore lengths and widths, as well as excipular-cell diameters, to the nearest 1 μm. Thallus thickness and apothecium diameter were estimated to the nearest tenth of a millimeter.

Extracellular secondary products were detected by a standardized method of thin-layer chromatography (Gowan 1989). A saturated solution of iodine in 10% aqueous potassium iodide (KI) was used to detect amyloid medullae and thalli. A 10% potassium hydroxide solution (K) was helpful in clearing apothecial sections and for detecting a substance in apothecial tissues that turned reddish with K (K+ reddish). Small amounts of K were occasionally applied to medullae to detect the presence of stictic or norstictic acid (K+ yellow or red). Effervescence with a 10% hydrochloric acid solution (HCl) was taken to indicate that the substrates of the lichens likely contained carbonates.

Colors of fungal tissues follow Kelly’s (1965) color chart.

I summarized the North American distributions of phenotypes according to bioclimatic and physiographic zones. For nomenclature and partitioning of North America into zones, I followed various authors: For the arctic zone, Parsild (1958); for the boreal zone, Ahti (1964), Ahti et al. (1968), and Hämet-Ahti (1981); and for the temperate zone, Braun (1950) and Küchler (1964). Gowan (1983) gives precise definitions of the biogeographic terminology used here.

**Species Concept**

Most lichen species, including those of *Porpidia*, are based solely on phenotypic characters because so little is known of the phylogenies, evolution, and extent of interbreeding populations (review: Kärnefelt 1979). In the present study, species were recognized on the basis of differences discerned in a large number of herbarium specimens. A post hoc analysis of these species shows that groups of individuals that are treated as different species either 1) differ in two or more well defined characters that are unlikely to be related genetically or developmentally; or 2) are geographically disjunct and differ by either one well defined character or a few less well defined characters. These “well defined” characters are the major thallus or apothecial characters such as spore and hymenium sizes, excipular pigmentation, pruina, color, or chemistry. Differences in these features are usually accompanied by more subtle differences such as in epithelial pigmentation, frequency of a blue subhymenial pigment, tendencies in apothecial size, or mean thallus thickness.

There is considerable debate over the validity of theoretical interpretations of species delimited by phenotype and geography (review of species concepts: Wiley 1981). I will not review the controversies but will state my interpretation in simple terms. Character correlation suggests nonrandom mixing of the characters, suggesting reproductive and phylogenetic discontinuity between phenotypes; and geographic disjunction accompanied by phenotypic difference suggests that the two disjunct groups of individuals have been separated long enough or over a large enough distance that they are now acting as different reproductive populations and evolutionary units.

The breadth of the species accepted by different authors varies. Kärnefelt (1979), for example, adopts a broad species concept, and places some widely disjunct phenotypic variants within one species. On the other end of the scale, some species exist that we do not detect with our normal methods of investigation (review: Culberson 1986). My approach has been to recognize species when there is phenotypic evidence of evolutionary divergence between groups of individuals. These are the units that will be useful in phylogenetic studies of the genus.

Most species distinctions I have recognized are based on correlated differences in major characters, and are therefore in the first category of distinctions mentioned above. The second category, incorporating geography, is illustrated by *Porpidia albocaerulescens*, *P. carlottiana*, and *P. glaucophaea* (refer to descriptions and maps). *Porpidia albocaerulescens* may or may not produce soredia, but soredium production is apparently not correlated with other characters (including the abundance of apothecia), there is a range of soralia density from esorediately to densely sorediate, and the two morphotypes are partly sympatric. Because of sympatry and inter-
gradation, I have included the two morphotypes in a single species. In contrast to the two morphotypes of *P. albocaerulescens*, the two morphotypes exhibited by *P. carlottiana* and *P. glaucophaea* are placed in two different species. *Porpidia glaucophaea* is analogous to *P. albocaerulescens* in including individuals with different soralia densities, and in Europe also includes esorediate individuals (Schwab 1986). *Porpidia carlottiana*, however, is disjunct and not known to produce soredia, and I have based the distinction between *P. carlottiana* and *P. glaucophaea* on disjunction and relative soredium and apothecium production.

The taxonomic significance of two classes of characters in lichens has been debated and is poorly understood: 1) Reproductive structure (Poelt 1970, 1972, 1974; Tehler 1982), and 2) secondary-product chemistry (e.g., Culberson & Culberson 1973). Both classes of characters vary in *Porpidia* and are important in species distinctions. As for other characters, the species distinguished on the basis of these types of characters fall into the two categories outlined above.

*Sorediate and esorediate phenotypes.*—The only two species of *Porpidia* that include sorediate and esorediate individuals are *P. albocaerulescens* and *P. glaucophaea*. In both cases, the two morphotypes are interpreted as belonging to the same species because they are sympatric and intergrade, and sorediate individuals are also commonly apotheciate. Three pairs of North American species are distinguished primarily by soredium production versus apothecium production (Table 1). Among these, there is some debate whether *P. flavocœrulescens* and *P. flavicunda* are the same species (compare Inoue 1983b and Schwab 1986). I discuss my treatment below for each species. The important factor in their taxonomic separation is that sorediate and esorediate morphotypes do not appear to intergrade with respect to density of soralia. In addition, at least in North America, sorediate specimens do not produce apothecia.

*Morphologically identical chemotypes.*—Phenotypes of *Porpidia* that produce different secondary products (called different chemotypes) are not necessarily different species. In general, a single morphotype (a morphologically uniform group of individuals) includes either a single chemotype, or one chemotype containing secondary products and another lacking them. In these cases, there is no obvious geographic or ecological correlation with the presence and absence of secondary products, and I recognize a single species.

In three species—*P. albocaerulescens*, *P. flavicunda*, and *P. flavocœrulescens*—morphotypes are represented by two or more qualitatively different chemotypes. In these as well, there is no clear geographic correlation with the chemical variation. The distributions of some of the chemotypes are not identical (*P. albocaerulescens*: Fig. 23–24), but I hesitate to recognize species based on this evidence.

In *P. flavicunda* and *P. flavocœrulescens*, compounds normally found only in different specimens have been confirmed together in single specimens (Gowan 1989), and this further suggests that chemotypes are not necessarily species in *Porpidia*.

**Overview of Characters**

Most of the characters that have proved useful for distinguishing species of *Porpidia* are qualitative, consisting of character states distinguished by observation. Examples of these characters are thallus color, presence of pruina, presence of soredia, and density of the pigmentation in the exciple. I also measured seven anatomical or morphological features. The variation in these seven characters and in two ratios formed from them is represented in Table 2. The means for the quantitative characters are given as the middle number in the ranges presented in the descriptions of species.

Pycnidia are rare in *Porpidia*. Hertel (1984) and Knoph (1984) have observed them in a few European and subantarctic species, but I have not yet seen them in North American material. All the black spots that I have sectioned were lichenicolous fungi. The rarity of pycnidia raises the question of how *Porpidia* and many other lichens reproduce sexually in the absence of spermia.

**Thallus (Fig. 1–7).**—The thallus of *Porpidia* ranges from endolithic (Fig. 1), living between crystals below the rock surface, to epilithic. Epilithic thalli are from less than 0.1 mm (e.g., *P. tahawasiana* and *P. thomsonii*) to over 1.5 mm thick (*P. cinereoastra*). Epilithic thalli are continuous in all species except *P. superba*, which forms dispersed, convex (bullate) areolae, and *P. tuberculosa* and *P. grisea*, which consist of patches of thallus on a well developed prothallus (Fig. 2). Continuous thalli may be almost completely uncracked (a few specimens of *P. albocaerulescens*), finely cracked or subrimose (e.g., *P. pseudomelinodes* and *P. tuberculosa*: Fig. 2–3) or strongly rimose-areolate (*P. flavicunda*: Fig. 4). Some thalli are verruculose or rugulose (common in *P. crustulata* and *P. macrocarpa*: Fig. 5). Only in *P.

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**Table 1.** North American species pairs in *Porpidia*, distinguished by soredium and apothecium production.

<table>
<thead>
<tr>
<th>Sorediate but nonapotheciate</th>
<th>Normally apotheciate but esorediate</th>
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<tbody>
<tr>
<td><em>P. glaucophaea</em></td>
<td><em>P. carlottiana</em></td>
</tr>
<tr>
<td><em>P. flavocœrulescens</em></td>
<td><em>P. flavicunda</em></td>
</tr>
<tr>
<td><em>P. tuberculosa</em></td>
<td><em>P. grisea</em></td>
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</tbody>
</table>
TABLE 2. Means and their 95% confidence intervals of seven structural or morphological measurements of *Porpidia* and two ratios formed from them. The numbers in parentheses are the numbers of observations. Spore lengths and widths are based on averages of 1–11 measurements taken from each specimen; Spore shape is the ratio of average spore length to average spore width; hymenium and subhymenium heights and excipular cell diameters are midpoints between the highest and lowest measurements taken on specimens; hymenium/subhymenium is the ratio of these hymenium and subhymenium heights; thallus thicknesses and apothecium diameters are maximum values.

<table>
<thead>
<tr>
<th>Spore length (µm)</th>
<th>Spore width (µm)</th>
<th>Spore shape</th>
<th>Hymenium height (µm)</th>
<th>Subhymenium height (µm)</th>
<th>Hymenium/subhymenium</th>
<th>Excipular cell thickness (µm)</th>
<th>Thallus thickness (µm)</th>
<th>Apothecium diameter (µm)</th>
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<tr>
<td><strong>P. alboaculelosa complex</strong></td>
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<tr>
<td>alboaculelosa</td>
<td>19.5 ± 1.0(11)</td>
<td>8.2 ± 0.9(11)</td>
<td>2.4 ± 0.2(11)</td>
<td>91.9 ± 3.5(34)</td>
<td>33.6 ± 2.8(34)</td>
<td>2.9 ± 0.2(34)</td>
<td>2.7 ± 0.4(16)</td>
<td>0.30 ± 0.06(17)</td>
</tr>
<tr>
<td>carlottiana</td>
<td>18.1 ± 0.6(10)</td>
<td>8.1 ± 0.3(10)</td>
<td>2.3 ± 0.1(10)</td>
<td>99.2 ± 7.0(10)</td>
<td>32.7 ± 5.7(10)</td>
<td>3.2 ± 0.6(10)</td>
<td>2.8 ± 0.2(10)</td>
<td>0.26 ± 0.07(10)</td>
</tr>
<tr>
<td>flavicunda</td>
<td>18.2 ± 0.7(16)</td>
<td>9.3 ± 0.9(15)</td>
<td>2.0 ± 0.1(15)</td>
<td>97.1 ± 5.1(23)</td>
<td>35.3 ± 3.0(21)</td>
<td>2.8 ± 0.3(21)</td>
<td>2.7 ± 0.4(11)</td>
<td>0.72 ± 0.19(13)</td>
</tr>
<tr>
<td>flavoaculelosa</td>
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<tr>
<td>glaucophana</td>
<td>16.5 ± 19.1(2)</td>
<td>7.5 ± 6.4(2)</td>
<td>2.2 ± 0.7(2)</td>
<td>87.5 ± 31.8(2)</td>
<td>27.5 ± 31.8(2)</td>
<td>3.2 ± 2.5(2)</td>
<td>2.5(1)</td>
<td>0.47 ± 0.27(4)</td>
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<td>pseudomaloe</td>
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<tr>
<td><strong>P. macrocarpa complex</strong></td>
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<tr>
<td>contraonpona</td>
<td>16.8 ± 1.1(13)</td>
<td>7.7 ± 0.5(13)</td>
<td>2.2 ± 0.1(13)</td>
<td>96.4 ± 8.2(14)</td>
<td>23.1 ± 3.2(14)</td>
<td>4.3 ± 0.6(14)</td>
<td>4.1 ± 0.2(11)</td>
<td>0.21 ± 0.13(12)</td>
</tr>
<tr>
<td>crustulata</td>
<td>13.1 ± 0.2(115)</td>
<td>6.5 ± 0.1(115)</td>
<td>2.0 ± 0.4(115)</td>
<td>68.3 ± 1.2(124)</td>
<td>16.9 ± 0.7(120)</td>
<td>4.2 ± 0.2(120)</td>
<td>6.6 ± 0.2(73)</td>
<td>0.17 ± 0.03(61)</td>
</tr>
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<td>diversa</td>
<td>16.5 ± 1.0(18)</td>
<td>7.8 ± 0.5(18)</td>
<td>2.1 ± 0.1(18)</td>
<td>83.9 ± 4.6(19)</td>
<td>22.1 ± 2.7(19)</td>
<td>4.0 ± 0.5(19)</td>
<td>4.2 ± 0.3(16)</td>
<td>0.31 ± 0.11(11)</td>
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<td>herteliana</td>
<td>13.0 ± 0.5(22)</td>
<td>6.4 ± 0.3(22)</td>
<td>2.0 ± 0.7(22)</td>
<td>79.1 ± 3.7(22)</td>
<td>23.4 ± 2.6(22)</td>
<td>3.6 ± 0.5(22)</td>
<td>4.2 ± 0.2(18)</td>
<td>0.25 ± 0.09(14)</td>
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<td>macrocarpa</td>
<td>17.6 ± 0.3(86)</td>
<td>8.0 ± 0.2(86)</td>
<td>2.2 ± 0.0(86)</td>
<td>91.1 ± 2.2(100)</td>
<td>26.8 ± 1.4(95)</td>
<td>3.6 ± 0.2(95)</td>
<td>4.1 ± 0.1(78)</td>
<td>0.23 ± 0.04(64)</td>
</tr>
<tr>
<td>tahawasiana</td>
<td>13.3 ± 0.7(13)</td>
<td>6.3 ± 0.7(13)</td>
<td>2.1 ± 0.2(13)</td>
<td>82.3 ± 4.0(13)</td>
<td>24.6 ± 5.3(13)</td>
<td>3.7 ± 0.8(13)</td>
<td>4.2 ± 0.3(10)</td>
<td>0.10 ± 0.05(13)</td>
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<td>thomsonii</td>
<td>16.7 ± 0.3(75)</td>
<td>7.6 ± 0.2(74)</td>
<td>2.2 ± 0.1(74)</td>
<td>88.4 ± 2.6(76)</td>
<td>24.5 ± 1.6(76)</td>
<td>3.9 ± 0.3(76)</td>
<td>5.7 ± 0.2(69)</td>
<td>0.13 ± 0.05(32)</td>
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<tr>
<td><strong>P. speirea complex</strong></td>
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<tr>
<td>cinereostea</td>
<td>13.6 ± 0.6(16)</td>
<td>6.6 ± 0.4(16)</td>
<td>2.1 ± 0.1(16)</td>
<td>80.2 ± 5.9(17)</td>
<td>27.4 ± 4.0(17)</td>
<td>3.2 ± 0.4(17)</td>
<td>4.2 ± 0.5(13)</td>
<td>0.82 ± 0.17(15)</td>
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<td>grisea</td>
<td>13.0 ± 1.6(5)</td>
<td>6.2 ± 0.7(5)</td>
<td>2.1 ± 0.3(5)</td>
<td>70.0 ± 18.2(5)</td>
<td>27.0 ± 17.9(5)</td>
<td>3.1 ± 1.5(5)</td>
<td>4.0 ± 0.0(4)</td>
<td>0.20 ± 0.13(4)</td>
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<td>kowiana</td>
<td>12.6 ± 0.7(5)</td>
<td>6.9 ± 0.9(5)</td>
<td>1.8 ± 0.2(5)</td>
<td>75.0 ± 13.9(5)</td>
<td>34.4 ± 11.1(5)</td>
<td>2.3 ± 0.8(5)</td>
<td>4.0 ± 0.0(4)</td>
<td>0.30 ± 0.12(5)</td>
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<td>speirea</td>
<td>14.2 ± 1.5(8)</td>
<td>6.7 ± 1.2(8)</td>
<td>2.2 ± 0.5(8)</td>
<td>69.1 ± 7.9(8)</td>
<td>34.4 ± 11.7(8)</td>
<td>2.3 ± 0.8(8)</td>
<td>4.1 ± 0.2(7)</td>
<td>0.26 ± 0.05(7)</td>
</tr>
<tr>
<td>tuberculosa</td>
<td>14.0 ± 12.7(2)</td>
<td>6.5 ± 6.4(2)</td>
<td>2.2 ± 2.6(2)</td>
<td>72.5 ± 31.8(2)</td>
<td>37.5 ± 95.3(2)</td>
<td>2.0 ± 4.2(2)</td>
<td>4.0(1)</td>
<td>0.30 ± 0.31(4)</td>
</tr>
<tr>
<td><strong>P. superba complex</strong></td>
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<tr>
<td>oscidea</td>
<td>17.8 ± 3.2(5)</td>
<td>9.2 ± 0.6(5)</td>
<td>1.9 ± 0.2(5)</td>
<td>102.2 ± 22.6(5)</td>
<td>29.4 ± 10.2(5)</td>
<td>3.6 ± 0.9(5)</td>
<td>5.2 ± 0.6(5)</td>
<td>0.86 ± 0.45(5)</td>
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<td>superba</td>
<td>20.7 ± 2.9(3)</td>
<td>9.0 ± 2.5(3)</td>
<td>2.3 ± 0.7(3)</td>
<td>119 ± 2.9(3)</td>
<td>24.3 ± 15.0(3)</td>
<td>5.1 ± 3.2(3)</td>
<td>6.0 ± 5.0(3)</td>
<td>0.53 ± 0.28(3)</td>
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<td>zeoides</td>
<td>19.2 ± 1.4(6)</td>
<td>9.0 ± 1.2(6)</td>
<td>2.1 ± 0.2(6)</td>
<td>109.5 ± 13.2(6)</td>
<td>23.0 ± 4.1(6)</td>
<td>4.8 ± 0.77(6)</td>
<td>5.4 ± 0.7(5)</td>
<td>0.43 ± 0.16(6)</td>
</tr>
</tbody>
</table>
calcarea and P. superba is the thallus bullate (Fig. 6).

A prothallus may be present in most species. The prothallus may develop between patches of thallus (P. tuberculosa, P. grisea, and endolithic species such as P. thomsonii and P. tahawasiana). The prothallus is continuous in some of these species (P. tuberculosa and P. grisea: Fig. 2) whereas it consists of very thin irregular strands in other species (P. thomsonii and P. tahawasiana: Fig. 1). Species with continuous thalli normally form a narrow marginal prothallus, especially when the thallus abuts another lichen of the same or different species (Fig. 7).

The thallus of all species is heteromeronous with an upper cortex and a thin algal layer. The thickness of the white medulla varies with thallus thickness. The cortex may be orange, gray, or white. Species that grow on siliceous rocks normally have a smooth, slightly glossy upper surface; species that grow on carbonate-containing substrates normally have a white, chalky-to-scabrid surface (description of the chalky surface of calciferous species: Hertel 1967; illustration: Fig. 6).

Soredia (Fig. 2–3, 34).—Six North American species are sorediate. In P. glaucophaeae, soralia are irregular in shape and size (Fig. 34), and they form along cracks in the thallus. In all other species, soralia are round or roundish, slightly raised, usually discrete, and 0.2–1.0 mm in diameter (Fig. 2–3).

Apothecia (Fig. 8).—The apothecia of Porphidia are hemiangularcapric, arising from within the thallus and first visible as tiny black dots on the surface. Apothecia at this stage are enclosed by the apothecial margin except for a small apical opening, and are covered with pruina. The margins open to expose the disks, which are fully exposed at maturity. As the disks broaden, they can be distinguished as either pruinose or nonpruinose. The density of pruina varies within species, but subtle differences in pruina density can help distinguish some species. The difference between P. flavicunda and P. albocaerulescens provides an example. The former is more weakly pruinose than the latter (Fig. 15, 32).

The apothecia of some species remain depressed in the thallus (with exposed disks and margins) until maturity. Those of other species soon become sessile. With some exceptions (e.g., P. carlottiana), depressed apothecia normally occur on thalli more than approximately 0.4 mm thick, and sessile apothecia occur on thin thalli. In some species that typically have a thin thallus (e.g., P. crustulata and P. macrocarpa), the thallus may become moderately thick (to 0.6 mm). On such thick thalli, the normally sessile apothecia may remain depressed until maturity.

Apothecial anatomy (Fig. 9–14). — The exciples of Porphidia are lecideine in the broad sense, lacking algae. They can be distinguished as either cellular or hyphal. The hyphal type exists only in the P. albocaerulescens complex (complexes are defined below). This type of exciple consists of radiating, branched hyphae originating from the hypothecium, with cross walls cutting off oblong to linear segments 2–4 μm in diameter (Fig. 9–10). The cellular type of exciple, which occurs in all species outside the P. albocaerulescens complex, is composed of radiating rows of subglobose to oblong cells, 3–9 μm in diameter (Fig. 11–13).

Pigmentation in the excipular cell walls is a useful character to distinguish some species. The outer margin of the exciple is very heavily pigmented in all species, from greenish to brownish black. Occasionally a thin, hyaline, possibly gelatinous layer can be discerned outside this dark layer. It occurs sporadically in several species: It is illustrated in Figure 10 in P. flavicunda, and Inoue (1982) illustrates it in P. speirea.

The inner part of the exciple varies from unpigmented to almost black, depending on the species. In the P. albocaerulescens complex the inner exciple is moderately brown to unpigmented (unpigmented in P. albocaerulescens: Fig. 9; moderately pigmented in P. flavicunda: Fig. 10). The unpigmented exciples appear grayish and opaque in section.

In most members of the P. macrocarpa complex, the exciple is brown within, and varies among species from pale brown (P. macrocarpa: Fig. 12; P. crastulata: Fig. 13) to dark brown (P. thomsonii: Fig. 11).

A third pigmentation pattern characterizes the P. speirea complex and some members of the P. macrocarpa complex (Fig. 14). The exciple in these species is so dark as to appear black in all but the thinnest sections (thinner than about 10–15 μm). In such thin sections, the cell lumina are exposed and the pigment can be seen encrusting the cell walls between the lumina. This pigmentation pattern has been called carbonaceous (Lowe 1939) or kohlig by German authors (e.g., Hertel 1984).

In immature apothecia of the species with carbonaceous exciples, a hyaline layer can often be discerned within the outer dark layer. In most species the outer carbonaceous layer is the thicker (30–75 μm) and the inner hyaline layer thinner (10–20 μm). In P. speirea this situation is reversed, so that the outer layer is thinner (10–25 μm) and the inner layer thicker (20–40 μm). The inner layer is reduced and usually imperceptible in mature apothecia of all these species except P. speirea. In P. speirea this inner layer is still perceptible in mature apothecia.

The exciple of all species may be reduced in mature apothecia to a narrow, dark margin (20–40 μm). These reduced margins are especially common on convex apothecia, and the three pigmentation pat-
tars cannot be distinguished because of the reduction.

The hymenium can be distinguished from a hyaline subhymenium (Hertel 1967). Below the subhymenium is a dark-brown hypothecium. Paraphyses (illustrations: Hafellner 1984; Inoue 1983a,b,c) are conglutinate and interconnected by short hyphal segments perpendicular or oblique to the paraphyses (anastomosed). The upper 10–20 μm of the paraphyses are often fuscate or bifurcate. The extent of anastomosing and apical branching appears to vary slightly among species, being least in the *P. albocaerulescens* complex.

The paraphyses tips contain pigments varying from orange-brown through olive to green.

Asci are unitunicate and clavate, with a large tholus (illustration: Hafellner 1984). The major part of the tholus is weakly amyloid, and this region contains a strongly amyloid cylindrical region within it. The cylindrical region varies from about half the length of the tholus to completely filling it, and this inner region may be uncapped or capped (illustration of the tholus of *Stephanocyclos*, which contains a capped cylinder: Hafellner 1984). I did not make a systematic study of tholus variability, but can confirm Hertel and Ramboldt’s (1985) finding that the size of the cylinder in the tholus varies within species.

Spores are irregularly arranged and biseriate in the asci. They are ellipsoid (to tear-drop-shaped in *P. macrocarpa*), hyaline, and 1.8–2.8 times longer than broad. They retain a segment of the epithecium throughout maturity, visible as a hyaline halo 2–7 μm thick.

Chemistry.—The secondary-product chemistry has been treated by Gowan (1989). Two major biogenetic-pathway types exist in the genus, one leading

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to β-orcinol depsidones, and the other to long-sidechain orcinol depsides (a third pathway, to short-sidechain depsides, exists in closely related species of Amygdalaria). All of these compounds occur in repeating sets called chemosyndromes. Among the β-orcinol depsidones, two sets of compounds occur, one dominated by stictic acid, the other by norstictic acid. Among the orcinol depsides there are four sets of compounds: one dominated by 2′-O-methylypsophyllinic acid, one by methyl 2′-O-methylmircophyllinate, one by confluentic acid, and the final one sharing dominance between confluentic and 2′-O-methylperlatolic acids.

Some specimens of P. macrocarpa and related species produce a blue pigment in the medulla near the apothecial base.

All North American species of Porpidia sometimes produce a K+ reddish substance in the exciple and hypothecium. This substance has been used as a character to distinguish species in the past (e.g., in P. phylliscina: Lowe 1939), but it appears to be taxonomically insignificant since it occurs in all morphotypes and is not correlated with other characters.

An important character distinguishing P. grisea, P. tuberculosa, and P. speirea from other species of the genus is the amyloid medulla. All other species of the genus have algal layers that are amyloid, but the medullae are not amyloid.

Ecology.—All species of Porpidia are primarily saxicolous. Each species occurs almost always on either HCl+ or HCl− substrates. A single specimen of P. macrocarpa and one likely P. cinereoastra have been observed from lignum (likely Picea). Habitats vary from shaded (P. albocaerulescens) to unshaded (most species). All species thrive in humid climates, and a few species (e.g., P. carlottiana, P. contraponenda, and P. glaucophae) are restricted to oceanic regions.

Distribution.—Porpidia is common in the arctic and the temperate zones, relatively rarer in the boreal zone, but common in the oroboreal and alpine zones in temperate regions. Distribution patterns of North American lichens have been described by previous authors (Ahti 1964, 1977; Brodo 1968; Brodo & Gowan 1983; Dey 1977), and distributions of most species are consistent with patterns formed by other groups. Some species are still poorly understood because of the small number of collections and the lack of experimental work done to determine physiological types or other forms of sibling species. Some of the species that I recognize, however, have distributions that are inconsistent with well known patterns (e.g., P. thomsonii: Fig. 58). As the genus is presently understood, the distribution patterns can be summarized as follows.

The species collected solely or predominantly in the Arctic show three distribution types: The first type, represented by P. flavicunda and P. lowiana (Fig. 40–43, 52), extends across North America; the second, represented by P. superba and P. zeoroides (Fig. 62, 66), is western; and the third, represented by P. flavocoerulescens (Fig. 44–48), is mainly eastern but disjunct in the Aleutian Islands. These five species that center in the Arctic are not known to extend south in the western alpine zone, but one species (P. flavicunda) has been collected in the alpine zone of eastern North America, in the northern Appalachian Mountains.

Brodo and Gowan (1983) point out that most North American arctic lichens are broadly distributed in the northern hemisphere. Among North American species of Porpidia, P. flavicunda, P. flavocoerulescens, and P. superba are also known from parts of Europe and Asia. Porpidia zeoroides is known from Europe, and P. lowiana is known only from North America.

Porpidia pseudomelinodes (Fig. 54) is the only species of Porpidia most concentrated in the alpine of western North America, with one specimen known from the Arctic and a few from the eastern hemiboreal zone. This is a peculiar distribution for lichens. The taxonomy of P. pseudomelinodes requires more work in North America, and I suspect that the eastern individuals are distinct from the arctic and alpine ones. This species also occurs in the Alps, in habitats similar to those where it occurs in the Rocky Mountains (Schwab 1986).

Porpidia thomsonii (Fig. 64) is common in both the arctic and alpine zones with phenotypically similar individuals on the West Coast. Like the P. pseudomelinodes morphotype, P. thomsonii may contain different physiological types.

Porpidia grisea (Fig. 50) is about equally abundant in the arctic and northern boreal zones. I have seen very few specimens of this species and have included specimens with both IKI+ and IKI− medullae. Its taxonomy and distribution may also be clarified with more collections.

Porpidia speirea (Fig. 61) occurs both in the arctic and the eastern hemiboreal zones. Like P. grisea, this species is poorly collected and poorly understood. The disjunct distribution may suggest that there is more than one species included.

Three species are boreal and oceanic. Two of these, P. contraponenda and P. carlottiana (Fig. 27, 29), are on the West Coast. Porpidia glaucophae (Fig. 49), closely related to P. carlottiana, is eastern. A boreal oceanic distribution has been described for lichens, and examples from several genera are listed by Gowan (1983). Conspecific individuals or close relatives of these boreal oceanic species occur in Europe.

Five species, P. cinereoastra, P. diversa, P. herte-
liana, P. tahawasiana, and P. tuberculosa (Fig. 28, 31, 51, 63, 65), occur most abundantly in the eastern southern boreal, hemiboreal, and oroboreal zones (the Appalachian–Great Lakes Region of, e.g., Brodo 1968; Brodo & Gowan 1983). Among these species, the eastern specimens of P. tuberculosa appear to be conspecific with specimens from the western arctic and northern alpine zones. The Appalachian–Great Lakes distribution is well known for lichens. Among species with this general North American distribution type, world distributions vary (Gowan 1983). Within the genus Porpidia, Appalachian–Great Lakes species are either known only from North America and Europe (P. cinereoatra and P. tuberculosa) or they are endemic (all other species).

Porpidia calcarea (Fig. 26) is restricted to the shores of Lake Superior in the hemiboreal and southern boreal zones. This species is closely related to the two western arctic species P. superba and P. zeoroides. Disjunction between the Arctic and the north shore of Lake Superior is known in vascular plants (Gowan & Soper 1981) and lichens (Brodo & Gowan 1983). Porpidia calcarea is intermediate in some characters between P. superba and P. zeoroides, suggesting that P. calcarea may have been separated from the ancestor of P. superba and P. zeoroides before the latter two speciated. A likely time for the separation is the Pleistocene, when organisms of arctic climates were offered disjunct glacier-free refuges in the western Arctic and south of the glaciers (Dott & Batten 1981).

Three species have been collected mainly in the temperate zone. Porpidia albocaerulescens (Fig. 23–25) is restricted to the East. It has been collected throughout most of the forested eastern temperate zone (excluding the forested parts of the southeastern coastal plain), and has been most abundantly collected in the Appalachian–Great Lakes Region. Porpidia crustulata (Fig. 30) and P. macrocarpa (Fig. 53) are likewise distributed through most of the forested eastern temperate zone but are also known from farther west. All three of these temperate species follow the pattern of many other widespread temperate species in occurring also in Europe and Asia.

Other species, for example P. superba, are similar to some species of Amygdalaria, with a tall hymenium, large spores, and a bullate-areolate thallus (description of Amygdalaria, and discussion of the relationship between Amygdalaria and Porpidia: Brodo & Hertel 1987). Similarities can be noted between Porpidia and other genera of the Porpidiaceae. Several genera share a carbonaceous exciple with some members of Porpidia. The apothecia of P. tahawasiana are strikingly similar to those of Stephanocyclos hensennianus. As mentioned previously, the generic limits within the Porpidiaceae are unsettled. Porpidia appears to be a residual genus lacking the specialized characters of other genera.

Four phenetic subgroups can be recognized among North American species (Tables 2–3): 1) The P. albocaerulescens complex, with narrow excipular cells and heavily pruinose apothecial disks; 2) the P. macrocarpa complex, with thin thallus, nonpruinose or very rarely pruinose disks, and a blue subhypothecial pigment (absent in some individuals of every species); 3) the P. speirea complex with carbonaceous exciple, small spores, generally a short hymenium, and a short hymenium-to-subhymenium ratio; and 4) the P. superba complex, with tall hymenium and usually an HCl+ substrate.

The characters of Porpidia and the Porpidiaceae have been analyzed phylogenetically (Gowan, in prep.). The analyses suggest that, of the four phenetic complexes of Porpidia, only the albocaerulescens complex is monophyletic, whereas the others are paraphyletic. The albocaerulescens and superba complexes contain the most derived species in the genus. The speirea complex is the least derived and the macrocarpa complex is intermediate. These detailed analyses will be published separately.

About 30 unidentifiable specimens remained after the study. Most of these specimens had an IKI− medulla, HCl− substrate and confluent acid, and they belong either to the P. macrocarpa complex or the P. speirea complex. More collections will be needed to understand these species.

INFRAGENERIC RELATIONSHIPS

The 21 North American species of Porpidia consist of 14 previously described species and seven new ones. In including all these in one genus, I have accepted a broad range of phenotypes compared to the range in other genera of the Porpidiaceae. Some species are similar to Lecidea s. str., having small spores, a hyaline layer in the inner exciple, short hymenium, tall subhymenium and IKI+ medulla (especially P. speirea, P. grisea, and P. tuberculosa).
### Table 3. Characteristics of the four phenetic subgroups of *Porpidia* (see Table 2 for North American members).  

<table>
<thead>
<tr>
<th></th>
<th>Thallus thickness (µm)</th>
<th>Amyloid medulla</th>
<th>Chalky thallus</th>
<th>Blue sub-hypothecial pigment</th>
<th>Pruinose apothecia</th>
<th>Spore length (µm)</th>
<th>Hymenium height (µm)</th>
<th>Minimum hymenium/subhymenium ratio</th>
<th>Excipular cell diameter (µm)</th>
<th>HCl+ substrate</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>P. albocaerulescens</em> complex</td>
<td>0.2–1.2</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>−</td>
<td>14–26</td>
<td>75–120</td>
<td>&gt;2</td>
<td>2–4</td>
<td>−</td>
</tr>
<tr>
<td><em>P. macrocarpa</em> complex</td>
<td>0.0–0.6</td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>10–23</td>
<td>60–120</td>
<td>&gt;2</td>
<td>3–9</td>
<td>−</td>
</tr>
<tr>
<td><em>P. speirea</em> complex</td>
<td>0.1–1.5</td>
<td>±</td>
<td>±</td>
<td>±</td>
<td>+</td>
<td>13–18</td>
<td>60–100</td>
<td>&lt;2</td>
<td>3–5</td>
<td>±</td>
</tr>
<tr>
<td><em>P. superba</em> complex</td>
<td>0.5–1.0</td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>±</td>
<td>14–25</td>
<td>85–130</td>
<td>&gt;2</td>
<td>3–6</td>
<td>±</td>
</tr>
</tbody>
</table>

**thallus center; prothallus present (especially between adjacent thalli) or absent, black or sometimes orange when thalli are also orange, thin; medulla IK1+ or IK1−; soredia present or absent, either forming irregularly and diffusely in cracks in the thallus, or more commonly forming discrete and regular, round soralia.**

Apothecia present or absent (normally absent only in sorediate species), scattered or clustered, sometimes arranged in concentric rings, hemiangiocarpous, emerging from small pruinose dots on the thallus, becoming sessile in some species; disks black to dark brown, pruinose or bare; margin bare or sometimes with white or orange pruina extending upward from the thallus, even to crenulate or radially grooved, regular, flexuose or invaginated. Hymenium 60–130 µm high, hyaline to translucent green or olivaceous in the upper part or rarely below; paraphyses completely conglutinate to rarely basally free, anastomosed, often branched in the upper 15–20 µm; epithecium clear orange-brown to olivaceous to aeruginose, littered with granular material on pruinose apothecia, clear on others; subhymenium (10–)15–50(–60) µm high, hyaline. Exciple either completely black and carbonaceous (usually with a thin hyaline region to the inside when immature) or black only at the margin and paler to hyaline within, perceptibly radiating from the hypothecial region and consisting of conglutinate hyphae or of conglutinate rows of more or less ellipsoidal cells, often producing a K+ reddish substance; hypothecium dark brown to more or less black.

**Secondary products.**—Long-sidechain depsides or β-orcinol depsidones, or both, sometimes present; unidentified triterpenes and unidentified pigment SV-1 sporadic in most species.

**Habitat.**—Most species on hard siliceous rocks such as granites, diorites, and metamorphosed derivatives, less common on sandstone; some species on carbonate-containing (HCl+) rocks.

**North American distribution (north of Mexico).**—Temperate to arctic.

**World distribution.**—Tropical (possibly only in mountainous regions) to polar, in the northern and southern hemispheres.

### Key to the North American Species of *Porpidia*

1. Soredia present .................................................. 2
2. Soredia absent .................................................. 9
3. Thallus mostly orange, rarely with minor gray patches ............ 3
4. Thallus mostly gray, at most patchily orange ................. 5
5. Thallus very thin (0.2 mm); soralia irregular and often confluent, 0.2–1.0 mm diameter. Eastern boreal ................................ cf. *P. soredizodes* (see Excluded Species) ......... 4
6. Thallus thicker (0.2–0.8 mm); soralia regular, roundish and mostly remaining discrete .......... 4
7. Soralia 0.3–1.0 mm diameter; soredia white or flecked with gray; lacking conflucent acid; thallus more or less continuous, often finely cracked but rarely subrimose to rimose. Mainly western alpine; rare in arctic and eastern temperate mountainous regions .......... 4
8. Soralia 0.2–0.8 mm diameter; soredia flecked with black; containing conflucent acid; thallus subrimose to rimose. Arctic ......................... cf. *P. pseudomeliniodes* .......... 5
9. Containing stictic or norstictic acid, or both (medulla K+ yellow to red). Eastern temperate or arctic-alpine ............................................. 6
10. Lacking stictic and norstictic acid. Eastern boreal ........... 8
11. Soralia pale yellow; norstictic acid present but stictic acid absent (medulla K+ red); thallus continuous only when young, becoming dispersed areolate on a well developed prothallus. Arctic-alpine ................................ cf. *Porpidia sp.* (see Excluded Species) .......... 7
12. Soralia pale gray; stictic acid present with norstictic acid as a minor constituent (medulla K+ yellow or orange); thallus continuous. Rare in the eastern temperate zone .......... 7
13. Thallus thick (0.6–1.0 mm); soralia regular in shape, mostly not confluent ... *P. albocaerulescens* .......... 7
14. Thallus thin (0.2 mm); soralia irregular in shape, often confluent ................................ cf. *P. soredizodes* (see Excluded Species) .......... 8
15. Medulla IK1−; soralia irregular, forming along cracks in the thallus; containing 2′-O-methylsuperphyllinic acid. Oceanic ................................ cf. *P. glaucophaea* .......... 8
17. Medulla IKI+-; soralia round, forming discrete patches; containing conflucent acid.
Oceanic or continental P. TUBERCULOSA
18. Thallus orange, with occasional gray patches 10
19. Thallus gray to white, at most with small irregular orange patches .......................... 11
20. Medulla IKI +; soralia round, forming discrete patches; containing conflucent acid.
Oceanic or continental P. TUBERCULOSA
21. Thallus orange, with occasional gray patches ........................................ 10
22. Thallus gray to white, at most with small irregular orange patches ......................... 11
23. Medulla IKI +; soralia round, forming discrete patches; containing conflucent acid.
Oceanic or continental P. TUBERCULOSA
24. Thallus orange, with occasional gray patches ........................................ 10
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Oceanic or continental P. TUBERCULOSA
25. Thallus orange, with occasional gray patches 10

21. Containing methyl 2'-O-methylmicrophyllinate ........................................ 22
22. Containing stictic acid or lacking secondary products ........................................ 23
23. Containing methyl 2'-O-methylmicrophyllinate ........................................ 22
24. Containing stictic acid or lacking secondary products ........................................ 23
25. Containing methyl 2'-O-methylmicrophyllinate ........................................ 22

1984. (Fig. 9, 15, 23-25)


Thallus usually light greenish gray to whitish, sometimes dark greenish gray to olive gray, rarely with orange patches, continuous, usually very finely cracked to subrimose when dry, less commonly coarsely rimose (particularly in exposed habitats), nonrimose when wet, 0.2–0.30–1.0–1.5 mm thick (some quite thin thalli, ca. 0.2 mm thick, seen from the southern Appalachian Mountains), even to infrequently verruculose or rugulose; margin distinct, usually thinner than the thallus center; prothallus black, often weak or absent but usually present in thalli growing over or abutting others; medulla IKI—; soredia rare, only in exposed habitats in the Appalachian–Great Lakes Region; soralia round, 0.7–1.0 mm in diameter.

Apothecia usually abundant, especially toward thallus center, usually evenly scattered, infrequently contiguous or clustered, sunken in thallus when young, broadly sessile or remaining sunken when mature, 0.8–1.5–2.0 mm diameter when mature;
disk black or less commonly dark brown, with thick, white or whitish pruina (or sometimes bare when decrepit or growing on intermittently submerged rocks); margin bare, thin to thick, even to infrequently weakly crenulate, regular to weakly flexuose. Hymenium 75–92–110 μm high; paraphyses conglutinate and indistinct above or a few free over part of their length, weakly to moderately anastomosed, weakly branched in upper 10–15 μm; epithecium brown to olive brown, littered with granular material; subhymenium 25–34–40(–50) μm high. Exciple of conglutinate, branched hyphae, radiating from hypothecial region, dark brown to blackish at exciple margin, opaque gray or weakly pigmented brown within; excipular hyphae narrow (2–2.7–4 μm); immature asci common. Spores (15–)18–20–21(–26) × 8–8.2–12 μm.

Secondary products. – Chemotype I: Stictic acid (major constituent), cryptostictic acid, Per-1, constrictic acid, norstictic acid, traces of hypostictic or menegazziaic acids, or both, sometimes apparent on heavily spotted TLC plates; unidentified triterpenes and SV-1 rarely present. Chemotype II: Norstictic acid (major constituent) and a trace of connorstitic acid.

Habitat. — HCl–rocks, particularly common in humid, shaded areas; often along waterways.

North American distribution (Fig. 23–25). — Eastern temperate United States and adjacent Canada, north to the hemiboreal and possibly southern boreal zone, not known in the southeastern coastal plain (Virginia south). The norstictic acid chemotype is within the range of the stictic acid chemotype. The sorediate morphotype is known only from the Appalachian Mountains and the Great Lakes Region.

World distribution. – Middle Europe, eastern to southeastern Asia, Himalaya Mountains, Australia and New Zealand (Hertel 1977, 1981a,b; Hertel & Knoph 1984; Inoue 1983a).

Distribution maps. — Europe, eastern North America, and world (Hertel & Knoph 1984).

Porpidia albocaerulescens is very common and distinctive and it can be identified at sight in the field. Its smooth, light, rather thick thallus, pruinose disks and sunken or partially sunken apothecia distinguish it from other eastern temperate crustose lichens. The related eastern boreal oceanic species is P. glaucopea. Porpidia cinereoatra may appear similar macroscopically. Though these two species overlap in distribution, P. cinereoatra is more northern or montane in distribution; its thallus is darker gray and usually more distinctly rimose. The presence of stictic acid, noncarbonaceous exciple and large spores easily distinguish P. albocaerulescens.

Although the thallus of P. albocaerulescens is usually thick, thalli as thin as normal specimens of the P. macrocarpa complex can be found in the high-elevation spruce-fir forests in the southern Appalachian Mountains. Pruinose apothecia are usually reliable for distinguishing these specimens from other temperate species with a thin thallus.

The norstictic acid chemotype is the rarer one. It centers in mountainous regions in eastern Asia and eastern North America. Its North American range is completely within that of the stictic acid chemotype. It is not known whether the norstictic and stictic acid phenotypes behave in nature as a single population. Hertel and Knoph (1984) feel that their taxonomic recognition may be unwarranted. Without greater differences between the chemotypes and their distributions, I also recognize them as a single species.

Hertel and Knoph (1984) discuss the variation and relationships of P. albocaerulescens in Europe, and Inoue (1983a) discusses it in Japan. As in eastern North America, its European and Asian habitat is siliceous rock, mainly in temperate forests. The
Distinctic acid chemotype is the more common in North America and Japan (Inoue 1983a); in Europe it is the only one (Hertel & Knoph 1984). Contrary to some earlier reports (Degelius 1982; Santesson 1984), _P. albocaeurelenscens_ is rare in Europe and restricted to the central regions (Hertel & Knoph 1984). In Asia, it grows from subtropical to subalpine climates, extending from Australia to China and Japan (Hertel & Knoph 1984; Inoue 1983a).

Inoue (1983a) as well as Hertel and Knoph (1984) treat _Huilia yezoensis_ (Zahlbr.) Hertel as a “habitabit modification” of _P. albocaeurelenscens_. _H. yezoensis_ has previously been considered a distinct Asian species on the basis of its darker thallus, its slightly different reaction with IKI, and tendencies in three apothecial characters (Hertel 1977). In North America, there are no specimens with all the characteristics of _H. yezoensis_, and no clear division can be made between populations belonging to _P. albocaeurelenscens_ and those with some features like those described for _H. yezoensis_.

Exposed habitats in the Great Lakes Region and at high elevations in the southern Appalachians have populations of the stictic acid chemotype of _P. albocaeurelenscens_ that produce soredia. Sorediate individuals have not previously been reported for _P. albocaeurelenscens_. Production of soredia appears to be habitat induced in the Appalachians, since from field observations on Roan Mountain, North Carolina, soredia seem to appear progressively as the protection of forests is left at the tops of mountains. Sorediate individuals usually also produce normal apothecia with spores. This type of variation is most similar to what Poelt (1974) would recommend treating at varietal rank. Because of the very few specimens and scanty field observations, I have not distinguished this sorediate variant taxonomically.

**Representatives of the 371 Specimens Examined**


2. _Porpidia calcarea_ Gowan, sp. nov.

(Fig. 6, 16-17, 26)

_Porpidia superbae_ et _P. zeoroides_ similis sed thallus continuus verrucis bullatis et apothecis colore mutabilibus (brunneis vel nigris) instructus.

**Type:** Michigan. Keweena Co.: Isle Royale National Park, Passage Is., Wetmore 47460 (MIN).

Named for its chalky white thallus that usually grows on calcareous substrates.

Thallus white, scabrid and chalky, continuous, subrimsone with common convex (bolluate) verrucae, 0.5-0.86-2.0 mm thick; margin distinct and thinner than thallus center; prothallus black, thin; medulla IKI—; soredia absent.

Apothecia abundant, scattered to infrequently contiguous, soon becoming sessile, 0.8-1.2-2.0 mm diameter; disk black to brownish black, nonpruinose; margin bare, even to weakly crenulate or flexuose. Hymenium 75-102-115 μm high; paraphyses conglutinate, strongly branched and anastomosed; epithecium orange brown to olive brown; subhymenium 15-29-40 μm. Exciple of conglutinate rows of cells radiating from hypothecial region, blackish at margin, moderately pigmented within; cells 4-5.2-6 μm diameter. Spores 14-18-23 × 7-9-11 μm.

**Secondary products.** — Only a trace of stictic acid seen (accessory).

**Habitat.** — HCl+ rocks in forests, in bogs, and on lake-shores.

**World distribution (Fig. 26).** — Shores of Lake Superior (northeastern temperate to hemiboreal zone).

This species is closely related to _P. superba_ and _P. zeoroides_, but differs in thallus characteristics, apothecium color, possibly mean spore size (see Table 2 and descriptions), and distribution. The relatively smaller spores than those of _P. superba_ and _P. zeoroides_ suggest a relationship with the _P. macrocarpa_ and _P. albocaeurelenscens_ complexes. The thallus characters and apothecium color are actually intermediate between those of _P. superba_ and _P. zeoroides_, suggesting that _P. calcarea_ either was ancestral to _P. superba_ and _P. zeoroides_, or arose by hybridization between them. _Porpidia calcarea_ is restricted to the shores of Lake Superior, and _P. superba_ and _P. zeoroides_ are western arctic. _Porpidia calcarea_ could have been separated from the arctic populations before speciation was complete between _P. superba_ and _P. zeoroides_. In the introductory section on Distribution, I suggest that the Pleis-
tocene could have been the time when the populations were separated.

**Specimens Examined**


3. **Porpidia carlottiana** Gowan, sp. nov.

(Fig. 18, 27)

Porpidiae glaucoaphae similis sed esorediata.  
Type: British Columbia. Queen Charlotte Is.: Graham Is., Port Lewis, Brodo 10489 (holotype, CANL; isotypes, COLO, US, WISC).  
Named for Charlotte Gowan and collected most frequently in the Queen Charlotte Islands.

Thallus usually light greenish gray to whitish, sometimes darker, to dark gray or olive gray, continuous, sometimes finely cracked to subrimose when dry, continuously continuous when wet, 0.2–0.26–1.5 mm thick, even to weakly verrucose or rugulose; margin distinct, thinner than thallus center; prothallus black, usually present when abutting another lichen; medulla IKI–; soredia absent.  
Apothecia abundant, scattered or often clustered, sunken in thallus when young, remaining more or less sunken or often becoming sessile on a broad base when mature, 0.5–1.4–2.5 mm diameter when mature; disk dark brown to black, normally with heavy whitish pruinina (but pruinina often absent when growing on rocks that become wet); margin bare, moderately thin to very thick, even to crenulate, regular to flexuose, sometimes radially cracked, especially on old apothecia. Hymenium 90–99–120 μm high; paraphyses conglutinate and indistinct above, sometimes a few free below, moderately anastomosed below, moderately branched above; epithecium yellowish brown to grayish olive green, littered with granular material; subhymenium 20–33–45 μm high. Exciple of conglutinate hyphae, radiating from hypothecial region, dark brown to black at exciple margin, opaque gray to weakly brown-pigmented within; excipular hyphae narrow, 2–2.8–4 μm. Spores 16–18–19 × 8–8.1–9 μm.

Secondary products. – 2’-O-Methylsuperphyllynic acid (major constituent), glaucophaic acid; SV-1 and unidentified triterpenes sometimes present; superconfluentic acid and insignin rarely visible by TLC, only on copiously spotted plates.

Habitat. — HCl– rocks, usually exposed, almost always along waterways in mountains or on seashore rocks.

World distribution (Fig. 27). — Oceanic western boreal to oroboreal; West Coast and coastal mountains from Oregon to southern Alaska.

I have segregated P. carlottiana from the European and eastern North American P. glaucoaphae on the basis of absence of soredia, production of abundant apothecia, and geography. These two species may represent a species pair in the sense of Poelt (1970). If so, they likely represent a recent species pair, in which soredia have not yet replaced spores as the only reproductive propagule. The specimens of P. glaucoaphae from eastern Canada have few or no apothecia, but the European specimens usually have apothecia (Schwab 1986).

**Representatives of the 40 Specimens Examined**


(Fig. 14, 19, 28)

Lecidea cinereatrum Ach., Lich. Univ. 167. 1810. Type: East Germany: Lausitz, Mosig 52 (lectotype, chosen here, Herb. Ach. 100, H!).


Thallus light to medium gray, continuous, rimose areolate to subrimose, usually nonrimose when wet, 0.5–0.82–1.2–(2.0) mm thick, often uneven, verrucose to rugulose; margin distinct, thinner than thallus center; prothallus black, thin, present or absent; medulla IKI–; soredia absent.  
Apothecia abundant, usually scattered and non-contiguous, sunken in thallus or less commonly broadly sessile when mature, 0.5–0.94–1.5 mm diameter when mature; disk black, moderately pruinose when young, usually retaining light to moderate pruinina in age; margin bare, thin, even to weakly crenulate, regular to commonly invaginated or flex-
Acharius' original treatment describes *Lecidea cinereoatra* as rimose-verrucose-areolate and gray-greenish with the apothecia appressed, plane but becoming convex, irregularly confluent, immarginate and black. Of the two specimens identified by Acharius as *L. cinereoatra*, the smaller (Herb. Ach. 369) was collected by Harriman in England. The annotation "*Lecidea cinereo-atra*" was crossed out, apparently by Acharius, and the specimen reidentified as *Lecidea armeniaca*. This specimen may belong to *P. cinereoatra* but is not typical (I did not study apothecial sections). It has an extremely thick, areolate thallus with sunken, nonpruinose apothecia that appear to lack an exciple. The lectotype of the species (*Herb. Ach. 100*) was collected by Mosaic (52) in "Lusatia." It has a moderately thick, areolate thallus with depressed, lightly pruinose apothecia. It contains confluentic acid, 2'-O-methylmicrophyllinic acid, 2'-O-methylperlatoletic acid, and unidentified substances normally found with confluentic acid (TLC) (Gowan 1989). In cross section, it has the features of normal *P. cinereoatra* (olive-brown epithecium, distinctly anastomosed paraphyses, hymenium 80 μm high, subhymenium 15–20 μm, exciple completely black and of indistinct structure). In the one apothecium that I sectioned, I found no spores.

*Porpidia cinereoatra* has a thick thallus, broadly sessile or immersed apothecia with relatively thick and smooth margins, and usually lightly to moderately pruinose disks. It can be distinguished from other North American species by these characters in combination with a carbonaceous exciple, a high hymenium, and small spores. It is most similar to *P. lowiana*.

North American *P. cinereoatra* often has odd cephalodia-like structures with a heteromeros anatomy and a green alga (Fig. 19). I have seen similar galls on European specimens of *P. flavicunda*. The biological significance of them is unclear, though they may be an infection.

This species is very similar in appearance and identical in secondary-product chemistry to the European and Asian *P. musiva*. *Porpidia cinereoatra* is distinct in having pruinose apothecia and smaller spores (description of *P. musiva*: Knoph 1984).

The European material placed under *P. cinereoatra* may be heterogeneous. I have not studied this material anatomically (but see Knoph 1984). The thalli are quite variable, ranging from rimose to dispersed verrucose.

**Representatives of the 25 Specimens Examined**


5. **Porpidia contraponenda** (Arnold) Knoph & Hertel in Hertel & Knoph, Mitt. Bot. Staatsamml. München 20: 477. 1984. *(Fig. 20, 29)*


This species conforms to the description of *P. diversa*, except that apothecia are commonly over 1.0 mm in diameter, reach 1.8 mm in diameter and are on average 1.4 mm in diameter (Table 2), the epithecium and outer exciple are more commonly olive green to olive gray than bluish (and sometimes nonolivaceous brown), and the aeruginous subhypothecial pigment is usually absent. The thallus is more commonly rimose-areolate than in the eastern North American *P. diversa*.

**Habitat.**—HCl− rocks, usually exposed.

**North American distribution** (Fig. 29).—Oceanic western boreal; West Coast and mountains.

**World distribution.**—Western North America and Europe (Hertel & Knoph 1984; Knoph 1984).

The type specimen of *P. contraponenda* has an abnormally thick, rimose thallus. Apothecia are partly sunken and slightly pruinose. The prothallus is well developed. Spores are noted on the packet to be 18–22 × 6–8 μm.

This West Coast population is very similar in apothecial pigmentation and apothecium sizes to the few European specimens of *P. contraponenda* that I have seen. I have, consequently, not separated them taxonomically. A detailed comparison of the North American and European populations may reveal differences. Compared to *P. diversa*, *P. contraponenda* has larger apothecia and less strikingly pigmented apothecial tissues.

**Representatives of the 26 Specimens Examined**


6. *Porpidia crustulata* (Ach.) Hertel & Knoph in Hertel, Beih. Nova Hedwigia 79: 435. 1984. (Fig. 13, 21, 30)


**Synonymy and treatment.**—Hertel (1977); Inoue (1983b); Schwab (1986).

Thallus usually light greenish gray to whitish, infrequently darker, to medium greenish or olive gray, occasionally weakly and patchily oxidized orange, epilithic to rarely endolithic (only on granite); continuous to patchy (not dispersed areolate), smooth to finely cracked, rarely subrimsome, 0.1–0.17–0.4 (–0.6) mm thick, even to commonly verruculose or rugulose; margin usually distinct, sometimes indistinct on endolithic thalli; prothallus sometimes present, especially between contiguous thalli, thin, black; medulla IKI−; soredia absent.

Apothecia usually very abundant, scattered or less commonly clustered in small groups, frequently arranged in concentric rings, sessile from beginning on thin thalli, soon becoming sessile on thick thalli, 0.3–0.83–1.0(–1.5) mm diameter when mature; disk black or brownish black (often more brownish when wet), nonpruinose or rarely very weakly pruinose; margin thin to moderately thick, even to very weakly crenulate, regular to flexuose, rarely orange on thalli that are orange. Hymenium (55–)60–68–90 (–100) μm high, hyaline or becoming translucent greenish or olivaceous in upper part; paraphyses conglutinate and indistinct, strongly anastomosed and apically branched; epithecidium light to dark brown, less commonly olive brown, very rarely olive green, usually with narrow olive-gray zone adjacent to exciple; subhymenium 10–17–25(–40) μm high; blue pigment often present in medullary region around apothecial base; exciple of moderately to less commonly heavily pigmented, indistinctly radiating, conglutinate, branched rows of slightly elongate cells, dark brown at exciple margin, distinctly paler brown within; excipular cells broad, (4–)5–6.6–8 (–9) μm in diameter. Spores 10–13–17 × 5–6.5–9 μm.

**Secondary products.**—Stictic acid usually in low amounts (main constituent); cryptostictic acid, Per-1, constrictic acid, and norstictic acid occasionally visible on very heavily spotted TLC plates; menegazziaic acid very rarely detected; SV-1 and unidentified triterpenes sometimes present.

**Habitat.**—HCl− or very rarely (less than 5 percent of the specimens) HCl+ rocks, commonly on pebbles, usually exposed.

**North American distribution** (Fig. 30).—Eastern temperate to southern boreal, rarer in the western mountains and West Coast.

**World distribution.**—Unclear: This species has been reported from around the world, from temperate to alpine or arctic climates (Hertel 1977). It has been misidentified in herbaria, and a closer study of specimens will likely show it to be more restricted, possibly circumtemperate, perhaps also in the southern hemisphere (Hertel 1977, 1984).


Lowe (1939) describes *Lecidea soredifera*, from the Adirondack Mountains, as agreeing in all characters with *L. macrocarpa* except for the presence of soredia. The holotype, as well as the other two
specimens (Mich) collected by Lowe, lack soredia and have abundant apothecia. The holotype contains stictic acid and is typical P. crustulata. One of the two nontype specimens is P. macrocarpa, the other P. diversa.

As in Asia (Hertel 1977), North American specimens commonly have small thalli, growing on pebbles in open habitats; it is very common on roadsides.

Vainio (1934) was among the first to draw attention to the size distinction between P. macrocarpa and P. crustulata (cited by Hertel 1967). Porpidia crustulata is the most diminutive North American member of the genus (spore dimensions, hymenium heights, and apothecium diameters: Table 2). It is similar to P. macrocarpa but has narrower hymenia and subhymenia, smaller apothecia, and smaller spores, but it has larger, less densely pigmented cells in the exciple (compare Fig. 12, 13). In addition, the epithecal pigments differ slightly, with P. macrocarpa being more commonly olive brown and P. crustulata more commonly yellowish brown. The two grow in similar habitats, and though there is overlap in most characters, it is always possible, knowing a range of characters, to refer specimens to either P. crustulata or P. macrocarpa.

Different authors define the boundary between P. crustulata and P. macrocarpa at different (though usually similar) spore sizes, hymenium heights, and apothecium sizes (Brodo 1981; Hertel 1977; Inoue 1983b). Some authors have questioned the validity of the separation of these two species (Anderson 1964; Harris 1977). The confusion is largely due to several previously unsuspected species that belong to the group and have apothecial and spore dimensions that cloud the distinction between P. crustulata and P. macrocarpa (see notes with P. macrocarpa). I have placed specimens from the Arctic and from alpine to subalpine localities in western North America in another species, P. thomsonii. This distinction is based on distribution, different excipular anatomy, and intermediate spore sizes between P. crustulata and P. macrocarpa.

Porpidia crustulata can form moderately thick thalli, and in such individuals the apothecia may be sunken in the thallus, similar to the condition in the normally thicker species of the genus. These specimens may be distinguished from other species by chemical characters, by the verruculose rather than smooth thallus, and nonpruinose apothecia.

The exciple and hypothecium commonly produce the K+ grayish-red substance reported in Japanese specimens by Inoue (1983a). Not uncommonly there is an aeruginose pigment in the medulla surrounding the hypothecium, similar to that normally found in P. diversa. Excipular and chemical characters are the most reliable for distinguishing P. crustulata from P. diversa.

### Representatives of the 240 Specimens Examined


7. **Porpidia diversa** (Lowe) Gowan, comb. nov. (Fig. 22, 31)


Thallus usually light greenish gray to whitish, less commonly light gray, continuous to often partly dispersed, consisting of irregularly shaped, domed areolae or verrucae, 0.1–0.3–0.5 mm thick, verruculose or rugulose to less commonly smooth; margin distinct or not distinct, usually thinner than thallus center; prothallus thin, absent or present between areolae; medulla IKI–; soredia absent; aeruginose pigment usually present in medulla near apothecial base.

Apothecia usually abundant, scattered or clustered, soon becoming sessile, (0.5–)0.8–0.9–1.0(–1.5) mm diameter when mature; disk black or rarely dark brown, nonpruinose or very rarely (2 specimens) with lightly but distinctly pruinose apothecia; pruina may be orange on young apothecia; margin bare, moderately thick to thin, usually thinning in old or convex apothecia, even to weakly crenulate,
regular to weakly flexuose. Hymenium 75–84–110 (~120) μm high; paraphyses conglutinate and indistinct, strongly anastomosed and apically branched; epithecium olive black to greenish black, less commonly olive brown; subhymenium 10–22–30 μm high. Excie of conglutinate, branched hyphae, radiating from hypothecial region, dark bluish green to olive brown at exciple margin, moderately to heavily pigmented brown (to carbonaceous) within; excipular cells 3–4.2–5 μm thick. Spores 15–16.5–20 × 7–7.8–11 μm.

Secondary products.—Methyl 2′-O-methylmicrophyllinate (major constituent) and 2′-O-methylmicrophyllinic acid; olivenonide monomethyl ether and unidentified substances visible on heavily spotted TLC plates.

Habitat.—HCl–rocks, usually exposed, less commonly in forested areas.

World distribution (Fig. 31).—Appalachian–Great Lakes Region, north to the southern boreal zone, only in North America.

Described by Lowe (1939) from the Adirondack Mountains, this species has been identified as P. macrocarpa in most herbaria. Porpidia diversa is like P. macrocarpa except that 1) it has different chemical characteristics, 2) it usually has smaller apothecia, 3) its thallus is usually slightly thicker, and 4) the medulla around the hypothecium is normally olivaceous to bluish black, the outer exciple usually dark bluish, and the epithecium olivaceous black to greenish black. The excipe is as in P. macrocarpa in structure, but is more heavily pigmented.

The specimens identified as Lecidea diversa by Lowe (Mich) are a uniform set. The aereuginos pigment is always present below some apothecia on each thallus. This pigment appears to diminish in older apothecia, and may sometimes be nondiscernible.

The thallus usually varies considerably with habitat. When growing in forested habitats, it is usually thick and smooth, and the apothecia are often sunken. In exposed habitats, the thallus is more often subrimose.

Porpidia diversa is most similar to the western North American and European P. contraponenda. A comparison between the two species is given with notes on P. contraponenda.

Representatives of the 80 Specimens Examined


8. Porpidia flavicunda (Ach.) Gowan, comb. nov. (Fig. 4, 8, 10, 32, 40–43)


Thallus distinctly orange to orange-yellow, occasionally with white or gray patches (extremely rarely specimens may be predominantly white or gray), and commonly with gray margin, continuous, rimose-areolate, nonrimose when wet, 0.2–0.72–1.0(–1.5) mm thick, even to rugulose; margin distinct or consisting of scattered low verrucae, usually thinner than thallus center; black prothallus frequently present (usually present when abutting adjacent lichens), thin to prominent; thin orange prothallus also sometimes present; medulla IKI–(IKI+ thalli reported by Knoph 1984, but not seen in North America); soredia absent.

Apothecia usually abundant (especially toward thallus center), scattered to commonly clustered, soon becoming sessile with broad base (0.5–0.7–1.7–2.0(–2.5) mm diameter when mature (irregularly shaped ones often forming by the fusion of clusters of smaller apothecia); disk black, lightly to more commonly heavily pruinose (occasionally bare with age, especially when intermittently submerged or growing in a spray zone); margin bare, thin to moderately thick, even, smooth to weakly crenulate, often flexuose or invaginated on large apothecia, sometimes with brown or reddish pigment, especially in young apothecia. Hymenium (75–)85–97–110(–120) μm high; paraphyses conglutinate and
indistinct, weakly anastomosed and apically unbranched or weakly branched; epithecial olivaceous brown to greyish olive, often more brownish below, littered with granular material; subhymenium 20–35–45(–60) μm high. Exciple composed of conglutinate, branched hyphae radiating from hypothecial region, usually lightly pigmented (from moderately pigmented to almost hyaline), dark at exciple margin; frequently thinning so as to retain only exterior portion; excipular cells narrow (2–2.7–4 μm); spores 14–18–24 × 6–9.3–11 μm.

Secondary products.—CHEMOTYPE I: Confluentic acid (main constituent), 2′-O-methylmicrophyllinic acid, 2′-O-methylperlatolic acid; SV-1 and unidentified triterpenes sometimes visible by TLC; olivonide monomethyl ether and unidentified substances visible on heavily spotted TLC plates. CHEMOTYPE II: Norstictic and connorstictic acids. CHEMOTYPE III: Secondary products of chemotypes I and II. CHEMOTYPE IV: No substances.

Habitat.—HCl– rocks, exposed, usually in tundra.

North American distribution (Fig. 40–43).—Throughout the hemiarctic and low arctic zones, extending from the high arctic to the northern boreal zone. Specimens containing norstictic acid rare within the range of the main chemotype.


Distribution maps.—Inoue (1983b), Japan.

Hertel (1977) and Inoue (1983b) point out that Hornemann’s and later Degelius’ (1938) concept of Lecidea flavocoerulescens included both the sorediate and esorediate morphologies, and under this concept, P. flavicunda is synonymous with P. flavocoerulescens. Knoph (1984) and Schwab (1986) treat P. flavicunda and P. flavocoerulescens as synonyms, since thalli can be found with both apothecia and soredia. In North America, the two phenotypes do not intergrade, each being distinct where they are sympatric. The type of P. flavocoerulescens is sorediate, and not conspecific with the North American specimens of P. flavocoerulescens auct. The correct name for the esorediate species is P. flavicunda.
Porpidia flavicunda is a very distinct species restricted to arctic localities. Anderson (1964) mentions the importance of hyphal thickness in the exciple in distinguishing this species. The narrow excipular cells are distinctive of the entire P. albocaerulescens complex, to which P. flavicunda belongs.

The thallus occasionally has gray or white patches or margins. The largest patches occur on specimens collected from the underhangs of stones, where the thallus can be mostly without pigment. The apothecia usually become sessile while very small. In addition to the primary apothecia forming near the thallus margin, there is a tendency for young apothecia to develop in clusters on senescent apothecia near the thallus center.

Only the confluent acid chemotype of P. flavicunda is reported from Europe (Knoph 1984). Inoue (1976), however, reports stictic acid as an accessory substance with confluent acid in Lecidea flavicunda in Japan. In North America, P. flavicunda sometimes contains norstictic acid, but I have not seen any specimens with stictic acid. The norstictic-plus-confluent chemotype agrees morphologically with the main chemotype. The very few specimens of the norstictic chemotype have small areolae, but they are within the range of variation of the specimens containing confluent acid. More collecting may clarify this relationship.

Representatives of the 128 Specimens Examined


9. Porpidia flavocoerulescens (Hornem.) Hertel & Schwab in Hertel, Beih. Nova Hedwigia 79: 437. 1984. (Fig. 33, 44-48)


Synonymy and treatment.—Hertel (1977); Hertel and Knoph (1984); Schwab (1986).

Thallus orange to yellowish or brownish orange, frequently with small gray patches and very rarely almost completely gray or whitish, continuous, rimose areolate, 0.2–0.45–0.6(–1.0) mm thick, even to infrequently verruculose or rugulose; margin distinct, usually thinner than thallus center; prothallus black, usually weak or absent; thallus either thinning toward margin or not thinning; a black prothallus present or absent; medulla IKI—; soralia punctiform to slightly efflorescent, usually regular in shape and mostly remaining discrete, dark or speckled dark, greenish to blackish, often with whitish rim, 0.2–0.8(–1.0) mm diameter, scattered; soredia rather coarse.

Apothecia unknown in North American material.

Secondary products.—CHEMOTYPE I: Confluent acid (main constituent), 2′-O-methylperlatic acid, and 2′-O-methylmyrhhophyllinic acid; SV-1, olivetone monomethyl ether and other unidentified substances also sometimes present. CHEMOTYPE II: No lichen substances (one specimen). CHEMOTYPE III: 2′-O-methylperlatic acid and confluent acid in about equal concentration (major constituents), 2′-O-methylmyrhhophyllinic acid; olivetone monomethyl ether sometimes visible. CHEMOTYPE IV: Constituents of chemotype I, plus stictic acid, cryptostictic acid. Per-1, constictic acid, and norstictic acid. CHEMOTYPE V: Norstictic and a trace of connomstictic acid.

Habitat.—HCl— rocks, in tundra.

World distribution.—Europe (Hertel & Knoph 1984), Himalaya Mountains (Hertel 1977), and North America.

The use of the name P. flavocoerulescens to refer to esorediate material is complicated by its sorediate lectotype. It appears that Hornemann included both sorediate and esorediate material under this name. Degelius (1938) reports the lectotype to be sorediate, however, and I therefore agree with Inoue (1983b) in using the name to refer to sorediate material, previously placed under “P. melinodes,” and using P. flavicunda to refer to the esorediate specimens.

Except for the presence of soredia, this species has thallus characters identical to those of P. flavicunda. The chemical characteristics are also similar. When growing together, P. flavocoerulescens and P. flavicunda are distinctly different, either densely sorediate but nonapotheciate, or esorediate but apotheciate. Though P. flavocoerulescens can occasionally form apothecia in Europe, soredia production does not intergrade between the two species. The confluent-plus-stictic chemotype agrees with the main chemotype in both morphology and distribution. The related specimens containing stictic acid but lacking confluent acid form a distinct
morphological, geographical, and chemical species, which I call P. pseudomelinodes.

**Representatives of the 23 Specimens Examined**


(Fig. 34, 49)


**Type:** Uncertain (see nomenclatural note below).


This species conforms to the description of *P. carlottiana* except in having irregularly shaped soralia sometimes forming along cracks in the thallus; soredia are moderately coarse, and apothecia are rare and deformed in North American material.

**Habitat.**—HCl− rocks; habitats unclear from herbarium data.

**North American distribution** (Fig. 49).—Eastern boreal, oceanic, rare.

**World distribution.**—Europe (Hertel & Knoph 1984) and eastern North America; oceanic.

The type specimen of *P. glaucophaea* has not been determined. The following is from Koerber's original description: “Auf blöcklichem Granit in der Grafschaft Glatz (Flotow), wie an Gabbro auf dem Gipfel des Zobtens in Schlesien (Koerber).” I searched for these specimens (I), but could not find them.

Like the rest of the *P. alboicaerulescens* complex, this species has a thick, smooth thallus and apothecia with pruinose disks and narrow, lightly pigmented excipular hyphae. The apothecial pigmentation is slightly darker than that of *P. alboicaerulescens*. From the few specimens available, *P. glaucophaea* appears to have a stronger tendency for apothecia to become sessile rather than remaining sunken.

Knoph (1984) treats the sorediate and esorediate European specimens of *P. glaucophaea* as conspecific. This is justified because the two morphotypes are sympatric, soredia are formed very irregularly along cracks in the thallus, the extent of soredia formation varies widely, and apothecium density does not vary noticeably with soredia production. I have not seen soredia yet on the western North American specimens of this group, and I have consequently treated them as a separate species, *P. carlottiana*.

Thomson (1979) reports *P. glaucophaea* from arctic Alaska. I have seen specimens identified as *P. glaucophaea* from the Arctic, but most of them belong to a sorediate, nonapotheciate species that only possibly belongs to *Porpidia* (see Excluded Species).

**Specimens Examined**

(Two of each date)

Canada. Newfoundland. Lack Harbour, 1896, 1897, Waghorne (m).
11. Porpidia grisea Gowan, sp. nov.

Porpidiae tuberculosa similis sed esorediata et apothecios abundos producens.


Thallus medium gray to light greenish gray, consisting of scattered patches, each consisting of continuous, subcorticose to distinctly rimose-areolate thallus, 0.1–0.20–0.3 mm thick, even to weakly verruculose or rugulose; margin distinct, thinner than thallus center; prothallus continuous between thallus patches, black, thin; medulla IKI+ blackish (or possibly sometimes IKI--; see below); soredia absent.

Apothecia scattered, soon becoming sessile, to 0.8–1.1–1.5 mm diameter when mature; disk moderately pruinose; pruina whitish; margin bare, even and regular. Hymenium 60–70–90 μm; paraphyses conglutinate and indistinct, strongly anastomosed and apically branched; epithecium greenish black, littered with granular material; subhymenium 15–27–45 μm; exciple ca. 50 μm wide, very dark even in thin sections (carbonaceous). Spores 12–13–15 × 6–6.2–8 μm.

Secondary products.—Confluent acid (main constituent), 2'-O-methylmicrophyllinic acid, 2'-O-methylperlatolic acid, olivetonic acid monomethyl ether, unidentified substances sometimes visible on heavily spotted TLC plates (one specimen that seems to belong to this species, Thomson 17807, wisc, lacked substances).

Habitat.—HCl+ or HCl– rocks, exposed.

World distribution (Fig. 50).—Arctic-alpine to northern boreal, rare, only in North America.

Porpidia grisea appears to be the esorediate counterpart of P. tuberculosa. These two species match in thallus, apothecia, and ecology. A minority of the known North American populations of P. tuberculosa are arctic, whereas all of the few collections of P. grisea are arctic to alpine. These few collections may or may not reflect the total distribution. Species of Porpidia that grow on HCl+ substrate are poorly collected in North America, and this may reflect patterns of collection rather than the real distribution.

Both P. grisea and P. tuberculosa are relatives of P. speirea, having a narrow, heavily pigmented exciple, low hymenium, small spores, moderately pruinose apothecia, an IKI+ medulla and confluent- tactic. In my herbarium studies, I have included several specimens with IKI– medulla in P. grisea because they are not known to differ in any other characters. The whole P. speirea complex is poorly collected and with more work the relationships between the IKI+ and the IKI– specimens may become clearer.

Specimens Examined


12. Porpidia herteliana Gowan, sp. nov.

(Fig. 36, 51)

Porpidiae macrocarpae et speciebus affinis sporis parvis, hymenio alto et excipulo variabile carbonaceo vel sub- vel noncarbonaceae differt.


Named in honor of Hannes Hertel, an expert of lecidaceous lichens.

Thallus light olive gray to light greenish or yellowish gray, epilithic to rarely endolithic on granite, more or less continuous if epilithic, sometimes with bare patches within thallus, 0.1–0.25–0.5 mm thick, smooth to more commonly verruculose, rugulose, sometimes subareolate; margin distinct, thinner than thallus center; prothallus black, thin, usually poorly developed, usually present when absutting another lichen; medulla IKI–; soredia absent.

Apothecia abundant, usually scattered, infre- quently contiguous or clustered, sunken in thallus only when very young, soon becoming sessile; reaching 0.7–1.0–1.4 mm diameter when mature; disk black, bare or rarely weakly pruinose; margin bare, thick to thin, even to weakly crenulate, regular to infrequently flexuose. Hymenium (65–)70–79–90(–110) μm; paraphyses conglutinate and indistinct, moderately anastomosed and branched; epithecium olive brown to commonly grayish green or green; subhymenium 15–30 μm. Exciple of conglu-
tinate, radiating rows of cells, greenish to brownish black at exciple margin, moderately to very darkly pigmented within; cells 4-4.2-6 μm diameter, about 1.5-2 times longer than broad. Spores 12-13-14 (-16) × (5-)6-6.4-8 μm.

Secondary products.—Confluentic acid (major constituent), 2'-O-methylmicrophyllinic acid, 2'-O-methylperlactolic acid; olivetonide monomethyl ether and unidentified compounds visible on heavily spotted TLC plates.

Habitat.—HCl—rocks, usually granite or related igneous or metamorphosed derivatives, usually open and exposed (e.g., cliffs and shores).

World distribution (Fig. 51).—Eastern North America, from the northern temperate (possibly only the oroboreal zone in temperate regions) to southern boreal zones.

*Porpidia herteliana* has spores comparable in size to those of the *P. speirea* complex and species of the *P. macrocarpa* complex that have small spores. It has a hymenium similar in height to that of *P. lowiana* and species of the *P. macrocarpa* complex with relatively low hymenia. Three other species of *Porpidia* in eastern temperate North America produce confluentic acid. *Porpidia herteliana* differs from these three as follows: by nonpruinose, sessile apothecia and a thinner thallus than *P. cinereoastra*; an HCl—substrate, IKI—medulla, nonscabrid thallus and excipular pigmentation pattern different from *P. speirea*; and absence of soredia, IKI—medulla and different thallus structure than *P. tuberculosa*.

Unlike most other species of *Porpidia*, the exciple appears to vary from very heavily pigmented (carbonaceous) to moderately pigmented. The epithecium is distinctively olivaceous to greenish.

*Porpidia herteliana* resembles the European *P. musiva* in secondary-product chemistry, in apothecium anatomy, and in having bare apothecial disks. It differs, however, in having smaller spores and thinner thallus. Macroscopically it resembles *P. macrocarpa* and *P. crustulata*, and has contributed to the confusion between these two distinct species.

**Representatives of the 21 Specimens Examined**


13. **Porpidia lowiana** Gowan, sp. nov.

(Fig. 37, 52)

Anatomia apothecii ut in *Porpidia cinereoastra* sed thallo tenuiore et apothecios sessilibus.
This species is closely related to *P. cinereoatra*, from which it differs mainly in having a thinner, yellower thallus and sessile apothecia (mainly sunk in *P. cinereoatra*), and in occurring in the Arctic.

**Specimens Examined**


**Synonymy and treatment.** — Hertel (1977); Inoue (1983c); Schwab (1986).

Thallus usually light greenish gray to whitish, uncommonly darker gray, frequently patchily “oxidized” orange, rarely almost completely orange (but see below), epilithic to less commonly endolithic (especially on granite), continuous to patchy but not dispersed-areolate, generally thin, 0.1–0.23–0.6 mm thick, smooth to verruculose or rugulose, often more or less rimose on thickest thalli; margin often indistinct on endolithic thalli, distinct on epilithic thalli, thinner than thallus center; medulla IKI−; soredia absent.

Apothecia usually abundant, scattered or clustered in small groups, clusters of young ones often forming on large senescent apothecia, sometimes arranged in concentric rings, sessile or sunken in thick thalli (especially when young), 0.4–1.6–3.5 mm diameter; disk black to brownish black, bare or rarely very weakly pruinose, plane to commonly convex, frequently umbonate or with sterile tissue within in the hymenium; margin thin to moderately thick, thinning on old or convex apothecia, even to weakly crenulate, regular to flexuose, sometimes very slightly pruinose in young apothecia; larger apothecia often appearing to divide by formation of secondary margins within disk. Hymenium (70–)80–91–120 μm high, hyaline to translucent greenish or olivaceous, especially in upper parts; paraphyses conglutinate, strongly anastomosed and apically branched; epithecium usually olive brown, more rarely pure brown, yellowish brown or olive green (this latter most common in unshaded habitats); hypothecium (12–)20–27–40(–50) μm high; hypothecium dark brown to blackish; blue pigment rarely present in medulla below or surrounding apothecial base; exciple of conglutinate, branched rows of roundish to elongate cells radiating from hypothecial region, dark or deep brown to blackish at margin, only slightly paler within; excipular cells 3–4.1–6(–8) μm diameter. Spores (13–)16–18–23 × (5–)7–7.6–10 μm.

**Secondary products (all accessory).** — Stictic acid (main constituent), cryptostictic acid (strain I of Inoue 1983c); SV-1 and unidentified triterpenes sometimes present.

**Habitat.** — HCl− rocks, very rare on hard limnog, exposed or protected.

**North American distribution (Fig. 53).** — Eastern temperate, mainly in the Appalachian–Great Lakes Region, north to the southern boreal zone, rare in the western mountains.

**World distribution.** — Asia (Hertel 1977), Europe (Knopf 1964), and North America.

**Distribution maps.** — Inoue (1983c), Japan.

There is more confusion about *P. macrocarpa* than there is about any other North American species of *Porpidia*. The name *P. macrocarpa* has been applied to several species including *P. contraponenda*, *P. crustulata*, *P. diversa*, *P. herteliana*, *P. thomsonii*, and *P. tahawaiasiana*. Notes are provided in the discussions of these species that elucidate the differences between these and *P. macrocarpa*.

*Porpidia macrocarpa* is often endolithic when growing on granite. On substrates with finer crystal structure it usually has a perceptible epilithic thallus. Inoue notes that it also rarely grows on trees in Japan. I have not seen it on bark but have seen one specimen from lignum.

There are several North American specimens with an almost completely oxidized orange thallus, similar to *P. flavicunda* and *P. flavocoerulescens*. I accept these as *P. macrocarpa* based on their anatomy, morphology, and chemistry. The overriding orange color might well be habitat induced, since lichens of other genera (e.g., *Aspicilia*) on these rocks also seem to be more orange than normal. Also, specimens of *P. macrocarpa* can be found that grade from orange to gray.

Specimens with small apothecia may be superficially difficult to distinguish from *P. crustulata*. Observation of all these specimens suggests that most of those with small apothecia but high hymenium and large spores belong to *P. macrocarpa*. This is based on the correlation of small excipular cells with high hymenium and large spores, and also on the occasional observation of a large apothecium on a thallus that has apothecia mostly under 1 mm.

**Representatives of the 172 Specimens Examined**


**Newfoundland.** Bay of Is., *Waghorne 137*, 392 (MIN).

**Ontario.** Thunder Bay Dist.: Slate Is., *Wetmore 25144B*,

(Fig. 3, 39, 54)

*Type:* Austria. Steiermark: Kleinsölk, 1973, Poelt (GZU, holotype, not seen).

*Treatment.*—Anderson (1964), under Lecidea melinodes; Schwab (1986).

Thallus brownish orange to pale orange yellow, often with gray patches or margins, continuous, usually finely cracked, sometimes subrimose, rarely distinctly rimose, 0.2–0.26–0.6 mm thick, even to very weakly rugulose; margin distinct and thinner than thallus center; prothallus black, forming between adjacent thalli; medulla IKI--; soralia always present, round or irregular, plane to slightly efflorescent, 0.3–2.0 mm diameter; soredia white or flecked gray to rarely black.

Apothecia unknown in North American materials (described by Schwab 1986, from one European specimen).

*Secondary products.*—Stictic acid (major constituent), cryptostictic acid. Per-1, constrictic acid, norstictic acid, traces of menegazziaic acid sometimes apparent by TLC (also see below).

*Habitat.*—HCl− rocks; tundra, or open cliffs and rocky shores when south of the Arctic.

*North American distribution* (Fig. 54).—Alpine in western North America, rare in the arctic and possibly eastern hemiboreal to southern boreal zones (see below).

*World distribution.*—North America and Europe (Schwab 1986).

*Distribution maps.*—Schwab (1986), Europe and world.

This species is distinct from *P. flavocoerulescens* in having a paler, more continuous thallus, larger soralia, and apparently slightly finer soredia that are usually less heavily flecked than those of *P. flavocoerulescens*. The single arctic specimen containing stictic acid (Baffin Is., *Hale 566*, CANL) agrees morphologically with *P. pseudomelinodes*. It is morphologically different from *P. flavocoerulescens*, growing in the same locality. A few eastern specimens also appear to belong to this species. One of them (Quebec, *LePage 34387*, WISC) lacks secondary products.

*Porpidia pseudomelinodes* is not a counterpart species of any nonsorediate species. Its thallus morphology suggests that it is most closely related to *P. flavocoerulescens* and *P. flavicunda*. Schwab (1986) describes the apothecia as being lightly pruinose and having broad excipular cells. These features suggest a closer relationship with the *P. macrocarpa* complex.

The delimitation of *P. soredizodes* and its relationship with *P. pseudomelinodes* is unclear, and warrants some exploration (see Excluded Species).

**Representatives of the 13 Specimens Examined**


(Fig. 7, 55, 61)


Thallus light greenish gray to white, with chalky, scabrid surface, continuous, finely cracked to subrimose, 0.2–0.5–1.0 mm thick, even to weakly rugulose; margin distinct, thinner than thallus center; prothallus well developed, thin, black; medulla IKI+ violet-black; soredia absent.

Apothecia abundant, scattered to commonly clus-
tered or contiguous, remaining sunken or very broadly sessile when mature, 0.8–2.5 mm diameter when mature; disk black, pruinose when very young, becoming nonpruinose by maturity; margin thin, smooth to very weakly crenulate, regular to rarely flexuose. Hymenium 75–85 μm high; paraphyses strongly conglutinate, moderately anastomosed and branched in upper 10–15 μm; epithecium olive brown to olive green; subhymenium 30–35 μm high. Exciple of young apothecia with rather broad marginal black layer and narrow inner hyaline layer of radiating rows of cells 3–5 μm diameter, inner hyaline layer disappearing on old apothecia to leave a rather thin (20–30 μm) completely black exciple. Spores 11–15(–17) × 6–7 μm.

Secondary products.—Confluentic acid (major constituent), 2'-O-methylmicrophyllinic acid, 2'-O-methylperlatolic acid; olivetonide monomethyl ether sometimes visible on heavily spotted TLC plates; SV-1 sometimes present.

Habitat.—HCl+ rocks.

North American distribution (Fig. 61).—Arctic and eastern hemiboreal zones (Fundy National Park and Keweenaw Co., Michigan), rare.
World distribution.—Europe (Hertel 1967), Asia (Hertel 1977; Inoue 1982), and North America.

Distribution maps.—Hertel (1967), Alps.

Based on comparison with European material, these few scattered specimens appear to belong to *P. speirea* s. str. (see especially Hertel 1967). This species has been confused with *Lecidea confluens* by some North American workers.

**Specimens Examined**


(Fig. 56, 62)

*Lecidea superba* Koerb., Syst. Lich. Germ. 248. 1855. Type: Poland, Koerber s.n. (isotype, m!).


Thallus white, scabrid, consisting of completely dispersed to mostly contiguous bullate areolae, areolae sometimes basally constricted, 0.3–0.5–0.6 (–1.0) mm thick; margin usually indistinct; prothallus black, thin, absent or present between areolae; medulla IKI—; soredia absent.

Apothecia usually abundant, scattered among areolae, sunken on margins of areolae only when very young, soon growing between areolae, 0.5–1.3–2.0 mm diameter when mature; disk usually dark brown, becoming black when wet, bare or weakly pruinose; margin bare, thin, smooth and even. Hyphhenium 110–119–130 µm high; paraphyses conglutinate and indistinct, strongly anastomosed and apically branched; epithecium yellowish to brownish orange; subhymenium 20–24–45 µm high. Exciple consisting of rows of slightly elongate (oblong) cells, radiating from hypothecium, moderately to heavily pigmented within (similar to *P. macrocarpa*); excipular cells 4–6–8 µm diameter. Spores 18–21–25 × 7–9–12 µm.

Secondary products.—Only stictic acid seen (accessory).

Habitat.—HCl+ rocks, in tundra.

North American distribution (Fig. 62).—Western arctic, rare.

World distribution.—Europe (Hertel 1967), Himalaya Mountains (Hertel 1977), and North America.

Distribution maps.—Hertel (1967), Alps.


**Porpidia superba** is a very distinctive species, even macroscopically, with its white, scabrid surface, dispersed areolae and brown disks. Anatomical features such as the large spores and especially the orange epithecium are equally diagnostic. This species has been rarely collected in the North American Arctic, and has been misidentified as *P. macrocarpa*.

Though Hertel (1977) mentions its possible presence in the Rocky Mountains, I have not seen specimens from there. A related population on the shores of Lake Superior is intermediate between *P. zeoides* and *P. superba* (more or less continuous but subbullate thallus, and blackish-brown apothecia). I have placed these few specimens in *P. calcarea*.

**Specimens Examined**


18. **Porpidia tahawasiana** Gowan, sp. nov.

(Fig. 1, 57, 63)

*Porpidiae macrocarpae* similis sed sporis 12–18 × 6–8 µm et excipulo radiale rimoso; thallus plerumque endo- lithicus.
**Type**: New York, Adirondack Region: Newcomb, Lowe 4725 (holotype, MICH!).

Named after an Indian name for Mount Marcy (translated Cloud Splitter), in the Adirondack Mountains, where Josiah Lowe first collected and noticed this species.

**Synonyms**. — *Porpidia cinereoatra* sensu Lowe (1939).

Thallus whitish to medium gray, endolithic and almost imperceptible, to less commonly epilithic and thin, to 0.3 mm thick, continuous if epilithic, smooth to almost imperceptibly verruculose or rugulose; margin definite or indefinite; prothallus very weak and rarely developed; medulla IKI—; soredia absent.

Apothecia abundant or not abundant, sessile on thallus, often clustered, ca. 0.8–1.3–1.7 mm diameter when mature; disk black to commonly brownish black, bare or very weakly pruinose; margin bare, thin to moderately thick, almost smooth to more commonly crenulate to usually radially cracked, regular to strongly flexuose, sometimes double, with second margin forming concentric with and below first exciple. Hymenium 70–82–100 μm high; paraphyses usually indistinct, conglutinate, moderately anastomosed, with tips sometimes once or twice branched; epithecium orange brown; subhymenium 15–25–30 μm high, exciple black and carbonaceous (upon application of KOH, this exciple is shown to be of radiating rows of oblong cells, ca. 3–3.7–5 μm thick). Spores irregularly biseriate, 12–13–18 × 6–6.3–8 μm.

**Secondary products**. — Unidentified terpenes and SV-1 sometimes present.

**Habitat**. — HCl–rocks, commonly granite, exposure not clear from herbarium data.

**North American distribution** (Fig. 63). — Appalachian Region; temperate to tundra.

**World distribution**. — Eastern North America.

Lowe (1939) discovered this species in the Adirondack Mountains and attributed it to the very different *P. cinereoatra* because of its carbonaceous exciple. *Porpidia tahawasiana* is very distinctive, however, with its endolithic thallus usually growing between the crystals of granitic rock, and its sessile apothecia with radially cracked margin.

*Porpidia tahawasiana* is firmly among the Porpidiaeae but it may eventually be removed from *Porpidia*. Its ascus tip is porpidiaceous and its large halonate spores, high hynemium-to-subhymenium ratio, dark hypothecium, and K+ red substance in the exciple all suggest it either belongs to *Porpidia* or is a close relative. Because of the absence of pruina, thin thallus, and lack of secondary compounds, *P. tahawasiana* is most appropriately placed in the *P. macrocarpa* complex. Its apothecial morphology and anatomy are similar to *Stephanocyclis* (Hertel 1984), and it may well be transferred to this genus when intergeneric variation within the Porpidiaeae is better understood.

**Representatives of the 56 Specimens Examined**


19. *Porpidia Thomsonii* Gowen, sp. nov.

(Fig. 11, 58, 64)

*Porpidiae macrocarpaee* similis sed cellulis excepulium granioribus et thallo albiore plurumque endolithico.

**Type.** Canada. Northwest Territories. Keewatin District: South end of Dubawnt Lake, Thomson 20416 (holotype, WISC; isotype, CANL).

Named for John W. Thomson, who has done extensive lichenological exploration in the Arctic, and who collected many of the specimens.

Thallus light greenish gray to white, or sometimes oxidized orange, epilithic to mostly endolithic (growing between crystals of granitic rock, with scattered epilithic verrucae), 0.1–0.13–0.3(-0.4) mm thick, even to weakly verruculose or rugulose, subrimose on thicker thalli; margin distinct or indistinct, thinner than thallus center; prothallus present or absent, thin, black, generally poorly developed if present; medulla IKI—; soredia absent.

Apothecia abundant, scattered, broadly sessile when mature, 0.8–1.2–2.0 mm diameter when mature; disk black to brownish black, bare; margin bare, thin to moderately thick; even to very weakly crenulate, regular to weakly flexuose. Hymenium 70–88–110 μm high; paraphyses conglutinate, moderately to strongly anastomosed, branched in upper 10–15 μm; epithecium brown, olive or commonly green; subhymenium 15–24–35 μm high. Exciple of conglutinate, branched rows of oblong cells radiating from hypotecial region, dark brown to blackish at exciple margin; moderately dark brown pigmented within (usually slightly darker than temperate specimens of *P. macrocarpa*); excipular cells moderately broad (4–5.7–7 μm). Spores 13–17–20 × 7–7.6–10 μm.

**Secondary products (all accessory).** — Stictic acid (major constituent), cryptostictic acid; Pcr-1, constictic acid, and norstictic acid visible on heavily spotted TLC plates; SV-1 sometimes present.

**Habitat.** — HCl–rocks, rarely HCl+ rocks, in tundra.
and open rocky habitats when south of the Arctic. I have tentatively included a phenotypically identical West Coast population that grows on coastal rocks.

World distribution (Fig. 64). — Arctic, south in the western mountains to Colorado, and the shore of Lake Superior. (It is not clear from herbarium specimens whether this species is restricted to the alpine zone when growing in low latitudes.) The West Coast population extends from northern California to the Queen Charlotte Islands. Known only from North America.

These specimens are similar to *P. macrocarpa*. They differ in having more elongate, slightly thicker, and more heavily pigmented excipular cells; on average lower hymenium, smaller spores, and arctic-alpine distribution. The blue pigment below the hypothecium, characteristic of the *P. macrocarpa* complex, is also found rarely in this species.

There are a number of specimens with orange thallus that fall within the range of morphological variation of *P. thomsonii*.

*Porpidia thomsonii* sometimes resembles the arctic *P. zeoroides*, which differs in having larger spores, higher hymenium, excipular cells of a different shape, as well as a normally HCl+ substrate.

**Representatives of the 101 Specimens Examined**


20. **Porpidia tuberculosa** (Sm.) Hertel & Knoph in Hertel, Beih. Nova Hedwigia 79: 438. 1984. (Fig. 2, 59, 65)

*Spilonema tuberculosa* Sm. in Smith & Sowerby, Bot. Jahrb. Syst. 36, tab. 2556. 1814. Type: Britain: Newcastle, Robertson (not seen, see Hertel 1984).

**Synonymy and treatment.** — Knoph (1984); Schwab (1986).

Thallus usually medium gray, sometimes whitish, usually showing yellowish cast when pale, sometimes oxidized orangish, continuous to patchy, subrimose to distinctly rimose-areolate, 0.2–0.30–0.8 mm thick, even to verrucose or rugulose; margin distinct, thinner than thallus center; prothallus usually present, sometimes very well developed, especially between patches of thallus, black; medulla IK1+ black or blackish; soralia always present, round to roundish, 0.1–1.0 mm diameter, usually flecked gray or blackish, rarely white, usually remaining ± discrete, sometimes efflorescent, forming mostly in cracks in thallus.

Apothecia (seen on two specimens: New York, Thomson 11228, Wisc; and New Brunswick, Gowan 3030, CANL), scattered, soon becoming sessile, to 2.2 mm diameter; disk moderately to strongly pruinose; pruina sometimes orange on young apothe-
cia, whitish on older ones; margin bare, even and regular. Hymenium 65–72–75 μm; paraphyses conglutinate and indistinct, strongly anastomosed and apically branched; epithecium olive brown to olive gray, littered with granular material; subhymenium 20–37.5–45 μm; exciple narrow, very dark even in thin sections, of unclear structure. Spores 13–14–16 × 6–6.5–9 μm.

Secondary products.—Confluent acid (main constituent), 2'-O-methylmicrophyllinic acid, 2'-O-methylperlatolic acid; unidentified triterpenoids sometimes present.

Habitat.—Hemiboreal to boreoreal eastern North America, more rarely collected in the western arctic zone.

World distribution.—Europe (Knoph 1984) and North America.

Porpidia turbosula decidedely belongs to the Porpidia speirea complex, having an IKI+ medulla, lightly pruinose apothecia, low hymenium, small spores, and low hymenium-to-subhymenium ratio. Like P. prochthallina, it shows a yellowish cast when it is pale in color.

The features that distinguish this from other sorediatae species are the moderately thick, gray, subareolate to areolate thallus, and the IKI+ medullary reaction. The normally dark thallus is also helpful, though not always reliable.

Lecidea sorediza Nyl. is considered a synonym of Porpidia turbosula. There are numerous specimens identified by Nylander as L. sorediza Nyl. in Herb. Nyl. I did not study their chemistry or anatomy, but they appear to be nonuniform. They vary from being esorediate (var. esorediza), to forming soredia irregularly on cracks, and to forming quite regular soralia with well-defined margins.

Specimens Examined


Synonymy and treatment.—Hertel (1967; as Lecidea macarcorpa var. trullisata); Hertel and Knoph (1984); Knoph (1984).

Thallus yellowish or greenish white to white, with scabrid, chalky texture, continuous to partly dispersed areolate, weakly cracked to subrimose, 0.2–0.43–1.0 mm thick, weakly verruculose or rugulose to subbullate; margin more or less distinct, thinner than thallus center; prothallus sometimes present, very thin, dark gray to black; medulla IKI−; soredia absent.

Apothecia abundant, scattered or clustered in small groups, sometimes arranged in concentric rings, sunken in thallus when very young but soon becoming sessile with a broad base, 0.8–1.4–2.0 mm diameter; disk black to less commonly brownish black, bare or weakly (rarely moderately) pruinose (often variable on single thallus), plane to commonly convex; margin thin to moderately thick, bare or commonly with white pruinose rim exterior to excipulum, even to very weakly crenulate, regular to flexuose or involuted; clusters of young apothecia appearing to form on senescent apothecia. Hymenium 85–110–130 μm high; paraphyses strongly anastomosed and apically branched, conglutinate or free over part of their length; epithecium olive brown, usually becoming greener below, also often greener toward margins; subhymenium 18–23–30 μm high; exciple of conglutinate rows of oblong cells radiating from hypothecial region, black at margin, lightly brown pigmented within; excipular cells (3–)4–5.4–6 μm; spores (15–)17–19–24 × 6–9–11 μm.

Secondary products.—Only stictic acid and SV-1 seen (both accessory).

Habitat.—HCl− rocks; exposure not clear from herbarium data.

North American distribution (Fig. 66).—Rarely collected in the western arctic and northern alpine zones.

World distribution.—Europe (Hertel 1967; Knoph 1984) and North America.

Distribution maps.—Hertel (1967), Alps.

This species is similar to P. superba, both growing on calcareous (HCl+) substrates and having a chalky thallus and rather large spores and apothecial features. The main distinctions between P. superba and P. zeoroides are the brown apothecia and more dispersed and bulblet thallus of P. superba. Porpidia calcaria, on the shore of Lake Superior, appears intermediate in these two characters (see notes with latter).

Specimens Examined


Excluded Species

Brodo and Hertel (1987) transferred this species to *Amygdalaria* and summarized its North American variation. Based on most North American herbaria, its distribution is shown in Figure 67.

**Representatives of the 9 Specimens Examined**


Like *A. elegantior*, this species has been transferred to *Amygdalaria* (Brodo & Hertel 1987). The North American distribution is presented in Figures 68–70.

**Secondary products.** — **Chemotype I:** Gyrophoric and lecanoric acids, and unidentified substances. **Chemotype II:** Confluentic acid (main constituent), 2'-O-methylmicrophyllinic acid, 2'-O-methylperlatolic acid; oligovitonide monomethyl ether and unidentified substances visible on heavily-spotted TLC plates. **Chemotype III:** Constituents of chemotypes I and II.

**North American distribution** (Fig. 68–70). — Arctic to boreal.

**Representatives of the 42 Specimens Examined**


**Chemotype III.** — **Canada. Newfoundland. Leading Tickles, Waghorne s.n. (min). Quebec. Ungava Bay: Fort Chimo, Thomson 13806 (wisc).

**Huilia phylliscina** Nyl., Flora 56: 21. 1873.

**Type:** "Ad saxa argillaceo-schistosa in regione Onegeni," Norrlin (holotype, Herb. Nyl., fl).

This species, described from Europe, was reported by Lowe (1939) from the Adirondack Mountains and by Wetmore (1967) from the Black Hills. Reportedly, the main distinction of the species from *P. macrocarpa* is that it normally has a K+ reddish exciple. The anatomy and morphology of specimens identified as *P. phylliscina* fall well within the range of variation of *P. crustulata* and *P. macrocarpa*. The K+ reddish reaction in the exciple has been observed in some specimens of all North American species of *Porpidia*, including *P. crustulata* and *P. macrocarpa*, and this character does not support species distinction. I have therefore not given special taxonomic treatment to the specimens with a K+ exciple.

*HuiUia soredizodes* is described as a sorediate species with normally gray thallus and IKI–medulla (Knoph 1984). Two North American specimens possibly belong to *P. soredizodes*, but the absence of apothecia and paucity of distinguishing features prohibit a positive identification. One specimen (New Brunswick, *Gowan 3573, CANL*) contains stictic acid. The other (Newfoundland, *Waghorne 308, MN*), lacks lichen substances. Both have a thin thallus (0.1–0.3 mm). The former is verruculose and oxidized orange; the latter is smooth and unoxidized. I would separate the oxidized specimen from *P. pseudomelinodes* on the basis of a thinner, more irregular thallus. I would, however, require more specimens to treat them taxonomically.

cf. *Porpidia* sp.

Thallus yellowish white to pale gray, varying from dispersed areolate to continuous rimose-areolate; in general young thalli rather continuous and older thalli or marginal parts of thalli becoming more dispersed; areolae flat, round or angular in outline. A well developed black prothallus present; soralia round or roundish, 0.3–0.8 mm diameter, usually remaining discrete, less commonly irregularly confluent, concave to slightly convex; soredia moderately coarse, white to pale yellow, or more commonly speckled black; medulla distinctly IKI+ violet. Apothecia were not seen on North American material and therefore I cannot propose a taxonomic position for this species.

*Secondary products.*—Norstictic acid and a trace of connorstictic acid.

*North American distribution* (Fig. 71).—Low arctic and south in the western alpine to Washington.

This species is not clearly a member of the *Porpidiaceae*, but has commonly been misidentified as *P. glaucophaeae* in North American herbaria. Its chemical traits match the sorediate *Lecidea subsecundiza* Lynege (Dahl et al. 1937), but comparison with material studied by Lynege (o) shows that the two do not match in thallus color or morphology. Unfortunately, I have not seen fertile material.

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**Literature Cited**


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