# *LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY

# IN HONOR OF

# JOHN W. THOMSON

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John W. Thomson photographed by Lois Brako, 1998.

# *Lichenographia Thomsoniana*

## North American Lichenology

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## John W. Thomson

Edited by
M. G. Glenn, R. C. Harris, R. Dirig & M. S. Cole

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FRONT COVER: *Cetraria arenaria* Kärnefelt (Parmeliaceae) grows primarily on sandy soils of the Atlantic Coastal Plain, around the Great Lakes, and in the northern prairies of North America. Secondary habitats are shale barrens and exposed ledges in the Appalachians. The habitats are usually windswept, facilitating the dispersal of this beautiful olive-brown lichen by fragmentation. When long undisturbed, it can spread in solid, luxuriant mats. Drawn from living material from Long Island, New York, by Robert Dirig.

# EDITORS' NOTE

The genesis of this volume derives not so much from the celebration of a special occasion as from the realization during a mealtime discussion at the Third Tuckerman Workshop that, although John Thomson has received international recognition and honors, those he has encouraged most, his fellow North American lichenologists, have not previously had the opportunity to express their thanks and appreciation. From this small notion this large volume has grown.

These papers also provide a cross section of North American lichenology at the end of the century. The history of American lichenology is a cycle of peaks and valleys, the highs the work of brilliant men such as Edward Tuckerman and Bruce Fink, the lows the breaks in continuity left by their deaths. The gap in tradition which occurred with the death of Bruce Fink coincided with John's introduction to lichens through the Torrey Botanical Club, through the field trips and teachings of talented amateur botanists, especially Gladys Anderson, Guy Nearing and Raymond Torrey. From this beginning John and his students went on to make lichenology a respectable, innovative academic discipline. (John's treatment of *Physcia* was one of the first to apply uniformly specific status to vegetative morphs while his students did the same for chemotypes.) Today as academic biology more and more turns away from its descriptive aspects, and fields such as lichenology are left unsupported with a great deal yet to do, amateurs again are becoming active in maintaining knowledge of the ecology, distribution and systematics of North American lichens, lessening the impact of the lack of academic and foundation support. This is most visible in the creation of the California Lichen Society, the Eastern Lichen Network and the Northwest Lichen Guild. As the cycle spanned by John's career turns again from 'academic' to 'amateur' it seems wholly appropriate that the Eastern Lichen Network, composed mostly of hardworking, knowledgeable non-professionals, should make its unifying inspiration a treatment of the lichens of Eastern North America. The first three parts appear in this volume. Similarly, members of the California Lichen Society and Northwest Lichen Guild are adding to our knowledge of western lichens. John's distinguished career is a major part of the foundation on which this renaissance is built.

The topics covered by these papers represent work that continues to flow from John Thomson's research on lichens. The Editorial Committee has arranged the compendium beginning with a set of 15 taxonomic studies, then 10 floristic accounts, covering localities throughout the continent, and finally 4 papers on lichen ecology. Dr. Thomson is honored by a new species, ***Fuscidea thomsonii*** Brodo & V. Wirth.[1]

The Editorial Committee acknowledges with gratitude the efforts of the numerous reviewers, whose suggestions improved the quality of this work as it moved toward publication. These include Vernon Amadjian, Irwin M. Brodo, William L. Culberson, Katherine A. Glew, Helmut Mayrhofer, Bruce McCune, Thomas H. Nash III, Hannes Hertel, Sabine Huhndorf, Roger Rosentreter, Bruce D. Ryan, Claire Schmitt, Steven Selva, Larry St. Clair, Einar Timdal, Tor Tønsberg, Orvo Vitikainen and William A. Weber. We thank especially for their creative efforts, Rupert Barneby, Lois Brako, William R. Buck, and Dick Korf.

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[1]**Species named for John W. Thomson**

***Lecanora thomsonii*** Magn., Acta Hort. Gotoburg. 19(2): 47. 1952.
***Cladonia thomsonii*** Ahti, Bryologist 81: 334. 1978.
***Porpidia thomsonii*** Gowan, Bryologist 92: 54. 1989.
***Physconia thomsonii*** Essl., Mycotaxon 51: 97. 1994.
***Fuscidea thomsonii*** Brodo & V. Wirth, this volume, p 156.

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# A TRIBUTE TO JOHN W. THOMSON

This is John Walter Thomson's eighty-fifth birthyear. His former students, the authors of the papers published here, his fellow lichenologists throughout the world, and his many friends everywhere join together in offering him their best greeting and warmest wish.

John Thomson has published on American lichens for 63 years, monographs and synopses of major lichen genera in North America and numerous floristic studies. Most important of all, he has become the world's most knowledgeable Arctic lichenologist. His productive scientific life was not carried out in a museum, where research was the only professional expectation, but in teaching institutions, where non-teaching duties were also numerous and diverse. In spite of these impositions and myriad requests for help from young lichenologists (to whom he never said no), he doggedly pursued his love of the lichens and even in retirement pursues it still.

For younger lichenologists today, it is hard to imagine what our field in this country was like in first part of this century, the America of Thomson's youth. Travel in this immense land was slow, difficult, and expensive. The few botanists interested in lichens rarely saw each other, and none had had an opportunity to study in Europe. Those were years of great isolation. Thomson's interest in lichens began then, in the mid-1930s, and his first paper was published in 1934, when he was 21, a list of species collected on a field trip of the Torrey Botanical Club to a swamp in New Jersey. A few years later the world was plunged into war, and it would be 1945 before peace was to return. By then, Thomson was in Wisconsin where he would remain permanently, eventually joining the faculty of the University of Wisconsin at Madison.

Just prior to the outbreak of World War II, in 1939, the Swedish lichenologist Gunnar Degelius came to the United States to collect. His resultant papers, one on Maine (1940) and the other on the Great Smoky Mountains (1941), showed American lichenologists how a precise understanding of the European lichen flora would reveal that many American lichens that they previously called by European names were, in fact, different and native or endemic American species. By then Thomson had set himself two goals: first, to catalog the North American lichen flora as precisely as possible, a floristic goal; and, second, to examine major North American genera critically, a monographic or synoptic goal. He would spend the rest of his career working toward these objectives.

Early on he produced treatments of *Cladonia* and *Peltigera*, first for Wisconsin (1942 and 1946) and in 1950, *Peltigera* for all of North America. He also wrote on *Physcia* (1963) in the broad sense, before it was divided into the smaller genera known today. He next returned to the genus *Cladonia,* a book-length synoptic summary (1967), bringing together his own original work on that genus and the monumental, scattered, but never-summarized research of Alexander W. Evans (d. 1959). (It was Evans who, after the War, championed Yasuhiko Asahina's microchemical techniques at a time when the chemical aspects of lichenology were scorned and dismissed in Europe.) This book also brought together the work of a small but sharp-eyed group of American Cladoniologists, including L.W. Riddle (d. 1921), C.K. Merrill (d. 1927), and C.A. Robbins (d. 1930).

Thomson's intense interest in floristics comes from his love of field work. He is a vigorous and critical collector, adding many new species and records to the American flora. In the early 1950s, he started a long series of collecting trips to various regions of the American Arctic, regularly generating reports of his finds. He later summarized part of his work in the book *Lichens of the Alaskan Arctic Slope* (1979) and subsequently wrote the 500-page *American Arctic Lichens: 1. The Macrolichens* (1984). The second volume, treating the American Arctic microlichens, just off the press, brings the number of lichen species covered close to a thousand. And always true to his interest in floristics, he is currently at work on a flora of the lichens of his adopted state, Wisconsin, a genuine labor of love.

In retirement, John lives in the same farmhouse that Mason Hale and I knew when we were his students in the early 1950s. His beloved wife Olive, a botanist of flowering plants, is always with him. John and Olive raised their children in this home and cultivated their garden and tended their livestock on this farm in that beautiful region of America where the deciduous forest merges into the Great Plains. Although he was born 85 years ago in Scotland, John Thomson is a quintessentially American scientist, the Dean of American Lichenology. This collection of papers is in his honor, and we salute him with pride.

William Louis Culberson

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# FORM, CONVENTION, AND EVOLUTION IN *CLADONIA*: THE CHALLENGE OF LICHEN DEVELOPMENTAL MORPHOLOGY

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**ABSTRACT:** Form in the Cladoniaceae is initiated by meristem-like fungal tissue found at the apex of the podetium. This tissue has historically been ignored or misinterpreted, but it is crucial if we wish to elucidate evolution in *Cladonia* and its allies.

> "Form! Form is the great crime."
> --Emile Zola.
>
> "The highest excellence in man is without form..."
> --Goethe

## INTRODUCTION

When John Thomson compiled "The Lichen Genus *Cladonia* in North America" (Thomson 1968), American lichenology was as yet little influenced by the converging scientific upheavals that had revolutionized organismic biology. Schwenender's hypothesis (1869), which was a century old, had barely affected the classification system of lichens. Although within a few years the question would be resolved empirically (Ahmadjian 1964, 1967, 1993; Ahmadjian et al. 1978), lichens were still not fully considered as fungi. A century had elapsed since Asa Gray had recognized the power of Darwinian natural selection (Dupree 1959), but that important moment in botany would seem to have passed lichenology by. Evolutionary process in lichens, though perhaps taken for granted, was still a matter of conjecture. The elucidation of the double helix was a little more than a decade old, but it would be nearly thirty years until technology allowed us to synthesize our understanding of that molecule with an evolutionary scheme for lichen fungi. In the 1960s lichenology was fairly untouched by the theoretical breakthroughs of the previous century and the technological advances of our century, which had transformed biological science. To state it more aptly, lichenology had fallen through the cracks. How did it happen?

The condition of lichenology at mid-century posed a challenge to Thomson, who was well aware of the scientific advances a century had brought. In his volume he endeavored to give fair play to lichen evolution, but his main goal was to summarize the contributions of his mentor, Alexander Evans. Evans had undertaken serious work on the Cladoniaceae of North America late in his career, after many decades as a bryologist and hepaticologist. An aggressive collector and curator, Evans catalogued the Cladonias and their names with great care. His apparent love of detail did not blind him to the reality of the numerous contradictions that persisted in *Cladonia* nomenclature and species concepts, nor did the contradictions prevent him from doing productive work. Evans attempted to reconcile the problems in *Cladonia*, and like many talented systematists, his approach mixed quantities of tradition and change. He was conservative in that he used the names and concepts of the past, most of which stemmed from the monographer Vainio. But Evans was eager to accept new species that found their way into the literature by way of the work of amateurs like Charles A. Robbins, George Knox Merrill, and others (see Thomson 1968 for citations). As early as the 1920s, Evans maintained an active correspondence with Merrill, with whom he conferred regularly about lichen species concepts. Evans was also a vigorous proponent of chemotaxonomy, and it was through Evans that the concepts and techniques of Asahina gained acceptance in North American Cladoniology. Through Evans, chemotaxonomy became a mandatory technique in lichenology. This was particularly the case for the Cladoniaceae, a group of lichens whose morphology was considered to be less than useful as a taxonomic tool. The contributions and pitfalls of Evans' work found their way into Thomson's volume and to Dr. Thomson's credit, although he did not consider *Cladonia* morphology to be "easy," he demurred at the use of chemotaxonomy as a panacea. For example, see his discussion (1968: pp. 105-107) of *Cladonia chlorophaea* (Spreng.) Sommerf.

Nevertheless, lichenologists were uncomfortable with *Cladonia* morphology, which was seen as scanty, variable, and uninformative. Morphological species concepts were considered by some as a thing of the past, a temporary problem in Cladoniology--a problem that would some day be supplanted by a more rigorous, more sophisticated approach to this difficult group. Perhaps lichen taxonomists expected to run before they had fully learned to crawl, for the morphological evidence was always before them under the dissecting scope. How did a group of organisms such as the Cladoniaceae, which are rich in morphological characters, come to be ignored, even disliked from a morphological standpoint? The rest of this essay will trace this question, especially as it relates to some of the underlying taxonomic conventions that showed up in "The Lichen Genus *Cladonia* in North America."

## EARLY FOUNDATIONS: IDEALS, EXPECTATIONS, AND DESCRIPTIONS

The story begins with the foundations of lichenology, which were developed within a theoretical framework laid down by the Early Masters of Botany. The Early Masters were scientist-naturalists who predated Darwin chronologically, and whose approach to lichens had more in common with the ancient Greeks, who coined the term lichen (*leikhein*: to lick). Early *Cladonia* taxonomy was based on gross thallus morphology, which was derived from the appearance of mature specimens (or pictures of them). Polynomial nomenclature and later taxonomic descriptions were written based upon fully developed specimens. Both lichen morphology and the taxonomy of lichens were considered as static, part of a Great Chain of Being. Further, lichens were considered to be plants, and logically they could be expected to grow like plants. The system of early lichen taxonomy was predicated on an idealized morphology, what lichens were *expected* to look like, often on the basis of illustrations rather than specimens. Certainly developmental processes, which are essential to an understanding of form in *Cladonia*, were not considered by early workers.

The mature lichen thallus is a strange looking thing, and our Early Masters had a field day with it. Linneaus, who didn't think much of lichens anyway, took many of his concepts from the pages of Dillenius' *Historia Muscorum* (Dillenius 1742), where the descriptions and illustrations are as fanciful as they are attractive. Consider the polynomials attributed to certain *Cladonia* species by Dillenius: "The Handsome Fine Cut Crisp *Coralloides*" and "The Black Lace *Coralloides*." What was Dillenius thinking when he wrote these descriptions?! Browne (1756), to whom the name *Cladonia* is attributed (Ahlner 1954), included eight taxa within the genus, with descriptions like "The Pendulous Branched *Cladonia* with a Foxy Stalk" and "The Whitish Tubular *Cladonia* with Ciliated Cups at the Ends of Branches." Hudson (1762) and Hoffmann (1762) included similar descriptions as well as short synonomies of polynomials. It is interesting that many of the authors of this period were unclear about how to circumscribe lichens. Most of them included algae, bryophytes, and liverworts in their concept of "lichen," and used terms like liverwort and lichen interchangeably to describe plants or plant-like organisms that grew close to the soil. Curiously, the ubiquitous terms crustose, foliose, and fruticose are quite old. They were used to describe lichens in the broadest sense as early as Micheli (1729), who may have derived them from his reading of Dioscorides.

In an attempt to provide a natural classification for lichens, Acharius (1803) stressed fungal sexual characters over vegetative morphology. This was an advance over previous systems (see Choisy 1929), but one consequence was that gross thallus morphology was neglected. After Acharius, poorly described morphologies continued as the mainstay of lichen taxonomy, and later authors superimposed the framework of Acharius' sexual system on an incomplete understanding of morphology. By the beginning of the 19th century, long lists of synonomies were the emergent convention (see for example Schaerer 1836), usually accompanied by vague taxonomic headings and unenlightening descriptions. Lichen taxonomy was becoming more complex as our conceptual understanding of lichens seemed to decline.

Based upon this set of circumstances, it is no wonder that the monographer Vainio considered *Cladonia* morphology as unreliable. The consequence is that he described what he considered to be great variability within a relatively few, broadly conceived species of *Cladonia* (Vainio 1887, 1894, 1897). By accommodating previously accepted taxa within broad species complexes, he attempted to bring all of the perceived variability in *Cladonia* (and *Cladina* Nyl.) into a taxonomically unified system. Vainio tried to pigeonhole the unruly, confusing Cladoniaceae into a logical system. But by establishing broad circumscriptions for many species he subsumed in them what are now considered to be distinct taxa. A good example is seen in his treatment of *C. fimbriata* (L.) Fr. Later workers, whose contributions made their way into the work of Evans and Thomson, based their taxonomic decisions on Vainio's system. They interpreted *Cladonia* conservatively, attributing great variability to species and still, as it were, toying with morphology rather than making use of it as a serious tool. For example, Asahina, who based many of his species on narrow chemical criteria, treated morphology in a rather offhanded manner. Morphology was secondary in Cladoniology. Developmental morphology was irrelevant. It is telling of this situation that when I described variations in the podetial axillary openings in section *Perviae* (Del.) Matt. within a developmental context (Hammer 1993a), one reviewer (who happened to share Dr. Thomson's handwriting) wrote in the margin "fantasy!"

With no real handle on growth dynamics in lichens, it is not surprising that the morphology of these organisms is so poorly understood. And with the present lacunae in our understanding of *Cladonia* form, it follows that the taxonomy is still weak. Developmental morphology in lichens has been neglected, but why? Frustration may be one reason. Morphological work is slow and inductive. Precious research time is spent in defining a problem that has usually been staring up through the microscope for months. Once a problem is recognized and defined, it must be reworked and reformulated, specimen by specimen, species by species-- a daunting task. To understand the scale and result of this kind of work, we can borrow from Jane Austen, who described her oeuvre as a "little bit (two inches wide) of ivory on which I work with so fine a brush as to produce little effect after much labour" (Cecil 1978). There is no fast track to getting morphological work done. And while Austen's characters were social, morphological research makes awful cocktail party talk. Yet with some luck, the work will finally speak for itself. The sketches and photographs will assemble themselves into a developmental series, and things will start to make sense. This outweighs the frustrations of isolation, the wasted time, and, to paraphrase Jane Austen, the forever scratching away at that bit of scrimshaw. The developmental morphologist gains immensely by seeing the organism as it is, by imposing upon it as few preconceptions as possible. Form emerges where typologies drop away. But tracing the development of a lichen requires patience, careful microscopy, extensive note taking, and sketching, techniques, all of which are rather poorly taught in graduate school. Ultimately, however, an impressive depth of biological understanding comes from deciphering something obvious but unknown.

## EVOLVING CHARACTERS OR *SCALA NATURAE*?

I chose a narrow focus for my preliminary studies, the genera *Cladonia* and *Cladina*, but this work can be extended to the family Cladoniaceae and perhaps to other lichens as well. I have arranged my questions within three overlapping issues in morphology. Questions regarding developmental morphology include: How does the thallus take its distinctive shape? What are the underlying principles of thallus architecture? Which variations are inherited and which are environmentally induced? The questions surrounding comparative morphology are slightly different: Which characteristics are homologous--allowing for comparison among the species? Are there autapomorphies that distinguish groups within the genus? What characters link *Cladonia* to other genera? My third area of focus is rather more difficult. It asks bothersome questions about the meaning of characters (see Stevens 1980). Which characters are discrete? Which characters are continuous? Are evolutionary advances represented in certain morphological characters? And, if these represent derivation, do they help us identify so-called primitive characters? Underlying all of my questions is this: How does morphology reflect lichen evolution? In this essay I lay the questions on the table without trying to answer them. They have been discussed, although by no means exhaustively, in a series of papers (Hammer 1995a; 1996a, b, c; 1997a, b) that mark, coincidentally, one hundred years of *Cladonia* morphology.

And dark years they have been. At about the time Vainio wrote his monograph, a classic study on *Cladonia* morphology came out of central Europe (Krabbe 1891). The title of that study, which includes the word "polymorphic," tells us much about the way scientific attitudes formed over the next century. *Cladonia* came to be known as a group of lichens without a reliable architecture. Patterns of growth and form in the genus were considered too variable to study effectively. They could not be predictive. *Cladonia* was also seen as character-poor, lacking in morphological distinctions past the generic level. The podetium, the erect, cup-shaped or branched *thallus verticalis*, was viewed as the one distinguishing character in *Cladonia*. At the same time, it was considered the least reliable, most variable part of the thallus. Another problem arose from the biological context in which the podetium was understood. In the podetia he illustrated, Krabbe depicted cells that came to be accepted as ascogonial, a product of gametic fusion. In the idealized concept of the podetium according to Krabbe, the presence of these cells (subsequent authors have mistakenly called them "generative") would indicate that the podetium is a sexual structure. Ascogonial cells have not been adequately documented in *Cladonia*, but they have been frequently *drawn*, albeit more crudely than in Krabbe. Their putative presence (see Jahns 1970) spawned an entire literature on the "podetium-problem" in *Cladonia*. This "problem" has done much to draw attention to Cladoniology, but it has not reflected particularly well upon our judgment as scientists (Hammer 1993b). While Krabbe contributed to *Cladonia* anatomy, he endangered the future utility of developmental morphology in the taxonomy of the genus. "Polymorphic" is not a prescription for success, if you are going to classify organisms on the basis of form.

From what we know so far about the history of Cladoniology we might ask whether Vainio and his intellectual descendants *could* be expected to use morphological characters to produce a natural classification of the Cladoniaceae. It may be argued that they never saw past the idealized features they had come to expect. We can envision a struggling Vainio at the end of the nineteenth century, who believed in descent through modification, in the uncomfortable position of arranging taxa that were named in the 1740s as part of a *Scala Naturae* that reached back to the Middle Ages. What could Vainio have done to reconcile the huge problems that Cladoniology presented? Was he, in a sense, in a position that was much different from that of Evans? Like Evans, Vainio accepted much that was old. But despite his adherence to taxonomic convention, he considered himself to be a revolutionary in that he erected a phylogeny for the genus. Phylogenies were a trend at the turn of the century, along with morphological work such as Krabbe's, but fifty years later both were all but forgotten. And along with Vainio's phylogeny and Krabbe's morphology, a larger, overarching intellectual development of the *fin de siècle* was also discarded--the idea that form in lichens was an evolutionary phenomenon, the result of natural selection. Botanists at this time had begun to struggle with the possibility that lichens had arisen through an evolutionary process. For example, Goebel (1900) suggested that the morphology of the lichen thallus was linked to the selective pressure to increase photosynthetic surface. He hypothesized that the evolution of form in *Cladonia* could be traced to the development of an orthotropous thallus (a podetium) from a dorsiventral ancestor (a squamule). Goebel may have derived this idea from Reinke (1896), who compared the trend from dorsiventral to radial growth in lichens, to the evolution of plant form. These authors seemed to be on the right track. They recognized natural selection as the driving force in evolution. So what went wrong? Why did scientific thought about the evolution of form in lichens disappear?

## PHILOSOPHY, FLORAS, AND THE DECLINE OF MORPHOLOGY

At least three factors led to the decline of morphological studies in lichens. These factors may fall under broad cognitive headings such as *belief* (philosophy), *pattern recognition*, and *analysis*. Although lichens and lichen morphology are part of biology, the decline of morphology had less to do with the organisms than with how they were perceived. How science perceived its mission was also part of the problem. As has always been the case, scientific disciplines such as morphology and taxonomy were influenced by the way scientists saw themselves in the looking glass of society.

Certain philosophical trends from within the discipline of morphology possibly contributed to its demise. For instance, the study of organismic form is rooted in the traditions of morphology, which historically have been linked to questions such as phyllotaxis and the spiral. Some botanists with an interest in cryptogams studied phyllotaxis (Schwenender 1878; Church 1968), but the idea was not extended to lichens. This may be because lichens are seen as architecturally simple (they lack "organs" like leaves and stems), or because spiral formations in lichens, though present, are subtly articulated (Des Abbayes 1939). More importantly, the spiral has been linked to distinctly unscientific metaphysical doctrines. For example, "modern" botanical metaphysics can be attributed to the poet-philosopher Goethe, who sought universal, ideal forms in plants (see Ritterbush 1972). His approach was eventually discredited by mainstream science, but a partial interpretation of Goethe survives in popular esoteric literature on plants. As recently as the 1980s, some of this literature served as a bridgehead against evolutionary theory, so it is not without reason that transcendent morphology has been soundly rejected by science. Unfortunately, as Goethe's metaphysical ideas were discredited, so was the impetus for morphological studies.

A second factor that obscured morphological studies may have been flora writing, which in contrast to metaphysics, survives as an established and respected discipline. Like morphology, floristic work is rooted in pattern recognition, and the author of a flora may ask some of the same questions as a morphologist. For example, both disciplines are concerned with species variability. But a larger concern in floristics is the circumscription of a species. In a perhaps oversimplified sense, a flora is a binary system in which a taxon, once defined, is either present or absent at a set of localities. A flora is likely to be set firmly in the present, while developmental morphology demands that one think about sequences of events. Both flora writing and morphology are complex time-consuming tasks. They both require well developed pattern recognition skills, but they demand different kinds of decision-making. Usually there is little time for a busy flora writer (Evans was a perfect example) to use both modes of thinking. Thomson's volume is a compendium of floristic studies, and it played a crucial role in North American Cladoniology by summarizing all of the known taxa in an important geographic region. It remains a document of great practical value. Good floras are practical, and while the contributions of a flora to science may be controversial (see Stevens 1990), flora writing is nevertheless the *sine qua non* of the taxonomist. But the biology behind taxonomic issues and the biology that underlies morphological questions may be quite different. The disciplines seldom manage to co-exist within the boundaries of a floristic monograph.

While floristics involves fieldwork, the third factor that changed lichenology as a discipline originated in the laboratory. Analysis, the attempt to reduce unruly life to a datum, has a long and respected history in Western science. It is tempting to criticize nineteenth century analysis as reductionist, but it should be noted that from a scientific standpoint, it is preferable to build concepts from bits of information rather than fitting observations to ideal concepts. The analytic method has almost as long a history in botany as morphology. Thus, on the same dusty shelf as the 19th century morphological inquiries of Naegli, Schwenender, Goebel, Krabbe, Sachs and Reinke, we find Zopf's (1908) analysis of the secondary chemicals in *Cladonia*. Even earlier than Zopf, lichenologists such as Nylander (1866) had worked with potassium hydroxide (the familiar "K") as a reagent. Not all of Nylander's contemporaries (Tuckerman, for example), accepted this approach as discussed by Culberson (1964), but the possibilities must have seemed powerful indeed. With the application of a drop of reagent, a botanist studying lichens could now cut through the difficulties of uncertain morphology and obtain a reliable identification of the specimen at hand. This marked the beginning of what was to be a wonderful new way to deal with the perceived morphological variability in lichens. It led to modern lichen chemotaxonomy, shaped by Asahina in Japan in the 1930s and 1940s, and perfected in North America by Chicita Culberson and her colleagues.

If we go back to the treatments of *Cladonia* by Evans (1930, 1952, 1955), we find that while he relied heavily on the identification of secondary substances, his morphological species concepts were often vague. This became a problem in the history of names and concepts when mixed collections of more than one species, which were not adequately studied morphologically, had a particular chemistry attributed to them. Perhaps something about the substance names "stuck," or maybe it was the respect attributed to the analytical process, but in some instances, chemotaxonomy was a misleading approach (see Hammer 1989, 1993a). By the 1970s, chemistry came to be used as the main tool for identification in *Cladonia*, with morphology considered much less reliable. But the utility of chemotaxonomy is also limited. Secondary compounds can be helpful with identification, but they may not provide information about lichen evolution. For example, the substances may be formed by various biosynthetic pathways (Culberson 1986), and they appear independently in unrelated taxa (White & James 1985). Nevertheless, as the detection and analysis of lichen substances grew as a focus, the "whole" organism became less important as the object of study.

## THE WHOLE FUNGUS

The thesis of this essay is that the whole organism is worth studying. A broad-based inquiry into the lichen and its workings is rewarding, and unexpected morphological distinctions among lichen fungi exist in abundance. Indeed, these distinctions can be used to make meaningful taxonomic decisions. While writing a flora for my dissertation, one of the challenges I faced was to find and describe distinctions among the species. The taxonomic conventions that I inherited from John Thomson only took me part of the way, especially since many of the species I found in the western United States had not yet been described (Hammer 1995b). The solution seemed to consist of staring deep and hard at many thousands of podetia that I collected or borrowed from herbaria. In doing so, I gradually came to recognize the basics of developmental dynamics of the *Cladonia* thallus. The obvious thing that taxonomists had seemed to overlook (although Professor Ahti discussed it with me in many conversations), was that *Cladonia* species actually had regulated, predictable patterns of growth. Even more interesting, thallus growth appeared to be controlled by a relatively tiny, 50-100 $\mu$m bundle of fungal tissue. Incredibly, this component of thallus anatomy was ignored in over 300 years of lichen literature. Could this meristem-like group of cells provide clues to the long-forgotten problem of the evolution of form in *Cladonia?*

In the last paragraphs of this essay I will summarize what I have learned about *Cladonia* developmental morphology. I will try to argue that these findings provide information about evolution in the Cladoniaceae. I propose that the study of form in *Cladonia* can contribute to building a natural classification, whether ontogeny, outgroup analysis, or other forms of phylogenetic model-building are used.

All *Cladonia* and *Cladina* species have bundles of cells like those described above. As homologous structures, they are an excellent character for comparison. The bundles are purely fungal and they represent unequivocally the organism for which the lichen is formally named. The growth dynamics of the fungus, which differ among species, provide insights about how distinguishing characters such as cups and branches are formed. By studying the growth dynamics of the fungal meristem, we can elucidate the mode by which each thallus attains its unique architecture. Because the initial meristem bundles are very young thallus parts, it is safe to assume that the phenomena we observe in them are relatively free of environmental disturbance. The developmental dynamics and variability of the thallus can be analyzed at the most basic level by following the early development of the fungal meristem. It is noteworthy that the meristem-like bundles of fungal cells behave differently among species, and the expression of developmental differences may be evident at several levels. For example, we may study the expression of form in a species by analyzing the synchronization of activities, the plane on which growth takes place (lateral or vertical), and patterns, both continuous and interrupted, such as meristem enlargement and division. At some time in the future, these differences in meristem behavior may provide part of a matrix of characters for a phylogenetic analysis. Presently, however, they have been illustrated in fewer than a dozen species (Figures 1-6). One morphologist has his work cut out for him! What are some examples of these differences? Why are they reliable? How might they provide evolutionary information?

Let us start with something fairly well known, a "typical" cup-forming podetium. For example, in the familiar cup-forming species *Cladonia ochrochlora* Flörke, a narrow band of non-lichenized tissue defines the margin of the cup. In earliest ontogeny, before the cup has formed, the tissue is a solid bundle of roughly vertically-oriented cells approximately 50 $\mu$m in diameter. As ontogeny progresses, the bundle flattens and thins, and the diameter of the cup widens.

As the podetium and the cup mature, the bundle of meristem tissue grows radially in a pattern that is characteristic of many non-lichenized fungi. As the center of the tissue thins and finally disappears, the meristem assumes an annular conformation. Finally, it breaks into small bundles along the margin of the cup. These resemble the initial meristem bundle, reaching approximately 50 $\mu$m in diameter. The cells in the fungal meristem seem not to change, but the shape of the tissue and its conformation change. During the development of the thallus, the cells in this tissue give rise to all of the hyphae that eventually comprise the podetium. The marginal bundles that form when the contiguous annular meristem has split may give rise to pycnidia, apothecia, or lichenized marginal proliferations. As we shall see below, the change from contiguous meristem tissue to divided meristem tissue is significant, ontogenetically and perhaps phylogenetically.

We may assume that for most cup-forming species, this thumbnail ontogenetic account will suffice. Different cup shapes have been described in the literature, such as "trumpet-shaped" or "goblet-shaped," and these are based largely upon varying synchronization of development of the meristem. Thus, the ontogeny of cup-forming podetia appears to be basically the same throughout the genus *Cladonia*. Can we rebuild our classification based on this ontogenetic information? Perhaps. As we study variations on the simple cup, informative differences emerge. For example, in *C. asahinae* Thoms., the ring of tissue grows slowly as the cup widens but does not break into smaller bundles. The slow growth of the cup is reflected in the symmetrical habit and the thick internal cartilaginous layer of this species, which was illustrated in Hammer (1995a). In verticillate species such as *C. cervicornis* (L.) Hoffm., the characterstic central proliferation does not arise until the ring of tissue on the supporting tier has broken into bundles. We may infer from this that the ring of fungal tissue controls certain processes such as vertical growth of the thallus, and that the meristem on one part of the thallus may constrain the activity of the meristem elsewhere on the thallus, similar to vascular plants (Hammer 1996b). The marginal bundles of *C. grayi* Merr. give rise to branching proliferations, which may be inrolled or otherwise curved, following the growth trajectory of the helicoid apical meristem tissue (Hammer 1997b). Branches in *C. grayi* increase the photosynthetic surface of the thallus, and branches are most commonly found among specimens that grow in the shade. Not surprisingly, podetia of *C. grayi* that are exposed to high levels of light tend to form fewer branches or no branches, behaving more like *C. chlorophaea*. While this observation supports Goebel's (1900) theory of light reception and thallus evolution, it is also disturbing. It leads us to ask whether *C. grayi* and *C. chlorophaea* are indeed related taxa, or whether the cup-forming habit is a convergent growth form. Is there a *C. chlorophaea* "group," or have we established this moiety on the basis of our own inadequate observations?

So far, we have concerned ourselves only with cup-forming species. What about branched species? Can comparative

Figures 1-6. Diagrammatic representation of meristem morphogenesis in Cladoniaceae thalli. Developmental sequence from left to right (columns a-d). Figures 1-3. Top view of meristem. Figures 4-6. Longitudinal section of meristem and podetium. Shaded areas indicate meristem tissue. Dotted lines in Figures 4-6 surround internal lacunae in developing podetia. Figures 1,4. Cup-forming podetium. Figures 2, 5. Cup-forming podetium bearing branch-like marginal proliferations. Figures 3, 6. Branching podetium. Scale bar = ca. 100 $\mu$m.

morphology provide the basis for redefining or realigning taxa? For example, what is the status of *C. dimorpha* Hammer, in which the cup-forming annular meristem, once divided, gives rise to branches similar to *C. furcata* (Huds,) Schrad.? As we move our focus from cup-forming to branched podetia, more problems appear. Questions arise within *Cladonia* and between *Cladonia* and other genera, for example the much-disputed *Cladina* (Ahti 1984). Branch initiation in *Cladonia* sections *Perviae* and *Unciales* (Del.) Ahti, which is laid down very early in the ontogeny of the bundle, is similar to branching in the genus *Cladina*. This suggests branch initiation may be homologous in all of these taxa. This in itself does not cast doubt on the independent status of *Cladina*, but a further problem may. Branch initiation in taxa previously considered as "distantly" related as *Cladina subtenuis* (Abb.) Hale & Culb., *Cladonia cristatella* Tuck., and *Cladia retipora* (Labill.) Nyl. is surprisingly similar. Are these taxa more closely related than conventionally thought? Was Vainio really so far from correct when he included them in the genus *Cladonia*? Ahti (1961) called the predictable development in *Cladina* species "regular," but a similar "regularity" can be seen in many species of *Cladonia*. What distinguishes *Cladina*? In gross morphology and chemistry it may be distinct from many of the taxa with which we compare it, but in the early ontogeny of the thallus, it is quite similar.

Can ontogenetic trends provide information about derived characters? Perhaps, if we step carefully. Evolutionary advance may be inferred from specialization (autapomorphies). One trend toward specialization may be the early initiation of thallus branching. Branching in most species is initiated from fungal bundles that arise directly from the primary thallus, without the intermediate step of forming a cup. Early branching without the intermediate cup allows vertical growth. It also provides the increased potential for reproductive opportunities through the development of greater numbers of apothecia. Branched podetia may develop greater photosynthetic surface, secure more territory, and experience genetic recombination faster than cup-forming species by by-passing the constraints of a cup-forming stage. Since divided bundles arise from contiguous bundles and not the other way around, can we assume that branching is an advance over cups? Before we jump to conclusions on this question, we would be wise to consider carefully the possibilities of heterochrony: paedomorphosis, neotony. Homoplasy is also an issue. The questions are great fun, but right now, we need more primary study and less speculation.

What about outgroup comparison? Axillary openings such as those in *Perviae, Unciales,* and *Cladina* species, arise from the development of branches, but branched species, for example, *C. cristatella*, may not produce openings (Hammer 1997c). It may be helpful to consider the biogenetic law of Haeckl (see Nelson 1978), which states that general characters are primitive (plesiomorphic) and less general characters are advanced (apomorphic). If this model holds for *Cladonia*, we may find that branched species, which are more general (common) than branched and open-axil species, are also basal to open-axil species.

The data are inconclusive, and if applied incautiously, they may lead to incorrect assumptions. Critical readers might correctly accuse me of old-fashioned evolutionary systematics. Stevens (1980) urged taxonomists to be prudent when establishing polarity for the characters they study. He stressed a balanced approach, in which ontogeny, outgroup analysis, and other options were combined with skepticism. He also implied that scientists who look deeply into ontogenetic characters must be willing to change their assumptions about taxa and their relationships. In *Cladonia*, these assumptions have been forming, and in some cases ossifying, for almost three centuries.

## THE CHALLENGE OF A PLANT-LIKE FUNGUS

What is the challenge of developmental morphology in *Cladonia*? It is now understood that form in the Cladoniaceae is initiated by meristem-like fungal tissue found at the apex of the podetium. The morphogenesis of this tissue is full of information. Until quite recently this tissue has been ignored or misinterpreted, but it is crucial if we wish to elucidate the evolution of form in *Cladonia*. The first step in rectifying this problem is to study the fungal meristem as it develops in each species. Growth dynamics in lichens provides a dramatic and unexpected unfolding. To frame the process in plant terminology, we can say that the lichen fungus "aestivates," although it does not flower. Likewise, the "vernation" of the lichen thallus is accomplished without leaves. While it is tempting to use plant terminology for lichen growth, it is important to recall that the meristem tissue of lichens is fungal. How this fungal tissue regulates the symbiotic thallus is still not understood. Eventually, description will require experimental corroboration. How is growth regulated? What controls the expression of lichen morphogenesis? The answers to these questions will hopefully inform the hypotheses posed by molecular systematics, so that biologically meaningful comparisons can be made among taxa. The goal is a natural classification that is based upon evolutionary relationships. Inherited thallus form in *Cladonia* is highly constrained and remarkably consistent, yet it is the product of evolutionary processes involving change and diversification. It is our best guide to the daunting landscape of lichen evolutionary biology.

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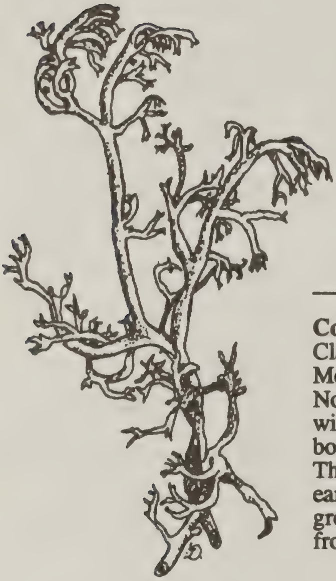

**Common Reindeer Lichen** [*Cladina rangiferina* (L.) Nyl., Cladoniaceae], sometimes popularly known as "Reindeer Moss," is widespread in northern and mountainous regions of North America. Its beautiful intricately branched podetia, with branches mostly in fours, have a distinctive greyish or bone white color, and may reach 4 inches (10 cm) in height. This lichen spreads in large cushions in sandy pine woods and early successional habitats, often intergrowing with yellow-green *Cladina* species. Drawn by Robert Dirig from material from the Catskill Mountains, New York.

*Lichenographia Thomsoniana*: North American Lichenology
in Honor of John W. Thomson.
Eds: M. G. Glenn, R. C. Harris, R. Dirig & M. C. Cole.
Mycotaxon Ltd., Ithaca, NY. 1998.

# *CLADONIA JALISCANA*, A NEW LICHEN SPECIES FROM MEXICO

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**Abstract.** A new species, *Cladonia jaliscana*, is described from Mexico, where it is especially common in the montane oak forests in the state of Jalisco. It belongs to sect. *Cocciferae*, frequently bearing red hymenial discs in abundance. Its major secondary constituents are thamnolic acid and didymic acids. *C. jaliscana* has often been referred to *C. cristatella* in Mexico but that species has not been found Mexico.

During a revision of Mexican material of the family Cladoniaceae we have been puzzled for years by a frequently fertile, red-fruited *Cladonia*. It has been placed to *C. cristatella* Tuck. by Mexican authors (e.g., Álvarez & Guzmán-Dávalos, 1993), or found in herbaria as *C. floerkeana* (Fr.) Flörke or *C. abbreviatula* G.Merr. In recent years many specimens of this red-fruited lichen have accumulated in Guadalajara (IBUG). Also we have observed it together in the field. An analysis of this material indicated that it must represent a new, variable species, which is described below.

**Cladonia jaliscana** Ahti & Guzmán-Dávalos, *sp. nov.*

Type: Mexico. Jalisco. Mpio. de Zapopan: Bosque La Primavera, 9 km from Periférico on the road Prolongación de Mariano Otero, alt. 1920 m, oak woods, on sandy erosion bank, 1 February 1996, *Ahti 52711, Guzmán-Dávalos, Álvarez & Fanti* (IBUG, holotype; ASU, B, DUKE, H, MEXU, NY, US, XAL, isotypes).

*Thallus primarius persistens, squamulosus. Podetia 0.5-1.5 cm alta, simplicia vel parce racemosa, frequenter fertilia; superficie microsquamulosa, verruculosa vel sublaevia, areolato-corticata. Hymenia purpurea. Acidum thamnolicum et acidum didymicum continens.*

*Primary thallus* persistent, consisting of elongate, incised, suberect to imbricate, green squamules, 2-5 mm long and 0.5-1 mm wide; underside arachnoid, white, turning orange-yellow at the very base, occasionally an orange streak extending higher up; rhizomorphs of hypothallus orange, often clearly visible in the soil, extending several cm outward from the squamules. *Podetia* when mature (fertile) 0.5-1.5 cm tall, rather stout, 0.5-2 mm thick, sometimes absent and apothecia sessile on squamules, simple to sparingly branched;

ascyphose but sometimes with scyphoid axils. *Surface of podetia* greenish-gray (rarely browning), rather smooth, areolate-corticate or, more frequently, verruculose-granulose to heavily microsquamulose, esorediate; with few decorticate patches. *Conidiomata* on basal squamules, sometimes on the podetial microsquamules near tips of podetia; usually fairly large, 0.2-0.4 x 0.15-0.2 mm, ampullaceous, sessile to shortly stalked; containing red slime; conidia 8-10 x 1 µm. *Hymenial discs* very common, purple red, coalescent to form 2-5 mm wide compound discs, initially with tiny, often darker red, botryose ascogonial primordia (trichogynes visible) at tips of very young podetia; spores 11-12 x 5 µm, simple, oblong.

Chemistry. K+ yellow, P+ yellow; contains thamnolic and didymic acids as constant major secondary substances and inconstantly traces of usnic (rarely), decarboxythamnolic, condidymic and subdidymic acids (thin-layer chromatography).

Habitat. Growing on bare to humus-covered soil, more rarely on rotting wood or tree bases, e.g. *Pinus oocarpa* or *Quercus resinosa*, in submesophilous oak-pine woodlands at 1650-3880 m, but also collected in treeless mountain pastures. It often forms large, conspicuous patches of richly fertile podetia and well-developed cushions of squamules.

Distribution. Mexico; recorded from the states Chihuahua, Sinaloa, Durango, Jalisco, Veracruz, Michoacán, México, Puebla, Oaxaca and Chiapas. It is expected to extend to Central America, but it has not been detected in the material of more than 1000 specimens of *Cladonia* recently examined from Guatemala and other Central American countries.

Representative specimens examined: MEXICO. CHIHUAHUA. Casada de Basaseachic, 1950 m, 1976 *Nash 13589* (ASU, H, IBUG; to be distributed in the exsiccata by Sipman: Lichenotheca Latinoamericana). - SINALOA. Mpio. Concordia: La Capilla del Taxte, 1370 m, 1983 *Breedlove & Almeda 58809* (CAS). - DURANGO. Along Rte 40 between Durango and Mazatlán, 8 km W of La Ciudad, 1976 *Nash 13899* (ASU, H). - JALISCO. Mpio. San Sebastián del Oeste: near San Sebastián del Oeste, 1985 *Álvarez 127, 131* (IBUG). Mpio. Zapopan: Bosque La Primavera, numerous collections in IBUG, incl. *Ahti et al. 52715* (H, IBUG), *52719* (H). Mpio. Tecolotlán: Sierra de Quila, 3.5 km W of Quililla, 2000 m, 1990 *Guerrero 895* (IBUG). Mpio. Autlán: Sierra de Manantlán, Puerto Los Mazos, 1270 m, 1989 *Guzmán-Dávalos 4839* (IBUG). Mpio. Tapalpa: Sierra de Tapalpa, 1992 *Álvarez 899* (IBUG). Mpio. Tonila: rd. from Atenquique to Parque Nac. Volcán de Fuego, 3140 m, 1996 *Ahti et al. 52781* (H, IBUG). Mpio. Tecalitlán: Sierra del Halo, km 18 on rd. Tecalitlán to Jilotlán, 2000 m, 1988 *Guzmán-Dávalos 4339* (IBUG). - VERACRUZ. W of Cofre de Perote, rd. to Tembladeras, Presa del Alto Pixquiac, 2920 m, 1981, *Guzmán 19525* (ENCB, XAL). Rd. Xalapa-Perote, El Volcancillo, 1982, *López 2133* (H, XAL). - MICHOACÁN. Sierra de San Ándres, Los Azufres, Laguna Larga, 1958, *Bonet s.n.* (ENCB). - MÉXICO. Nevado de Toluca, Parque Los Venados, 3600 m, 1976, *Mora 167* (ENCB). Popocatépetl, Tlamacas, 3700 m, 1957, *Bravo 85* (MEXU), *Ruiz-Oronoz 86* (MEXU). - PUEBLA. Mpio. Atlanta: 2 km NW of Tlamacas, 3790 m, 1985, *coll. unknown s.n.* (FCME). - OAXACA. Rd. Tuxtepec - Ixtlán de Juárez, El Punto, 1963, *Miller s.n.* (ENCB). - CHIAPAS. Montebello, *coll. unknown 150* (MEXU).

The species shall be discussed in more detail in the treatments of the Cladoniaceae for the Flora Neotropica and Flora de México, which are under preparation.

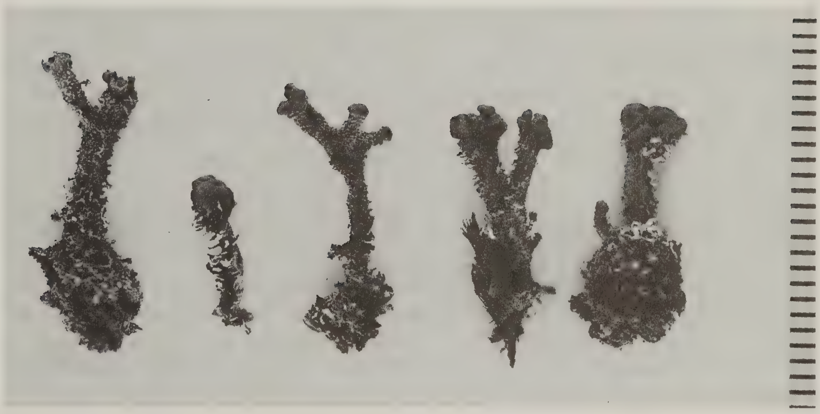

**FIG. 1:** *Cladonia jaliscana*, isotype (H). Scale in mm.

*Cladonia jaliscana* is distinguished from *C. cristatella* by its gray color due to the absence of the pigment usnic acid (usnic acid may be present in traces insufficient to affect the color). *Cladonia cristatella*, endemic to the eastern United States and southeastern Canada (Thomson 1968), is thinner, somewhat more branched, and contains barbatic acid (P-) as the principal constituent. A study of the major Mexican herbaria (IBUG, ENCB, FCME, MEXU, XAL) has shown that all Mexican material identified as *C. cristatella* was misidentified. The showy color picture of "*Cladonia crystatella*" on the front cover of the Mexican handbook "Etimología e iconografía de géneros de hongos" by Ulloa and Herrera (1994) resembles *C. jaliscana* but because of the lack of well developed cortex seems to be *C. didyma* (Fée) Vain.

*Cladonia floerkeana* can also resemble *C. jaliscana*, but is very slender and contains barbatic acid (though a very rare thamnolic acid strain is also known from Europe; Huovinen et al. 1989), while usnic acid is normally absent. *C. floerkeana* also often produces granulose soredia. It is present in eastern Canada and the United States, but the range is poorly known. Some doubtful material has also been seen from Honduras.

*C. abbreviatula* is perhaps the closest relative of *C. jaliscana*, since its chemistry can be similar (Evans, 1952; Huovinen et al., 1989): thamnolic, usnic (perhaps inconstant?) and the didymic acid complex. Harris (1995) reported usnic, squamatic and didymic, rarely grayanic acid, for *C. abbreviatula*. However, *C. abbreviatula* is regularly extremely small, with 1-5(10) mm tall, turbinate podetia almost exclusively growing on the soft bark of *Taxodium* in *Taxodium* swamps (Moore, 1968), and restricted to Florida and adjacent Georgia. *C. jaliscana* is a species primarily growing on soil at higher, colder elevations, extending to timberline.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
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# THE HETERODERMIA ERINACEA GROUP IN NORTH AMERICA, AND A REMARKABLE NEW DISJUNCT DISTRIBUTION

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ABSTRACT: A review of material from northwest Mexico and southern California (including the Channel Islands) generally identified as *Heterodermia erinacea* has revealed the presence of three species, one of which is new to the Mexican mainland, and one of which is new to North America. *Heterodermia ciliatomarginata*, which was originally described from Guadalupe Island (Mexico), is reported from Baja California. *Heterodermia namaquana*, previously known only from coastal Namaqualand in southern Africa, is reported from Baja California and Sonora state (Mexico), and southern California, including the Channel Islands. This appears to be the first report of a species level western North America-southern Africa distribution pattern. The heterobasidomycete *Syzygospora physciacearum* is a relatively common parasite on *Heterodermia namaquana* in southern California.

During collecting trips in southern California, the Channel Islands and Baja California, the authors collected many specimens of *Heterodermia* which bear conspicuous marginal or laminal cilia on the thallus. The only ciliate species known to occur in the area was *H. erinacea* (Ach.) W. A. Weber, a fertile, primarily epiphytic species easily distinguished from other ciliate or 'hairy' species in the genus by its possession of relatively small, *Physcia*-type spores which lack sporoblastidia (Kurokawa 1962, 1973). After preliminary study of the material, it became obvious that this group of ciliate specimens actually comprised three distinct species, two of which occur primarily as epiphytes and the third occurring on rock. Subsequent investigation has revealed that names already exist to accommodate all three species, which can be distinguished from one another on the basis of the criteria in the following synoptic key:

**A.** Thallus mostly caespitose, the lobes erect-ascending, cilia primarily marginal or submarginal; lower surface flat to weakly concave (not convex), obviously ecorticate in whole or in large part.

**B.** Lower surface ecorticate essentially throughout, esorediate, often appearing veined due to downward projecting ridges of the upper cortex appearing among the 'cottony'/hyphal medulla; apothecia common and often abundant, margin eciliate; ascospores 16-24 x 7.5-10 µm; epiphytic.
*Heterodermia erinacea* (Ach.) W. A. Weber

**B.** Lower surface ecorticate and sorediate throughout (especially in shorter, broader lobed specimens), or some narrower lobed specimens with sorediate areas only toward the (often broadened) ends, sorediate areas often appearing veined due to downward projecting ridges of the upper cortex among the soredia; apothecia often missing but not rare, the margin eciliate or occasionally ciliate; ascospores 17-22.5 x 6-8 µm; epiphytic, rarely on rock.
*Heterodermia namaguana* Brusse

**A.** Thallus more or less prostrate or only very indistinctly ascending toward lobe ends, cilia laminal and marginal (some of the latter acting like rhizines to weakly attach thallus to the rock substrate); lower surface flat or often weakly convex, with continuous, agglutinate medulla which usually appears smooth on the surface, almost (or indeed) like a cortex, never sorediate or 'cottony'/hyphal or veined; apothecia common, with ciliate margin; ascospores 12-20 x 6-8 µm; saxicolous.
*Heterodermia ciliatomarginata* (Linder) Essl.

***Heterodermia erinacea*** (Ach.) W. A. Weber in Egan **[Figs. 1 & 2]**
The Bryologist 90(2): 163. 1987.
Basionym: *Borrera erinacea* Ach., Lichenographia Universalis 1810, p. 499. Type: California, *Menzies* (H-Ach; not seen, but see discussion below).

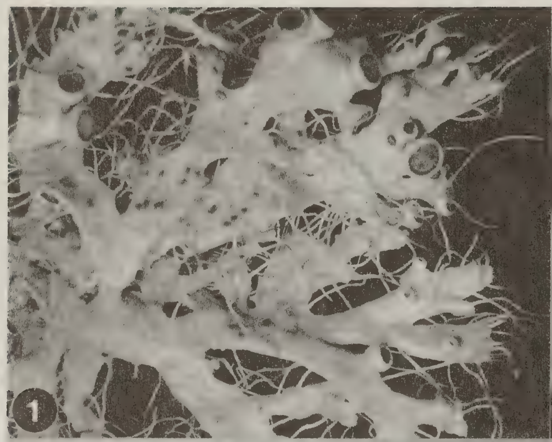
Thallus foliose to caespitose-subfruticose, up to 6 or 7 cm in diameter, with loosely adnate lobes, prostrate to more often ascending. Lobes (0.5-)1-2 mm broad, elongate, often crenate/flabellate near the end, upper surface usually more or less flat to weakly convex or (rarely) weakly concave, sometimes weakly lumpy, ciliate, the cilia mostly marginal or submarginal (less frequent on the upper surface), 2-7 mm long and 50-100 (-125) µm thick at the base, simple or rarely branched, white or darkening in the upper parts. Lower surface flat to weakly concave, uneven, ecorticate throughout and appearing 'cottony'/hyphal (Fig. 2), never sorediate, usually irregularly veined due to downward projecting ridges of the upper cortex and weak agglutinations of medullary hyphae. Apothecia very common (near 100% frequency) and often abundant, laminal and short stipitate, up to 2.5 mm diameter, flat to weakly convex, the disk black and becoming more or less pruinose, the apothecial margin eciliate; spores 16-24 x 7.5-10 µm, *Physcia*-type. Pycnidia common, 150-350 µm wide, sometimes bulging the tissues above, black around the ostiole and usually conspicuously emergent, conidia 3.5-4.5 x <1 µm, bacilliform, sometimes more pointed on one end. Upper cortex K+ yellow, lower surface (medulla) K+ yellow. TLC: atranorin, chloroatranorin, zeorin, and unidentified trace terpenoids (see discussion of chemistry under *H. namaquana*). On shrubs, trees, and cacti (not presently known from rock?); from near sea level to 500 m elev.

The type of *H. erinacea* is in the Acharian herbarium in Helsinki and is therefore unavailable for loan. Dr. Orvo Vitikainen was kind enough to examine the specimen for me and confirmed that it has an ecorticate and esorediate lower surface. Furthermore, he sent a small specimen from the Nylander herbarium (H-Nyl 32436) which is apparently a 'kleptotype' taken from Acharius' specimen. It is only fragmentary, about 6 mm across, but very distinctly belongs to *H. erinacea* as defined here.

In southern California and Baja, *H. erinacea* occurs in habitats similar to those of *H. namaquana* and the two species sometimes grow intermixed. *Heterodermia erinacea* is not known from South Africa, the original report of that species (Brusse 1988) having been based on material of *H. namaquana* (Brusse 1992). A questionable report of *H. erinacea* exists for China (Wei, 1991). The report of *H. erinacea* from Santa Barbara Island (Bratt 1993) was based on a specimen of *Heterodermia namaquana*, and although *H. erinacea* has been reported from several other California islands (e.g. Santa Catalina [Kurokawa 1962], San Clemente [Bowler et al. 1996]), in this study it was found only on Santa Rosa Island. Generally, *H. namaquana* seems to be more common than *H. erinacea* in California and on the Channel Islands.

Additional specimens examined (**TLE** is the herbarium of T.L. Esslinger, and **B-T** is the combined herbarium of Charis Bratt and Shirley Tucker):

**U.S.A. California**. San Diego Co.: San Diego, *Hunt*, 1914 (TLE), *Palmer*, 1888 (MIN); Point Loma, *Hasse 2288* (MIN), *Lichenes Exsiccati ex Herb. Dr. H. E. Hasse Relicti 178* (B-T). Santa Barbara Co.: mesa W of La Parisima Mission, Lompoc, *Bratt 4433A* (B-T); Channel Islands, Santa Rosa Island, South Point (33°54'N, 120°07'15"W), 180-310 m elev., *Ryan 31221-b* (ASU), N rim of Bee Canyon, *Bratt 8454* (B-T). **Mexico. Baja California Norte**: Miller's Landing, *Wiggins*, 1946 (B-T); along the Pacific Ocean NW of Bahía Falsa and at end of road W from San Quintín, ca. 7 m elev., *Nash 29497* (ASU); near Bahia San Quintin, ca. 46 m elev., *Nash 8710* (ASU); Camino a la Bufadora, ca. 100 m elev., *Patron 76* (ASU); Punta Banda Peninsula, 24 km S of Ensenada, Banda Peak, 275-305 m elev., *Rundel & Bowler 7579* (ASU); Punta Banda W of Ensenada (31°44'30"N, 116°43'30"W), 60 m elev., *Wetmore 75968* (MIN); Punta Santo Tomas, 20 km S of Ensenada (31°33'30"N, 116°42'W), 0-100 m elev., *Esslinger 10198* (TLE), *Wetmore 63468* (MIN); 2 km S of Colonet along Hwy. 1(31°04'N, 116°13'W), 50 m elev., *Esslinger 10276, 10285, 10297* (TLE), *Egan 13722, Wetmore 63551* (MIN); 8 km E of San Quintin, 60 m elev., *Nash 8765* (ASU, MIN); San Quintin, Cerro Kenton (30°28'N, 116°00'W), 30-200 m elev., *Esslinger 10334, 10371, 10380* (TLE), *Egan 13761, Wetmore 63632, 72405, 72418* (MIN), *Ryan 21275, Bratt 6932, 6942, 6984,*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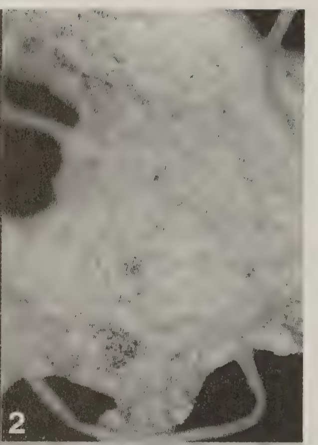
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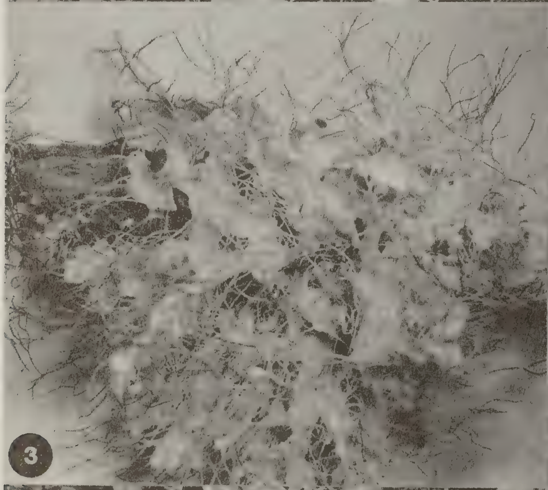
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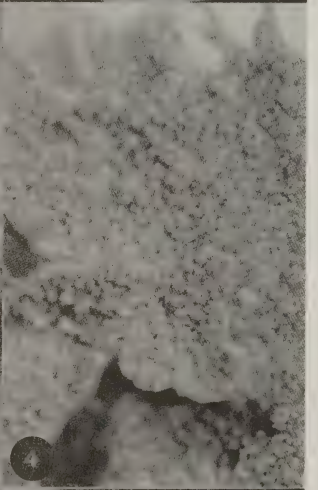
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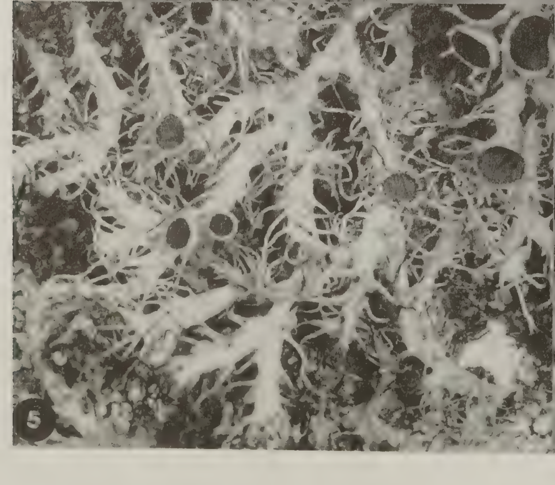
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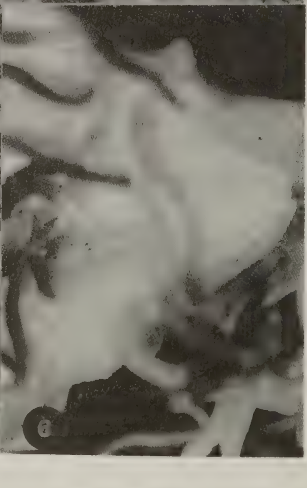
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*6993, 7002, 7049* (B-T); about 10 km N of El Rosario in Cañon del Rosario (30°08'N, 115°46'W), ca. 90 m elev., *Esslinger 10482* (TLE); 6 km N of El Rosario along Hwy. 1 (30°07'N, 115°46'W), ca. 280 m elev., *Nash 34047* (ASU), *Wetmore 72378A* (MIN); 31 km E of El Rosario near El Aguajito (30°03'N, 115°25'W), ca. 500 m elev., *Esslinger 10788A* (TLE); 23 km E of El Rosario (30°02'N, 115°31'W), ca. 200 m elev., *Esslinger 10525* (TLE); Punta Santa Rosalillita, 15 km W of Hwy. 1 (28°40'N, 114°13'W), 40 m elev., *Wetmore 70278* (MIN); along side road to Punta Rosarito, 0.3 km W of Hwy. 1 and 11 km S of Rosarito (28°34'N, 114°04'W), 30 m elev., *Wetmore 64011* (MIN); Isla Cedros (28°22'N, 115°15'30"W), ca. 300 m elev., *Nash 34418* p.p. (ASU); Punta Santo Domingo (28°15'N, 114°08'W), 60 m elev., *Nash 12804* (ASU); between Laguna Manuela and Punta Santo Domingo (28°14'N, 114°06'W), 0-50 m elev., *Esslinger 10619* (TLE), *Nash 26194* (ASU), *Egan 13972* (MIN); ; 28 km N of El Socorro along Hwy. 1, 60 m elev., *Nash 4532* (ASU); 3.2 km N of Colonet along Hwy. 1, 150 m elev., *Nash 4474* (ASU); 5 km S of Colonet along Hwy. 1, 90 m elev., *Nash 4499* (ASU); 28 km N of El Socorro along Hwy. 1, 60 m elev., *Nash 4509* (ASU). **Baja California Sur**: along road to Punta Eugenio, 3 km W of junction with Hwy. 1 (27°39'N, 113°25'W), ca. 60 m elev., *Esslinger 10754A* (TLE); 31 km W of San Ignacio (27°20'N, 113°07'W), ca. 180 m elev., *Esslinger 10631* (TLE); 3.5 km along road to Punta Abreojos from Hwy. 1 (27°15'N, 113°10'W), *Wetmore 72227* (MIN); 10 km WSW of San Isidro (26°09'30"N, 112°11'W), 220 m elev., *Wetmore 70236* (MIN); 36 km NNW of Ciudad Insurgentes (25°40'N, 111°58'W), ca. 50 m elev., *Nash 30495* (ASU), *Wetmore 70207* (MIN); 16 km NE of Puerto San Carlos, *Nash 8930* (ASU); 50 km NNW of Ejido Insurgentes (25°32'N, 111°56'W), 40 m elev., *Nash 17085* (ASU), *Lichenes Exsiccati A.S.U. No. 63* (B-T, TLE); 22 km N of Hwy. 1 and SW of El Arco, *Nash 8836* (ASU); 3.2 km N of San Carlos (24°48'N, 112°06'W), 6 m elev., *Nash 12817* (ASU).

***Heterodermia namaquana*** Brusse, Bothalia 22: 183. 1992. **[Figs. 3, 4, & 7]**

Type: South Africa. Cape Province: Springbok, Gemsbokvlei, Namaqualand coastal plain, Brusse 5930 (COLO, isotype).

Thallus foliose to caespitose-subfruticose, with loosely adnate, ascending lobes, mostly 1-3 cm in diameter, rarely up to 5 or 6 cm. Lobes 1-2.5 (-3) mm broad, elongate but often somewhat irregular or laciniate, often broader toward the ends, the upper surface flat to weakly concave or convex, often appearing uneven or lumpy, ciliate, the cilia primarily marginal or submarginal (infrequent on the upper surface), (1-)2-6 mm long and 50-100 (-125) µm broad at the base, simple or rarely branched, white or darkening in the upper parts. Lower surface flat to weakly concave, uneven,

Figures 1-6. Habit photographs (x4.5) and lower surface photographs (x26) of *Heterodermia* species. Figs. 1 & 2: *H. erinacea*, Bratt 7042 (B-T). Figs. 3 & 4: *H. namaquana*, Bratt 8196 (TLE). Figs. 5 & 6: *H. ciliatomarginata*, Esslinger 10768 (TLE).

in mature thalli often becoming more or less totally ecorticate and sorediate (Fig. 4), sometimes the narrower more linear lobes develop soredia only toward the ends, the older parts having agglutinated (cortex-like) medulla, sorediate parts of the lower surface often appearing veined due to the thickened downward extensions of the upper cortex which are visible among the soredia, occasional cilia (rarely more numerous) present on the lower surface among the soredia (originating from lower surface of the upper cortex), patchy erosion of the medulla and soredia rarely exposing a more or less smooth lower surface (actually the lower surface of the upper cortex) . Apothecia occasional (present in ca. ⅓ of cited specimens), laminal and stipitate, up to 3 mm in diameter, more or less flat, the disk black and often somewhat pruinose, the apothecial margin smooth or ciliate (about ¼ of fertile specimens); spores (14-)17-22.5 x 6-8 µm, *Physcia*-type (Fig. 7). Pycnidia rather common, 150-200 µm wide, weakly or not emergent, conidia 4-5 x <1 µm, bacilliform but sometimes more pointed at one end. Upper cortex K+ yellow, medulla and soredia on the lower surface K+ yellow. TLC: atranorin, chloroatranorin, zeorin, and trace terpenoids. Usually on tree and shrub branches, occasional on cacti, palm leaf bases, rock or sandy soil; from near sea level to 500 m. elevation.

As pointed out by Brusse (1992), this species is similar and related to *H. erinacea*, with which it shares habit, a generally ecorticate lower surface, *Physcia*-type spores, and chemistry. That species differs from *H. namaquana* by its lack of soredia, and the concomitant retention of a 'cottony'/hyphal medulla on the lower surface, which is interrupted only by the weak venation . The two are not a true primary/secondary species pair however, since other morphological characters distinguish them as well. Thalli of *Heterodermia erinacea* totally lack the agglutinated (cortex-like) medulla present in the narrow-lobed forms of *H. namaquana* (see below). *Heterodermia erinacea* thalli are frequently larger than those of *H. namaquana*, and most specimens also have somewhat narrower, slightly more elongate lobes, a trend that is particularly evident in mixed collections of the two species where they were found growing together in Baja. Also, the spores and pycnidia of *H. erinacea* range somewhat larger. Interestingly, the lichenicolous heterobasidiomycete *Syzygospora physciacearum* Diederich was found parasitizing (often heavily) nine specimens of *H. namaquana* (all from California; denoted by an asterisk in the specimen citations), but was not observed on any of the ca. 70 specimens of *H. erinacea* examined for this study. *Heterodermia erinacea* was originally reported as one of several physciaceous hosts for this parasitic fungus (Diederich 1996), but this parasite is either much more common on or restricted to *H. namaquana*.

There is a form of this species (especially common on Isla Cedros) with narrower, elongate lobes which retain an agglutinated (lower cortex-like) medulla in older thallus parts, bearing soredia only toward the lobe ends, which tend to be broader. The terminal soralia in some of these specimens mimic the domed, helmet-shaped terminal soralia of *Physcia adscendens* (see below). The more common form of *H. namaquana*, with generally shorter and broader lobes and nearly continuous soredia on the entire lower surface, at first seems distinct from the these narrow-lobed forms, but the variation between the two is continuous. Some of these narrow-lobed thalli were found to have few or no soralia (*Nash 34421* and part of *Nash 34393*, both from Isla Cedros), but all other characters agree with their placement here.

Among other species of *Heterodermia* growing in the region, only members of the *H. leucomelos* (L.) Poelt group are likely to be confused with *H. namaquana* or the other species treated here. *Heterodermia leucomelos* and its relatives have a less caespitose habit, with much longer, generally narrower, strongly linear, and regularly branched and intertwined thallus segments, which are often weakly circinate at the ends. The ecorticate lower surface in these species is clearly bordered by the reflexed upper cortex and has soredia in patches, usually only in the end regions of branch segments. Well-developed specimens of *Physcia adscendens* (Fr.) H. Olivier or related *Ph. tenella* (Scop.) DC. may be superficially similar to *H. namaquana* in habit, but they are easily distinguished by the corticate lower surface with soralia forming only on or under the lobe ends, and by a generally smaller size with narrower lobes and sparser, shorter cilia (up to 1-2 mm long). Specimens of *H. namaquana* which are very small and poorly developed and which have agglutinated medulla/cortex on the narrower portions of the lobe lower surface, may have the soredia forming only near lobe ends and edges. These specimens in particular might be confused with *Physcia adscendens* or *Ph. tenella*, although the unevenly thickened and prosoplectenchymatous upper cortex of *H. namaquana*, as revealed in a longitudinal section of a lobe, will easily distinguish such difficult specimens.

The disjunct distribution of *H. namaquana* is remarkable. Although various bipolar disjunctions are well known in lichens (Culberson 1972, Galloway 1991, Galloway and Aptroot 1995), no previous report of a species level western North America-southern Africa disjunction pattern was found in the literature. The southern California/Baja area shares a similarly arid, near-Mediterranean climate with South Africa, and they therefore have structurally somewhat similar lichen floras at the family and genus level, but apparently only a few near ubiquitous or otherwise widespread species have been found in both areas (Almborn 1988).

The thin-layer chromatography (TLC) results reported here were obtained using the standardized TLC methods described by Culberson & Kristinsson (1970) with its various later modifications by Culberson (1972, 1974) and Culberson and Ammann (1979). Some early TLC results indicated that some specimens of *H. namaquana* and *H. erinacea* might contain chloroatranorin rather than atranorin as the major phenolic component, but the distinction between these two substances is not easily made by TLC. Dr. Chicita Culberson kindly analyzed a small number of specimens using HPLC, and confirmed the presence of chloroatranorin in both species, but in extremely variable concentrations. In some specimens, atranorin was major, with only traces of chloroatranorin, and in others that situation was reversed. At least one specimen with significant amounts of both atranorin and chloroatranorin (ca. 3:1 ratio) was found. Further and more detailed study of the chemical variability of these two species is required, especially to determine whether any environmental factors are influencing the production of atranorin vs. chloroatranorin.

Brusse (1992) reported that the ascospores of this species are *Pachysporaria*-type when examined in water and *Physcia*-type when examined in KOH. However, ascospores from an isotype specimen from south Africa (cited above) were examined and proved to be *Physcia*-type in both water (Fig. 7 ) and KOH, just like those from the American specimens. In all specimens, immature spores may have rather rounded-oblong lumina with thin side walls, but the mature spores are distinctly *Physcia*-type, whether observed in water or in KOH.

Additional specimens examined (* indicates specimen parasitized by *Syzygospora physciacearum*):

**U.S. A. California**: San Luis Obispo Co.: south of Morro Bay, Los Osos, across road from Los Osos Middle School (35°19.5'N, 120°49.1'W), *Esslinger 15165, 15181, 15182** (TLE), *Tucker 34644* (B-T); Los Osos Oaks State Reserve, Los Osos Valley Road, *Bratt 3841**, *4030, 4060, 4065* (B-T). San Mateo Co.: near Point San Pedro, cliffs above sea, 76 m elev., *Herre 513* (MIN). San Francisco Co.?: San Francisco, Pt. Lobos, 23 m elev., *Herre 885* (MIN). California Channel Islands: Santa Barbara Co.: Santa Barbara Island, northwest face of Signal Peak, *Bratt 5186* (B-T); Santa Cruz Island, Islay Canyon Rd. plateau, 300 m elev., *Bratt 5661** (B-T); Santa Rosa Island, along South Point Road, Boulder Hill, *Bratt 8507* (B-T), along bluff top, N rim of Bee Canyon, *Bratt 8454A, 8460* (B-T), just W of Bee Canyon (120°12'W, 33°58'15"N), *Nash 32702** (ASU), lower portion of Lobos Canyon (34°00'15"N, 120°05'15"W), *Ryan 31303* (ASU); San Miguel Island, Devils Knob, S of Harris Point, *Bratt 9001** (B-T), NW of Station in Nidever Canyon, *Bratt 9042**, *9044** (B-T), across 1st barranca NW Stn., Nidever Canyon, *Bratt 9051, 9058, 9062** (B-T), Lester Point, *Bratt 8909** (B-T), North Shore, W of Green Mtn., *Bratt*

Figure 7. *Physcia*-type ascospores in the isotype (Brusse 5930, COLO) of *Heterodermia namaquana*, mounted in water.

*9018* (B-T). Ventura Co.: West Anacapa Island, campground east ¼ mi to 2nd draw, *Bratt 9186*, 9218, 9223* (B-T), Willow Canyon, *Bratt 8706* (B-T); San Nicolas Island, sand dunes along Tufts Rd., *Bratt 8196* (B-T, TLE), south side, south of Research Station, on bluff top, *Bratt 7990* (B-T), south side, below Twin Towers at edge of bluff, *Bratt 7874* (B-T), near buildings on Tufts Road, *Tucker 33777* (herb Bratt), West End terrace overlooking Red Eye Beach, *Rindlaub L0001* (B-T, TLE). **Mexico. Baja California Norte**: base of San Pedro Martir, *Nash 9042* (ASU); 1.6 km NE of El Arco, *Nash 8848* (ASU, MIN); along Hwy. 1, 30 km S of turnoff for Bahía de Los Angeles (28°45'N, 114°07'W), ca. 170 m, *Nash 33989* (ASU); 6 km N of El Rosario along Hwy. 1 (30°07'N, 115°46'W), ca. 280 m elev., *Nash 34034* (ASU); 10 km S of bridge over El Rosario wash along Hwy. 1 (30°03'N, 115°35'W), ca. 230 m elev., *Nash 34017* (ASU), *Wetmore 72335* (MIN); along Hwy. #1 about 2 km S of Colonet (31°04'N, 116°13'W), ca. 50 m elev., *Esslinger 10285* (TLE); Cerro Kenton between Bahia Falsa and Bahia San Quintin (30°28'N, 116°00'W), ca. 20 m elev., *Esslinger 10312* (TLE); along Pacific Ocean from NW of Bahia Falsa and west of San Quintin (30°28'N, 116°02'W), *Esslinger 10449A* (TLE); 4.8 km N of El Rosario along Hwy. 1, 180 m elev., *Nash 4665* (ASU); along Hwy. #1 about 10 km N of El Rosario in Cañon del Rosario (30°08'N, 115°46'W), ca. 90 m elev., *Esslinger 10463, 10482A* (TLE); along Hwy. #1, 31 km E of El Rosario near El Aguajito (30°03'N, 115°25'W), ca. 500 m elev., *Esslinger 10786, 10788* (TLE); 23 km E of El Rosario along Hwy. #1 (30°02'N, 115°31'W), ca. 200 m elev., *Esslinger 10543* (TLE); along Hwy. #1 about 21 km S of Rosarito, just N of Arroyo San Regis (28°31'N, 114°03'W), ca. 50 m elev., *Esslinger 10589* (TLE); Isla Cedros (28°22'N, 115°15'30"W), ca 300 m elev., *Nash 34393, 34399, 34418, 34421* (ASU), (28°22'N, 115°15'W), ca. 400 m elev., *Nash 34288* (ASU), (28°08'N, 115°12'45"W), 510 m elev., *Nash 34537* (ASU); south end of Guadalupe Island, Lower California, *Howell 47* p.p.(FH, a very small admixture in the isotype of *H. ciliatomarginata*). **Baja California Sur**: along road to Punta Eugenio, 3 km W of its junction with Hwy. #1 (27°39'N, 113°25'W), ca. 60 m elev., *Esslinger 10754* (TLE); 31 km W of San Ignacio along Hwy. #1, NE slope of cerro at junction of road to Punta Abreojos (27°20'N, 113°07'W), ca. 180-200 m. elev., *Esslinger 10631A* (TLE), *Bratt 7125* (B-T); 36 km NNW of Ciudad Insurgentes (25°40'N, 111°58'W), ca. 50 m elev., *Nash 30512, 30516* (ASU); 48 km SW of San Javier along San Javier wash (25°37'N, 111°44'W), 150 m elev., *Wetmore 70066* (MIN); 20 km ENE of Ciudad Insurgentes along Hwy. #1 (25°21'N, 111°37'W), ca. 75 m elev., *Esslinger 10695* (TLE); 21 km W of Ciudad Constitución along Hwy. #22 (24°59'N, 111°51'W), ca. 30 m elev., *Esslinger 10709, 10712* (TLE), *Bratt 7158* (B-T); 16 km W of Ciudad Constitución (24°59'N, 111°51'W), ca. 30 m elev., *Nash 30424* (ASU); 22.4 km WSW Villa Constitución (24°57'N, 111°51'W), 30 m elev., *Nash 12861* (ASU); 20 km W of hwy. 1 along road to Puerto Cancun (24°35'N, 111°36'W), 70 m elev., *Wetmore 72089* (MIN); 1 km SW of Santa Rita along Hwy. 1 (24°35'N, 111°29'W), ca. 120 m elev., *Nash 29829* (ASU); 9 km NE of Puerto Chale (24°31'N, 111°29'W), ca. 20 m elev., *Nash 17056* (ASU); E of Guerrero Negro, *Nash 8996*

(ASU); Isla Santa Margarita (24°24'N, 111°43'W), ca.375 m elev., *Nash 33921* (ASU). **Sonora**: 3.2 km NW of Huatabampito (26°43'N, 109°35'W), 9 m elev., *Nash 12308* (ASU); 2 km WNW of Huatabampito (26°42'N, 109°33'W), 6 m elev., *Nash 12328* (ASU).

***Heterodermia ciliatomarginata*** (Linder) Essl., **comb. nov**. **[Figs. 5 & 6]**

Basionym: *Anaptychia ciliatomarginata* Linder, Proc. Calif. Acad. Sci., 4th series, 21(18): 217. 1934. Type: South end of Guadalupe Island, Lower California, Nov. 16, 1931, *Howell 47* (FH, isotype).

*Anaptychia erinacea* f. *ciliatomarginata* (Linder) Kurokawa, Beih. Nova Hedwigia 6: 46. 1962.

Thallus foliose to subfruticose, up to 6 or 7 cm in diameter, with loosely adnate lobes which are more or less prostrate throughout (although held above the substrate by cilia) or weakly ascending toward the ends. Lobes 0.5-1.2 mm broad, elongate and linear, upper surface more or less convex, smooth to weakly lumpy, ciliate, the cilia laminal and marginal, up to 5 or 6 mm long and ca. 75-150 μm broad at base, simple or sometimes irregularly branched in upper parts (especially those which project downward and make contact with the substrate), white or darkening in upper parts. Lower surface flat to weakly convex, the dense agglutinated hyphae of the medulla forming what appears to be a more or less smooth (but dull) lower cortex (Fig. 6) (fibrous nature often visible at the tips and edges of the lobes). Apothecia common, usually present, laminal and short stiptitate, up to 4 mm in diameter, more or less flat, the disk black but often pruinose, the apothecial margin ciliate; spores 12-17 (-20) x 6-7.5 μm, *Physcia*-type. Pycnidia large, up to almost 500 μm wide, often bulging the tissues above, black around the ostiole and more or less emergent, conidia 3-4 x 1 μm, ellipsoid to bacilliform, rarely more pointed at one end. Upper cortex K+ yellow, lower surface K- to K+ yellow (positive especially near some lobe tips but also rarely in some older parts), internal medulla K-. TLC: atranorin and faint traces of several terpenoid compounds. Known only from rock.; from near sea level to 200 m elevation.

This species was treated as a form of *H. erinacea* by Kurokawa (1962), but now that more material is available it is easily distinguished from *H. erinacea* as well as *H. namaquana* by the thick, agglutinated medulla, the slightly stouter cilia regularly distributed on the upper surface, the smaller spores, and the more prostrate habit. The pycnidia are also distinctive, being generally much larger than in the other two species (up to 0.5 mm broad) and sometimes becoming eroded when old to leave large rough pits on the upper surface. *Heterodermia ciliatomarginata* differs from the other two species treated here by its lack of zeorin. This species was not tested for chloroatranorin by HPLC.

Kurokawa (1962) regarded the type specimen in FH (cited above) as the holotype, but Linder (1934) clearly indicated that the type was placed in the herbarium of the California Academy of Sciences and the FH material was designated as a 'cotype.' Furthermore, the excellent photographs of type material in the protologue show thalli that are not present in the FH specimen.

Additional specimens examined:
**Mexico. Baja California Norte**: 9.6 km S of Millers Landing, *Nash 9002* (ASU); Punta Baja, 4.8 km SW of El Rosario, *Nash 4874* (ASU); Punta Santa Rosalillita, 15 km W of Hwy. 1 (28°40'N, 114°13"W), 40 m elev., *Wetmore 70272* (MIN); 11 km S of Rosarito along Hwy. 1 and 0.3 km W on side road toward Punta Rosarito (28°34'N, 114°04'W), ca. 30 m elev., *Esslinger 10768* (TLE), *Egan 14076*, *Wetmore 64026* (MIN), *Bratt 7173* (B-T); 12.3 km S of Rosarito, *Nash 8831* (ASU); along Hwy. 1 about 21 km S of Rosarito, in an arroyo just N of Arroyo San Regis (28°31'N, 114°03'W), ca 50 m elev., *Esslinger 10582* (TLE), *Wetmore 63836* (MIN). **Baja California Sur**: W of San Ignacio, *Nash 8973* (ASU); Peninsula Vizcaino, along road to Bahia Tortugas, 152 km W of Hwy. 1 (27°38'N, 114°32'W), *Nash 29617* (ASU); along Hwy. 1, 31 km W of San Ignacio at junction of road to Punta Abreojos (27°20'N, 113°07'W), 180-200 m elev., *Wetmore 63980*, *Egan 14000A* (MIN).

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Mycotaxon Ltd., Ithaca, NY. 1998.

# *RINODINA RIPARIA* (LICHENIZED ASCOMYCETES, PHYSCIACEAE), A NEW CORTICOLOUS SPECIES FROM NORTH AMERICA

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## Abstract

*Rinodina riparia* is described from western North America. It has an unusual spore ontogeny and conidiophore morphology which are compared with other species in the genus. The species may be most typical of *Populus* species in river valleys and moist draws of low rainfall areas but it has also been collected on *Juniperus* in a more xeric wooded habitat.

Taxonomic studies of the lichen genus *Rinodina* in North America have resulted in a better circumscription of the genus (Mayrhofer et al. 1992, Sheard 1974, Sheard 1992, Sheard & May 1997) but few of the new species discovered within the genus have yet been described (Sheard 1995, Sheard & Tønsberg 1995). New species frequently have been encountered in collections, particularly from western North America, sent to the author for identification. The present species was among specimens verified for the paper which follows later in this volume (Will-Wolf 1998).

## *Rinodina riparia* Sheard sp. nov.

**Diagnosis:** Ad corticem arborae, ascosporae 20.0-28.0, 24.0 x 11.0, 9.5-13.0 μm, typi "dirinaria", tumidae ad septum in sporae immaturae, paries non ornatus.

**Type:** U.S.A., COLORADO: JEFFERSON CO., alongside Deer Creek, 4.7 km West of jnct. Colo. 470 and Deer Creek Rd. Growing at base of *Populus angustifolia*, 1650 m, 5 May 1974, *M.B. Carmer 2525* (COLO - holotype).

**Description:** Thallus thin, grey, minutely verrucate at first, becoming areolate, areolae to 0.60-0.80 mm wide, plane and matt. Thallus indeterminate, without perceptible hypothallus. Apothecia sessile but broadly attached, frequent and mostly contiguous, to 0.50-0.80 mm diam. Disc dark brown to black and persistently plane, margin concolorous with thallus, 0.05-0.10 mm wide, entire and persistent, excipular ring sometimes present.

Thalline exciple 50-90(-120) μm wide laterally, 40-110 (-140) μm below. Cortex cellular, 5-10 μm wide laterally, sometimes expanded below to 10-40 μm wide. Cortical cells not or lightly pigmented, to 5.0-7.0 μm wide, algal cells to 10.5-16.5 μm diam. Proper exciple ca. 10 μm wide laterally, expanded above to 20-30 μm wide.

Hypothecium colorless, (40-)60-80 μm deep. Hymenium (70-)100-120 μm high, gelatinized, paraphyses 2.0-2.5 μm wide, apices expanded to 3.5-5.5 μm, lightly pigmented and immersed in dispersed pigment forming a light red-brown epithecium. Asci (60-80) x (20-27) μm. Spores dirinaria-type (Mayrhofer 1984), 20.0-(23.5-24.5)-28.0, 24.0 x 11.0, 9.5-(11.0-11.5)-13.0 μm, mainly type A development (Giralt & Mayrhofer 1995), inflated at septum when young, more so on application of KOH; lumina angular (physcia-like) before walls become fully pigmented, becoming rounded and spores thin walled except at apex; walls darkly pigmented except at apices and sometimes appearing almost mucronate at maturity, not ornamented, some spores with a pigmented band around each cell; septal disc often present in immature spores; torus absent.

Conidiomata (Hawksworth 1988) immersed in thallus, not pigmented and hence very difficult to detect except as slight depressions in verrucae of juvenile thalli. Conidiophores Type II (Vobis & Hawksworth 1981), conidia bacilliform, 4.5-6.0 x 1.0 μm.

Thalline reactions negative, not tested by TLC.

## Discussion

Spore morphology is the most important character in the taxonomy of *Rinodina.* Spore types have been described by Mayrhofer (1982, 1984) and modified by Matzer & Mayrhofer (1996). The spores of *Rinodina riparia* first possess angular locules (physcia-like), a septal disc between the locules and a swelling at the septum which becomes larger on application of KOH (Figure 1A). An inner wall, characteristic of some dirinaria-type spores (Mayrhofer 1982, 1984), becomes visible in the apical region at maturity (Figure 1B). It finally develops into a structure which might be described as an endospore in over-mature, probably non-viable, spores (Figure 1C). This spore type usually develops apical wall thickenings before the septum is formed (Type B ontogeny, Giralt & Mayrhofer 1995) to create two locules (Matzer & Mayrhofer 1996). The majority of juvenile spores of *R. riparia* lack this feature. The mature spores are relatively large for the dirinaria-type, comparable to *R. monacensis* Ropin in length but broader due to the septal swelling, another corticolous species recently described from Europe (Ropin & Mayrhofer 1995) and the saxicolous *R. teichophiloides* (Stizenb.) Zahlbr. (Mayrhofer 1984). The relatively large spores invite comparison with another corticolous western species, *R. oregana* H. Magn., but this species has much larger, physcia-type spores averaging 30.5-32.5 x 14.0-16.0 μm.

Conidiophores are generally considered to be Type VI in *Rinodina* (Matzer & Mayrhofer 1996) and have been illustrated in Matzer et al. (Figure 8, 1994). The conidiophores of *R. riparia*, however, are neither septate or branched and belong to Type II. They are indistinguishable from those of *R. beccariana* Bagl. var. *beccariana* illustrated by Mayrhofer et al. (Figure 6, 1993).

*Rinodina riparia* has previously been reported from the Elkhorn Unit of the Theodore Rossevelt National Park, South Dakota by Wetmore (1985).

**Other specimens examined:** U.S.A. CALIFORNIA, Mariposa Co., Yosemite valley, 1900, *H.E. Hasse* (FH); COLORADO, Jefferson Co., Deer creek, 1973, *M.B. Carmer 900A* (COLOM), *1710* (BRY); SOUTH DAKOTA, Pennington Co., Edge of Sheep Mtn., 1981, *S. Will-Wolf 2070* (WIS); Shannon Co., Fog Creek, 1991, *S. Will-Wolf 2536* (WIS); UTAH, Summit Co., east of Kamas, 1990, *C. Newberry 1434* (BRY).

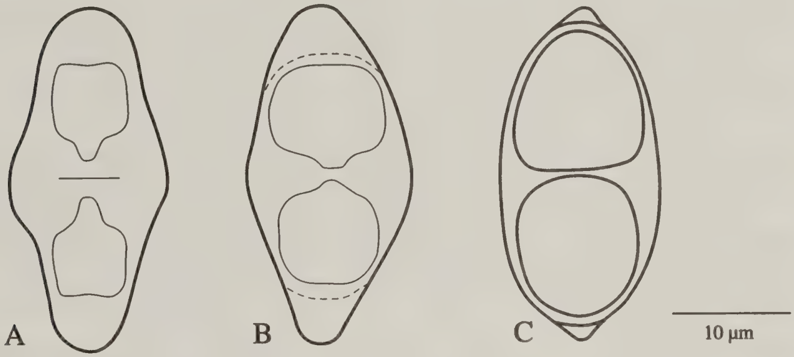

Figure 1. Dirinaria-type spore development in *Rinodina riparia*, illustrated after application of KOH. A. Immature, lightly pigmented spore showing angular locules (physcia-like), each with a prominent porus, and a septal disc separating the locules. Note the marked inflation at the septum. B. Mature spore, slightly curved and more darkly pigmented except at the apices and with more rounded locules. Note the appearance of an inner wall at the apices. C. Over-mature spore, darkly pigmented with a heavy inner wall and remnants of lightly pigmented apices. Walls may be partly collapsed in over-mature spores and their shape is not affected by KOH. Scale = 10 $\mu$m.

**Ecology:** The species has been collected from *Populus angustifolia* James and *P. deltoides* Bartr. ex Marsh, both species which frequent river valleys and moist, wooded draws, these habitats being reflected in the species name (Latin *riparius*). However, it also has been collected on *Juniperus* in South Dakota, suggestive of a drier habitat but in groves which are cooler and moister than the surrounding mixed grass plains (Will-Wolf personal communication). *Rinodina riparia* has been collected at altitudes between 900 m and 1880 m.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
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# IS *NEPHROMA SILVAE-VETERIS* THE CYANOMORPH OF *LOBARIA OREGANA*? INSIGHTS FROM MOLECULAR, CHEMICAL AND MORPHOLOGICAL CHARACTERS

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**Abstract**- The question has recently been raised whether *Nephroma silvae-veteris* Goward et Goffinet, an endemic species of the Pacific Northwest, might not appropriately be interpreted as the cyanomorph of *L. oregana*. This view is supported by comparison of fungal nucleotide sequences of the internal transcribed spacer and the 5.8S gene of the nuclear ribosomal DNA repeat from *N. silvae-veteris* with those of *N. arcticum* and *L. oregana*. The fact, however, that *N. silvae-veteris* and *L. oregana* differ in several morphological and anatomical characters, as well as in the nature of their associated chlorobiont, suggests they are not entirely genetically identical. *Nephroma silvae-veteris* appears to be morphologically intermediate between *L. oregana* and *N. arcticum*, and may perhaps be interpreted as a species that arose through hybridization between *L. oregana* and *N. arcticum*. It is concluded that although *N. silvae-veteris* may appropriately be accomodated in *Lobaria*, it should for the time being be considered distinct from *L. oregana*. Consequently the combination *L. silvae-veteris* (Goward & Goffinet) Goward & Goffinet is made.

## INTRODUCTION

The epiphytic lichen *Nephroma silvae-veteris* was recently described from old-growth forests of the Pacific Northwest of North America by Goward and Goffinet (1993). This may be described as a small cyanophilous foliose lichen, in which chlorophilous secondary lobules are often borne laminally. Although *N. silvae-veteris* is not known to produce apothecia, its placement in *Nephroma* was assumed to be justified by its close morphological resemblance to the cyanomorph of

*N. arcticum* (L.) Torss, from which, however, it clearly differs on chemical grounds. Goward and Goffinet (1993) also called attention to the morphological similarity of *N. silvae-veteris* to *Lobaria oregana* (Tuck.) Müll.Arg., with which it also shares an identical chemical profile. More recently, this latter similarity led McCune and Geiser (1997) to interpret *N. silvae-veteris* as the cyanomorph of *L. oregana.*

Photomorph pairs have been reported primarily from the Peltigerineae (*sensu* Tehler 1996), in which the chloromorphs are invariably foliose in habit whereas the cyanomorphs may be foliose or fruticose. In *Nephroma*, for example, all cyanomorphs reported to date are foliose (Tønsberg and Holtan-Hartwig 1983; White and James 1987, 1988). By contrast, secondary cyanomorphs in *Lobaria* appear to be invariably fruticose (Jordan 1972; Purvis 1992). Chloromorphs of *Nephroma* and *Lobaria* primarily differ in characters of their apothecia, and the morphology of their lower surface. These species further differ in the nature of their symbiotic partner. Chloromorphic *Lobariae* are lichenized with either *Myrmecia* (i.e., *M. biatorellae* [Tsch.-Woess & Plessl] Petersen; Tschermak-Woess 1981) or *Dictyochloropsis* (i.e., *D. reticulata* [Tsch.-Woess] Tsch.-Woess; Tschermak-Woess 1978 as *Myrmecia reticulata*), whereas the chlorobiont of *N. arcticum* is assumed to belong to *Coccomyxa* (Wetmore 1960; White 1992). *Nephroma silvae-veteris* likewise appears to be lichenized with a species of *Coccomyxa* (Goward and Goffinet 1993).

Consensus has yet to be reached on the appropriate taxonomic disposition of alternative photomorphs. The controversy is centered primarily on two points: first, the genetic nature of the mycobiont in either symbiotic relationship is in most cases not known; and second, physical independence, as well as ecological, geographic and sometimes also chemical differentiation could be seen as supporting the recognition of two distinct taxa (Galloway 1988; White and James 1988; see Laundon 1995 and Goffinet and Bayer 1997 for review). Armaleo and Clerc (1991) were the first to test the "one-fungus-photomorphs" hypothesis using molecular techniques. Their results suggest that the mycobionts of a photomorph pair are genetically very similar if not identical. Based on actual nucleotide sequences of the internal transcribed spacer (ITS) region of the nuclear ribosomal repeat sequences, Goffinet and Bayer (1997) recently reached a similar conclusion for joined photomorphs in *Peltigera* and *Nephroma*, suggesting that the mycobionts of both photomorphs are conspecific.

The present study attempts to answer three questions: 1) Do the chloromorphic and the cyanomorphic lobes of *N. silvae-veteris* share the same mycobiont, as defined by ITS sequence data? 2) Can molecular data provide insights regarding the systematic affinities of *N. silvae-veteris* to either *N. arcticum* or *L. oregana*? and 3) Do comparisons of vegetative characters among the three species yield results congruent with the molecular data?

## MATERIALS AND METHODS

**DNA extraction, PCR amplification, sequencing, and sequence alignment**: Thallus fragments (green lobules in the case of the chloromorph of *N. silvae-veteris*) were removed from single herbarium collections of *N. arcticum*, *N. silvae-veteris* and *L. oregana* (Table 1), then cleaned in distilled water and lyophilized. DNA extraction followed a modification of Doyle and Doyle's (1987) method (protocol available from senior author). The ITS region was amplified as outlined in Goffinet and Bayer (1997) using the universal primer ITS1 (White et al. 1990) and the ascomycete-specific primer NL6A (Egger 1995). The PCR protocol followed the one outlined in Goffinet and Bayer (1997). The double-stranded templates were sequenced using the Dye Terminator Cycle Sequencing Kit (Perkin Elmer), and the resulting fragments were separated on polyacrylamide gels (Long Ranger Singel ™; FMC BioProducts) using a ABI Prism ™ 377 DNA Sequencer (Perkin Elmer). Sequences obtained were edited using Sequencher 3.0 (Gene Codes Corporation), entered in PAUP 3.1 (Swofford 1993) and aligned to an available sequence of *N. arcticum* (Goffinet and Bayer 1997; U92881). The beginning of the first spacer (ITS1) was determined by comparisons with available sequences of Sclerotiniaceae (Carbone and Kohn 1993); whereas the length of the 5.8S gene and the end of the second spacer were inferred from comparisons with *Saccharomyces cerevisiae* (J01355 and K01048; see Gutell et al. 1993).

Table 1: Voucher specimens and associated GenBank accession number for sequences of the ITS region ([1] private herbarium of B. Goffinet; [2] UBC)

| Taxon | GenBank accession number | Voucher |
|---|---|---|
| *Nephroma arcticum* | AF014109 | Canada, Goffinet 1310[1] |
| *N. silvae-veteris* (joined photomorphs) | AF014110 | Canada, Goward 92-336[2] |
| *Lobaria oregana* | AF014111 | Canada, Goffinet 3141[1] |

**Morphological study**: Several specimens of *N. silvae-veteris* (Goward 81-1965, 91-1149a, 91-1400, 92-336), *N. arcticum* (Goffinet 1310, Goward 92-354, 91-988), and *L. oregana* (Goffinet 3141, Goward 81-1878, 83-137) were selected from different parts of temperate western North America for examination of vegetative characters. Hand-cut sections were mounted in water. All specimens are deposited at UBC, OSU or in the herbarium of B. Goffinet.

**Chemical study**: Selected specimens of *N. silvae-veteris* (Goward 95-603-cyanomorph, 92-336 and 91-1400 - chloromorph), *N. arcticum* (Goward 91-988-chloromorph, 92-354 both photomorphs), and *L. oregana* (Goward 81-1878, 83-137) were examined for their chemical constituents. Secondary substances were extracted in acetone or toluene, and each extract loaded on precoated Merck Silica gel 60 $F_{254}$ plates, and chromatographed in solvent A, B, or C following Culberson et al. (1981).

## RESULTS

**ITS sequences**: Nucleotide (nt) sequences of the ITS region generated using ITS-1 and ITS-4 as sequencing primers vary between 468 nts (*N. silvae-veteris*, *L. oregana*) and 507 nts (*N. arcticum*; Table 2). Both photomorphs of *N. silvae-veteris* share identical coding (5.8S) and non-coding (ITS1 and ITS2) sequences (absolute distance=0). The 5.8S sequence of *N. silvae-veteris* is identical to that of *L. oregana* but differs from the homologous sequence in *N. arcticum* by eight point mutations and one insertion or deletion (indel). The sequences of both spacers of *N. silvae-veteris* also completely overlap with those in *L. oregana*. ITS sequences of *N. arcticum* are nearly identical to those obtained previously by Goffinet and Bayer (1997). Except for one point mutation, all differences are accounted for by additional G (5nt) or C (2) in the *N. arcticum* sequence obtained here. These may reflect the increased sensitivity and resolution of the automated sequencing method rather than a true genetic divergence, as was observed between different populations of *Peltigera leucophlebia*, for example (Goffinet and Bayer 1997). Aligning the ITS sequences of *L. oregana* and *N. arcticum* required incorporation of numerous gaps and was not pursued here.

Table 2: Length in nucleotides (nt) of the spacers (ITS1&2) and 5.8S gene in *Nephroma arcticum*, *N. silvae-veteris*, and *Lobaria oregana*.

| | ITS1 | 5.8S | ITS2 | total |
|---|---|---|---|---|
| *N. arcticum* | 201 | 159 | 147 | 507 |
| *N. silvae-veteris* - chloromorph | 162 | 158 | 148 | 468 |
| *N. silvae-veteris* - cyanomorph | 162 | 158 | 148 | 468 |
| *L. oregana* | 162 | 158 | 148 | 468 |

**Morphological characters** (Table 3): The dominant cyanomorph of *N. silvae-veteris* often produces numerous green "stress lobules" that are about 4-5 mm in diameter. The lobules may occasionally be produced in great numbers, e.g. to about 20 lobes per $cm^2$. Their early development is signalled by the occurrence of brown, pycnidiiform initials over the upper surface of the cyanomorph. These lobules are morphologically nearly identical to "homologous" chloromorphic lobules

Table 3: Comparison of molecular, morphological and chemical characters for *Nephroma arcticum*, *N. silvae-veteris*, and *Lobaria oregana*.

| | *N. arcticum* | *N. silvae-veteris* | *L. oregana* |
|---|---|---|---|
| Chloromorph | | | |
| margin of lobules | **downturned** | **downturned** | upturned |
| cortex of lobules | **subparaplectenchymatous** | **subparaplectenchymatous** | paraplectenchymatous |
| upper surface | **dull,**<br>**not maculate** | **dull,**<br>**not maculate** | shiny,<br>(weakly) maculate |
| Chlorobiont | ***Coccomyxa*** | ***Coccomyxa*** | *Myrmecia* or *Dictyochloropsis* |
| Cyanomorph | | | |
| growth-from | **foliose** | **foliose** | ? (fruticose in all *Lobariae*) |
| Tomentum of lower surface | **continuous**<br>(both photomorphs) | **continuous**<br>(cyanomorph) | reticulate<br>(chloromorph) |
| ITS sequences | very different from those of *N.sv.* | - - | **identical to those of *N.sv*** |
| depsidones | all absent | **constictic,**<br>**cryptostictic,**<br>**norstictic,**<br>**stictic acids** | **constictic,**<br>**cryptostictic,**<br>**norstictic,**<br>**stictic acids** |
| others secondary metabolites | nephroarctin,<br>phenarctin,<br>zeorin, ± methyl gyrophorate | **all absent** | **all absent** |

of *N. arcticum*, that is young green lobules that arise from the surface of the cyanomorph of *N. arcticum*. In both species, the lobes may be characterized by their distinctly downturned tips, and dull to occasionally weakly scabrid upper surface that also lacks maculae and is not at all ridged. By contrast, the tips of young lobes of *L. oregana* are upturned, and the upper cortex is smooth and somewhat shiny, bearing weakly effigurate maculae, and is usually weakly to strongly ridged. The ridging in this species is very pronounced, and is readily observed in lobes as small as 5 mm in diameter. The lower surface of the cyanomorphic lobes of *N. silvae-veteris* is covered by a continuous tomentum as in *N. arcticum*, and not by a reticulate tomentum as in *L. oregana*.

Morphogical similarities between the chloromorphs of *N. silvae-veteris* and *N. arcticum* are also seen at the anatomical level. In both species the upper cortex is rather delicate, and may be described as subparaplectenchymatous compared to the distinctly paraplectenchymatous cortex of *L. oregana*. Furthermore, *N. silvae-veteris* and *N. arcticum* share a similar photobiont (*Coccomyxa* sp.?) that measures 3-5(-7) µm in length, whereas the photobiont of *L. oregana* , whose cells are 10-12 µm in diameter, appears to belong either to *Myrmecia* (*M. biatorellae*) or to *Dictyochloropsis* (*D. reticulata*; see Tschermark-Woess 1984 for distinguishing characters). The cyanobacteria in all three species appear to belong to the genus *Nostoc*.

**Chemical profile** (Table 3): Thin layer chromatography of extracts of either photomorph of *N. silvae-veteris* confirmed the presence of constictic, cryptostictic, stictic, norstictic and usnic acids. The presence of phenarctin in the chloromorph of this species (Goward et Goffinet 1993) could not be confirmed, nor were trace amounts of PCr4 detected. *Lobaria oregana* shared an identical array of secondary substances. *Nephroma arcticum* lacks all the above depsidones, and instead produces nephroarctin, phenarctin, usnic acid and zeorin, as well as methyl gyrophorate which is however absent from the cyanomorph.

## DISCUSSION

The 5.8S gene is a small gene characterized by a low evolutionary rate, which yields characters generally phylogenetically informative at the level of deep divergences dating back to the Paleozoic (Hillis and Dixon 1991). Although evolutionary rates for a given locus may vary among organisms (see Britten 1986), the lack of sequence variation between taxa most likely reflects the lack of genetic divergence as opposed to homoplastic changes leading to identical sequences shared by "distantly" related organism. The complete identity in nucleotide sequences of the 5.8S gene between *N. silvae-veteris* and *L. oregana* therefore suggests that these species are more closely related to each other than either species is to *N. arcticum*, whose 5.8S gene sequence differs by eight point mutations and one indel.

The ITS sequences of both photomorphs of *N. silvae-veteris* are completely identical, suggesting that these photomorphs share a single mycobiont, as do other pairs of attached photomorphs (Goffinet and Bayer 1997). Furthermore, this mycobiont shares with *L. oregana* identical nucleotide sequences for the transcribed spacers (ITS1 and ITS2). Along a taxonomic gradient, minimal or lack of divergence of ITS sequences is generally found at the species level. Although homologous sequences are not available for other species of *Lobaria*, ITS sequences in *Lobaria*, as in other Peltigerineae and other fungi or plants (see Baldwin et al. 1995; Goffinet and Bayer 1997, and references therein) are likely to differ "significantly" and consistently among species. The complete identity in nucleotide sequence of the ITSs between *N. silvae-veteris* and *L. oregana* therefore suggets that their mycobionts are very closely related if not conspecific. This hypothesis is further supported by the identical chemical profile of both species. A complete identity of ITS sequences does not, however, exclude genotypic differentiation between *N. silvae-veteris* and *L. oregana*, even if they merely represent alternative photomorphs of a single species (see Goffinet and Bayer 1997).

Chloromorphs of *L. oregana* and *N. silvae-veteris* differ in the nature of their chlorobiont. *Lobaria oregana* is lichenized with a species seemingly belonging to *Myrmecia*, whereas the green lobules of *N. silvae-veteris* include a much smaller photobiont, similar to that found in *N. arcticum* (i.e., a species of *Coccomyxa*). The genetic basis for the choice of the photobiont is not understood, but varying degrees of selectivity have been demonstrated between eukaryotic and prokaryotic photobionts (Stocker-Wörgötter and Türk 1994; Yoshimura et al. 1994) and between various taxa of chloroccocalean algae (Ott 1988; see also Honegger 1996 for review). The differences in the chlorobiont between *N. silvae-veteris* and *L. oregana* could be interpreted in two ways: 1) although closely related (see above), the mycobionts may be genetically distinct, at least with regard to the gene(s) controlling selection of the symbiotic chlorobiont; or 2) the two mycobionts are identical but may produce only small, juvenile lobes when occurring with *Coccomyxa*, as opposed to larger thalli when occurring with *Myrmecia*.

Although a single fungus species is apparently capable of establishing a symbiotic relationship with more than one algal species (e.g., *Parmelia saxatilis* Ach., Friedl and Büdel 1996; Honegger 1996), the chlorobionts involved are typically congeneric, and may thus entail minimal changes in the actual symbiotic relationship. By contrast, *Coccomyxa* and *Myrmecia* differ significantly in their cell wall composition (e.g., a resistant biopolymer is present in *Coccomyxa*, but is absent in *Myrmecia*; Brunner and Honegger 1985), and are on this account unlikely to provide suitable photobionts for a single mycobiont. It may be significant that the sporopollininlike polymer in the wall of *Coccomyxa* prevents the formation of haustoria (Honegger and Brunner 1981). Intraparietal haustoria formation was not studied in the symbiosis between *L. linita* and *M. biatorellae* (Tschermark-Woess 1981), but other *Lobariae* (i.e., those lichenized with *D. reticulata*, which shares cell wall charateristics with *M. biatorellae*; Brunner and Honegger 1985) do form haustoria on the cell wall of the photobiont (Tschermak-Woess 1978). Cell-wall characteristics of the photobiont may thus determine the type of cytological interactions between the symbionts. It appears likely that such cytological differences have a genetic basis, and do not merely reflect the phenotypic plasticity of the fungus. Consequently, the presence of distinct photobionts in the chloromorphs of *N. silvae-veteris* and *L. oregana* may be seen as evidence of genetic differentiation; and the resulting taxa may be interpreted as sibling species (Culberson 1986).

As mentioned above, an alternative explanation for the observed morphological and anatomical differences between the chloromorphs of *N. silvae-veteris* and *L. oregana* may be provided by thallus ontogeny. From this perspective, the occurrence of *Coccomyxa* in the chloromorph of *N. silvae-veteris* may represent an initiating or "stop-gap" measure in lobes that will eventually mature into typical *Myrmecia*-containing lobes of *L. oregana*. We tentatively reject this hypothesis on the following grounds. First, careful searching has failed to turn up any material in which the chloromorph of *N. silvae-veteris* is accompanied by *Myrmecia*. Second, no instances of joined thalli between these species have yet been detected. Third, *Myrmecia/Dictyochloropsis* are the only algae genera reported to date for chloromorphic *Lobariae*; *Coccomyxa*, by contrast, appears to be the sole photobiont genus present in chloromorphic *Nephromae*. And fourth, in all chlorophilous *Lobariae* for which cyanomorphs are known (e.g., *L. amplissima* [Purvis 1992], and *L. ravenelii* [Jordan 1972]), the cyanomorphs are fruticose, not foliose.

In our opinion, the above observations support the hypothesis that *N. silvae-veteris* may be genetically distinct from *L. oregana* and may thus appropriately be considered a distinct albeit closely related species. The strict identity of the ITS sequences is not in conflict with this interpretation, though it does strongly suggest that both species have diverged only recently. The mode of speciation is not clear, and a hybrid origin involving participation of *N. arcticum* cannot be excluded. This rather startling claim seems to be supported by four characteristics of *N. silvae-veteris*. First, the lower surface of its cyanomorph is covered by a continuous tomentum, as in both photomorphs of *N. arcticum* (Tønsberg and Holtan-Hartwig 1983), rather than by a reticulate tomentum as in *L. oregana* (Jordan 1973). Second, the green lobules of *N. silvae-veteris* and *N. arcticum* share a thin upper cortex as well as downturned margins, whereas "homologous" lobules in *L. oregana* have a thicker cortex and upturned margins. Third, the chloromorphs of *N. silvae-veteris* and *N. arcticum* both contain *Coccomyxa* as their chlorobiont. And fourth, the foliose growth form of the cyanomorphic thalli is more consistent with *Nephroma* than it is with *Lobaria* (see above). A hybrid origin may also perhaps be consistent with the extraordinarily narrow ecology and distribution of *N. silvae-veteris* (see Goward and Goffinet 1993).

A final taxonomic disposition for *N. silvae-veteris* must await further study, particularly regarding its ontogeny and genetic structure. Molecular and chemical evidence suggest that *N. silvae-veteris* is most appropriately placed in *Lobaria*, and may actually represent the cyanmorph of *L. oregana*. Given, however, the existence of various morphological, anatomical, and especially symbiological points of distinction between these two taxa, we prefer for now to recognize *N. silvae-veteris* as a distinct species. Doing so not only accords with our belief that this is an independent taxon, it also considerably improves the long term prospects for one of western North America's most endangered epiphytic macrolichens (Goward 1996).

***Lobaria silvae-veteris*** **(Goward & Goffinet) Goward & Goffinet** ***comb. nov.***

*Nephroma silvae-veteris* Goward & Goffinet. Bryologist 96: 242. 1992. TYPE: Canada: British Columbia. Skeena River Basin, Date Creek, 10 km WNW Kispiox, 55°22'N, 127°50' W, elev. 760 m, shrubby semi-forested seeps with old-growth *Tsuga heterophylla* and *Abies amabilis*, on branches of *Tsuga*, 15 July 1992, *Goward 92-336* with *Allen Banner* (holotype, UBC!; isotypes BM, CANL, H).

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# LICHEN FLORA OF EASTERN NORTH AMERICA: THE GENUS *PARMELIA* SENSU STRICTO

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**ABSTRACT**: Descriptions, keys, distribution maps, and illustrations are provided for the 7 species of *Parmelia* sensu stricto found in eastern North America (eNA): *fertilis, fraudans, neodiscordans, omphalodes, saxatilis, squarrosa,* and *sulcata.* The species with the most restricted ranges in eNA are *P. fertilis*, known only from southeastern Canada and Maine, and *P. neodiscordans,* restricted to the Appalachians from North Carolina to Maine. *P. fraudans* has the most northerly range, extending into the U.S. only in Minnesota and Michigan. *P. omphalodes* and *P. saxatilis* have very similar, boreal ranges, but *P. saxatilis* extends farther south into southern Ontario and along the Atlantic coast to Long Island, NY. The range of *P. squarrosa* is the most southerly, ranging south to Arkansas, Alabama, and South Carolina; in eNA it is found as far north as the fiftieth latitude, with a distribution overlapping broadly with that of *P. saxatilis* from the Great Lakes area through New York and New England to Quebec and Newfoundland. *P. sulcata* is the only *Parmelia* species commonly found in agricultural regions of the northern Midwest region of the U.S. and southern Ontario.

This review of the lichen genus *Parmelia* in eastern North America (eNA) is the first of a series of generic reviews by various authors that will, it is hoped, eventually cover all of the lichens of eNA, a region defined as extending from the arctic/boreal boundary at about 54° N., south to Florida and west to the midgrass/tallgrass boundary at about 97° W. It is planned that each generic treatment will include descriptions, keys, detailed distribution maps, and illustrations.

In the present study, distribution maps are based on specimens examined by the author and others (see Acknowledgments) as well as literature reports considered by the author to be reliable. The only distributional references cited, however, are those that include records not found in the specimens examined. A detailed list of every accepted specimen and literature report may be obtained from the author upon request. Herbaria have been abbreviated following Holmgren et al. (1990), except for the following private herbaria: CLAYDEN, DIRIG, HINDS, LADD, LAY, and SCHMITT. Distribution maps have been generated using decimal latitudes and longitudes and MapInfo Desktop software. References singled out as "Key References" below are not usually specifically cited in the text, even though they were relied upon in many instances, for example for chemistry and for spore, conidial, and anatomical measurements.

**PARMELIA** Ach., Meth. Lich.: 153 (1803). Shield Lichens. Etymology (Feige 1996): Greek *parme*, a fruit bowl + *-eileo*, enclosed, alluding probably to the lecanorine apothecia.

TYPE SPECIES: *Parmelia saxatilis* (L.) Ach.

KEY REFERENCES: Hale 1971, 1987; Skult 1987.

SELECTED PREVIOUS ILLUSTRATIONS: Color photos: McCune & Geiser 1997 (*saxatilis, sulcata*), Wirth 1995 (*omphalodes, saxatilis*, *sulcata*); B & W photos: Hale 1987 (all species in eNA), Hyvönen 1985 (*squarrosa*); Drawings: Brodo 1988 (*sulcata*), McCune & Geiser 1997 (*squarrosa, sulcata*), Thomson 1984 (*fraudans*, *omphalodes*, *saxatilis*).

HISTORY OF GENUS: *Parmelia* has had a remarkable contraction of concept, from Acharius' broad concept in 1803 of almost all crustose, foliose, and fruticose species with lecanorine apothecia to Hale's (1987) narrow concept of an adnate, eciliate, pseudocyphellate foliose species with black lower surface, rhizines, cylindrical microconidia < 8 μm long, simple spores 8 per ascus, and atranorin, not usnic acid, in the cortex. By the end of the 19th century *Parmelia* was generally held to include only foliose species with rhizines (excluding, e.g., *Hypogymnia*, *Lobaria*, and *Pannaria*), laminal apothecia (excluding, e.g., *Cetraria*), and simple spores (excluding, e.g., *Physcia* and *Xanthoria*). Starting in the mid-19th century with Massalongo's separation of *Menegazzia*, there were attempts to circumscribe the vast assemblage of species contained in *Parmelia*, with varying degrees of acceptance. Many of the proposed segregates are based largely on thalline characters, rather than purely fungal characters, and this has slowed their acceptance (e.g., Purvis et al. 1992)

VEGETATIVE STRUCTURES: Thallus foliose, 4-60 cm broad (in eNA, 5-30 cm), greenish to whitish mineral gray, or in some species turning brown or black in exposed habitats, with sublinear lobes divaricate, contiguous, or imbricate and 0.5-10 mm wide (in eNA 0.5-5 mm). Upper surface plane to foveolate, becoming cracked with age, and isidiate, sorediate, or lacking soredia and isidia, sometimes with a white pruina of oxalates, and always with pseudocyphellae appearing as irregular laminal or marginal white markings, often fusing into a loose reticulate network. Lower surface black with simple, furcate, or squarrosely branched rhizines, 0.5-2 mm long. Upper cortex paraplectenchymous and 4-6 cells thick (20-30 µm), algal layer and medulla 100-200 µm thick, and lower cortex less than 20 µm thick. Pseudocyphellae consisting of areas where the cortex has disintegrated and become filled with medullary hyphae, covered often by a thin, densely pored, polysaccharide layer.

REPRODUCTIVE STRUCTURES: Apothecia adnate to substipitate, 1-20 mm in diameter (in eNA, 1-12 mm), and disk brown or reddish brown with the rim usually pseudocyphellate and rugose; spores 8 per ascus and in eNA 10-18 x 5-11 µm. Pycnidia immersed and laminal with conidia usually cylindrical, 5.5-8 µm long.

CHEMISTRY: All species have atranorin and chloroatranorin in the cortex. Six of the seven species in eNA have salazinic acid in the medulla; one species, *P. neodiscordans*, has fumarprotocetraric acid in the medulla.

DISTRIBUTION AND SUBSTRATES: The center of evolution for *Parmelia* appears to be in eastern Asia and in Australia and New Zealand, with 12 and 14 species, respectively. Seven species occur on trees and rock in eNA, most commonly in northern regions but with one or more species found at least occasionally in most of the region, exclusive of the southeastern coastal plain.

## KEY TO SPECIES

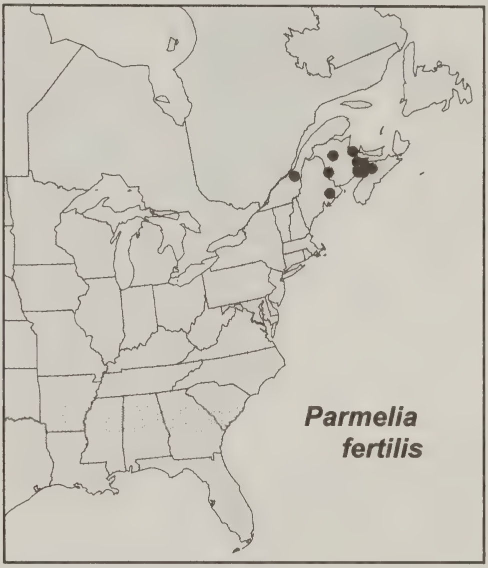
1. Soredіate
   2. Soredia laminal and marginal, white, granular; rhizines simple to squarrosely branched; pseudocyphellae laminal and marginal; on trees and rock ........................................ **P. sulcata**
   2. Soredia coarsely isidioid when mature, mostly marginal, yellowish (usnic acid); rhizines simple to furcate; pseudocyphellae mostly marginal; usually on rock .................. **P. fraudans**
1. Not sorediate
   3. Isidiate
      4. Isidia coarsely granular (actually soredia), mostly marginal .................................................. **P. fraudans**
      4. Isidia fine and cylindrical; laminal and marginal
         5. Rhizines squarrosely branched (simple at lobe margins) [if necessary, use knife to scrape rhizines onto white paper to visualize]; most common on trees ........ **P. squarrosa**
         5. Rhizines simple or furcate, rarely subsquarrosely branched; most common on rocks ......................... **P. saxatilis**
   3. Not isidiate (but can have secondary lobules)
      6. Medulla K- (or K+ yellowish turning dingy brown), P+ red [fumarprotocetraric acid]; lobes small, 0.5-2 mm wide with pseudocyphellae usually restricted to margins and forming a white line there ........... **P. neodiscordans**
      6. Medulla K+ yellow turning red, P+ orange [salazinic acid]; lobes generally larger (1-4 mm wide) with pseudocyphellae usually common laminally as well as marginally
         7. Rhizines simple to squarrosely branched; on trees; apothecia common; rare, in southeastern Canada and Maine .... **P. fertilis**
         7. Rhizines simple to furcate; on rocks; apothecia uncommon; widespread boreal species ........... **P. omphalodes**

**Parmelia fertilis** Müll. Arg., Flora 70: 316 (1887). Type collection (Hale 1987): Siberia (G, lectotype); Syn: *P. subdivaricata* Asah.

Morphology: Thallus adnate on trees, greenish to whitish mineral gray, with divaricate, contiguous, or overlapping lobes 0.5-3 mm wide; upper surface plane to weakly foveolate with conspicuous marginal and laminal pseudocyphellae fusing with age into a reticulate network; rhizines simple to squarrosely branched. Pycnidia and apothecia common, the latter substipitate and 2-7 mm in diameter; spores rare, 12-14 x 6-8 µm.

Chemistry: Medulla containing salazinic acid and consalazinic acid (K+ yellow changing to red, P+ orange).

Distribution (map based on 15 sites: CANL, CLAYDEN, MAINE, NBM, US): *P. fertilis* is common in eastern Asia, but it has only recently been reported in eNA (Hale 1987, Gowan and Brodo 1988). All known sites in eNA are in southeastern Canada or Maine, including four from Fundy National Park in New Brunswick.

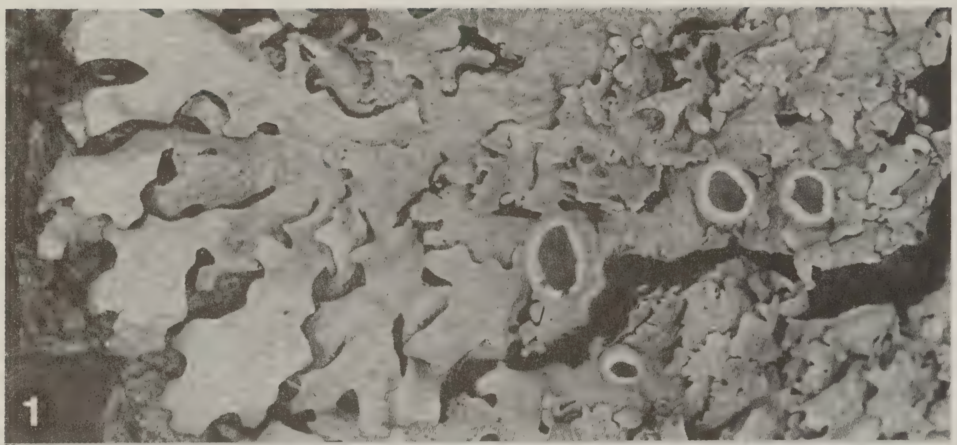


Remarks: Hale has suggested that *P. fertilis* is the parent morphotype to the isidiate *P. squarrosa* and the sorediate *P. sulcata.*

**Parmelia fraudans** (Nyl.) Nyl., Lich. Jap.: 28 (1890). *Parmelia saxatilis* (L.) Ach. * *fraudans* Nyl., Lich. Scand.: 100 (1861). Type collection (Hale 1987): Finland (H-NYL 34869, lectotype).

Morphology: Thallus adnate on rock (rarely on trees), greenish to yellowish to brownish mineral gray with contiguous to imbricate lobes 1-4 mm wide. Upper surface plane to rugose-foveolate with mostly marginal pseudocyphellae and coarsely granular, yellowish or grayish, densely clustered, mostly marginal, isidioid soredia; rhizines simple to furcate. Pycnidia and apothecia rare; spores 10-12 x 5-6 µm.

Chemistry: Medulla containing salazinic acid and protolichesterinic acid (K+ yellow changing to red, P+ orange); soralia with usnic acid.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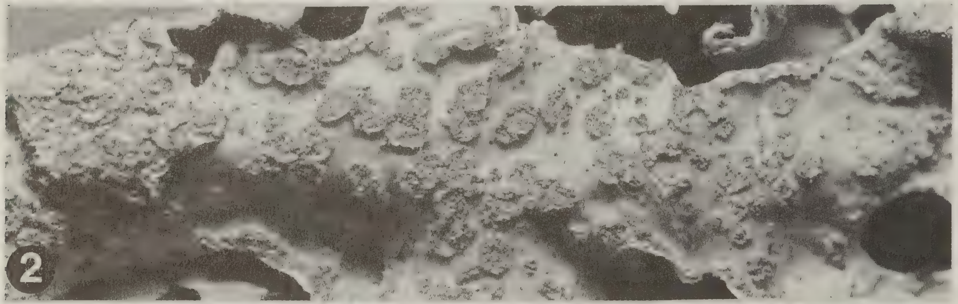
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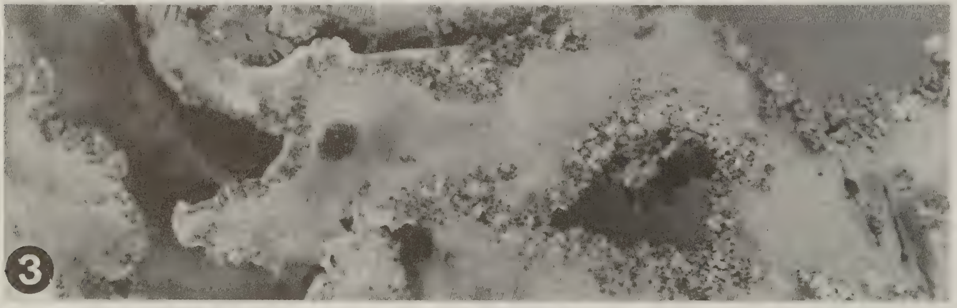
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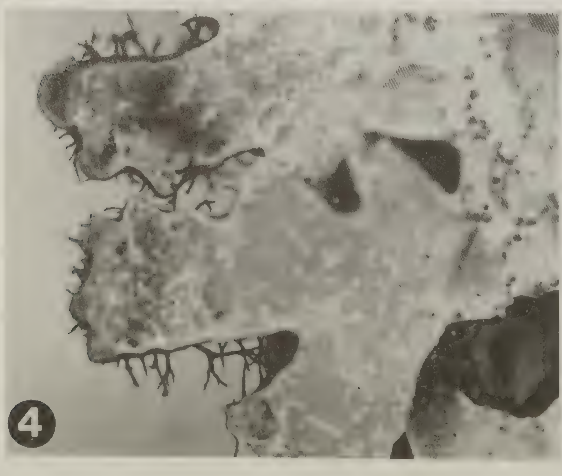
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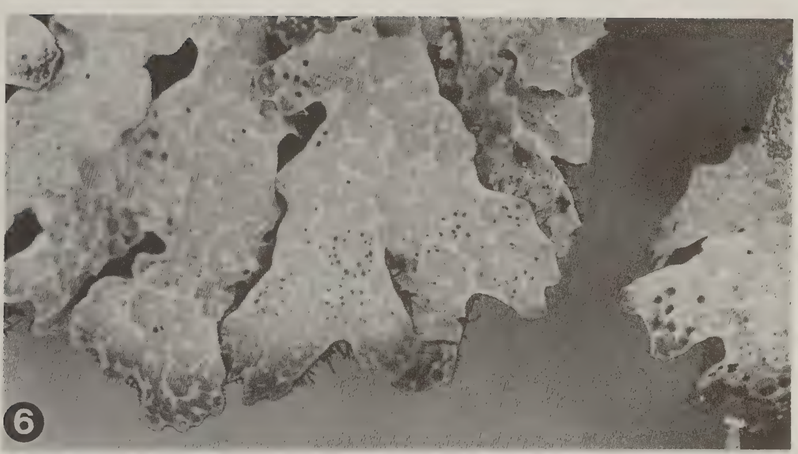

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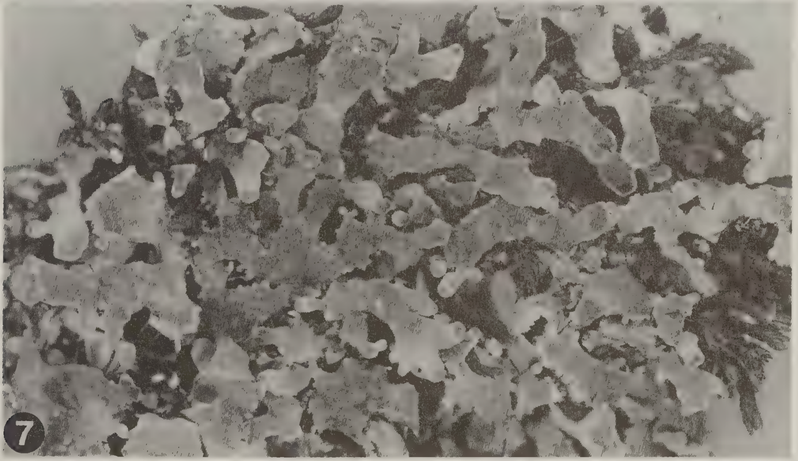

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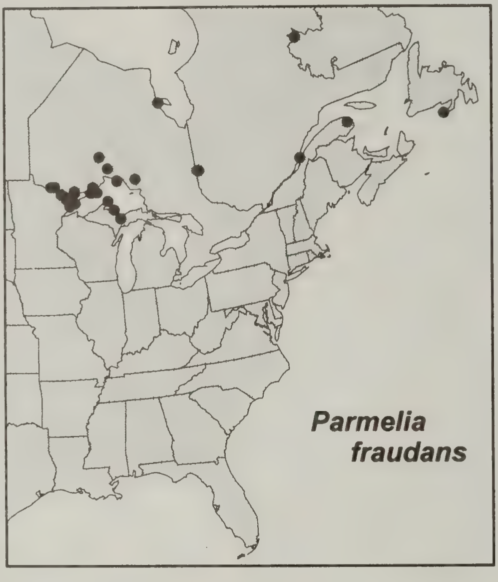
**Figures 1-7**. Species of *Parmelia*. **1**. *Parmelia fertilis* (Maine, *Biazrov W5/9*, MAINE): lobes with reticulated pattern of white pseudocyphellae; apothecia present; no soredia or isidia. X5. **2**. *Parmelia sulcata* (Maine, *Hinds 3178*, HINDS): laminal soralia of granular soredia. X7. **3**. *Parmelia fraudans* (Minnesota, *Wetmore 21800*, MIN): coarse, marginal, isidioid soredia. X9. **4**. *Parmelia saxatilis* (Maine, *Hinds 2105,* HINDS): fine laminal isidia (right) and coarse, furcately branched rhizines (left). X12. **5**. *Parmelia squarrosa* (Maine, *Hinds 2828*, HINDS): fine, squarrosely branched rhizines. X12. **6**. *Parmelia omphalodes* (Maine, *Hinds 2100*, HINDS): broad, branched lobes with laminal, reticulated pseudocyphellae. X7. **7**. *Parmelia neodiscordans* (Maine, *Hinds 2492*, HINDS): narrow, unbranched lobes with marginal pseudocyphellae. X7.

Distribution (map based on 55 sites: CANL, CLAYDEN, MIN, NY, US, Ahti 1964, LeGallo 1952, Thomson 1984): *P. fraudans* is a boreal and arctic species that is rare in eNA except near Lake Superior. The report of Slack et al. (1993) of *P. fraudans* in Connecticut is probably erroneous (E. Lay, pers. comm.)

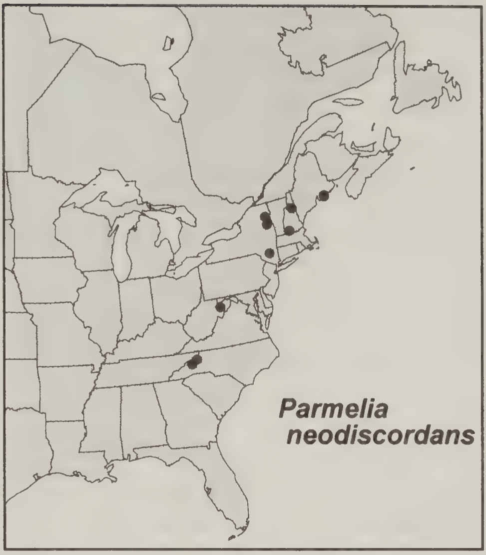


Remarks: *P. fraudans* is the only species in *Parmelia* s.s. to have usnic acid. Morphologically it closely resembles *P. hygrophila* Goward and Ahti of the Pacific Northwest (Goward et al. 1994), but differs from that species in its substrate (usually bark in *P. hygrophila*) and the position of its isidioid soredia (usually laminal in *P. hygrophila*).

**Parmelia neodiscordans** Hale, Smiths. Contr. Bot. 66: 1 (1987). Type collection (Hale 1987): USA, Maine, Acadia National Park (US, *Hale 37496*, holotype).

Morphology: Thallus adnate to loosely adnate on rocks, mineral gray to brownish, with imbricate lobes 0.5-2 mm wide, often with suberect lobules. Upper surface plane with pseudocyphellae forming a white marginal rim; rhizines simple. Pycnidia rare, apothecia not known.

Chemistry: Medulla containing fumarprotocetraric acid and accessory unidentified fatty acids (K-, P+ red).



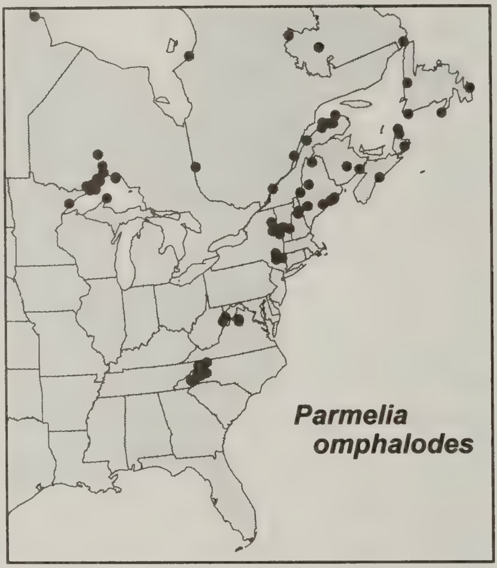
Distribution (map based on 12 sites: CANL, DIRIG, DUKE, HINDS, MIN, NY): This species has only been recently described (Hale 1987) and in eNA is known only from the Appalachian Mountains from North Carolina to Maine.

Remarks: Morphologically *P. neodiscordans* resembles small-lobed, marginally pseudocyphellate morphotypes of *P. omphalodes* ("*P. pinnatifida*") as well as *P. discordans* Nyl. of Europe (although that species is generally darker) and *P. skultii* Hale of arctic regions (although that species generally has wider lobes and often has pruina). It differs from all these species, however, in having fumarprotocetraric acid as its principal medullary substance. Although Hale (1987) reported that the species was only found in the Appalachians, it appears that it also occurs rarely in western NA. Skult (1987) reported 3 forms with the same morphology and chemistry from western NA and in 1986 annotated two of these specimens (from the Yukon) at CANL as "*P. neodiscordans* Hale?".

**Parmelia omphalodes** (L.) Ach., Meth. Lich.: 204 (1803). *Lichen omphalodes* L., Spec. Plant.: 1143 (1753). Type collection (Hale 1987): specimens and Dillenius, 1742, pl. 24, fig. 80A (OXF, lectotype); Syn: *P. omphalodes* subsp. *pinnatifida* (Kurok.) Skult, *P. pinnatifida* Kurok.

Morphology: Thallus adnate to loosely adnate on rocks, often on talus slopes, and very rarely on base of tree growing out of cliff (HINDS), whitish mineral gray to brown to black, with imbricate lobes 1-4 mm wide, often with dense secondary lobes. Upper surface plane to weakly foveolate with pseudocyphellae marginal and laminal forming a distinct network to mostly marginal. Rhizines simple to furcate. Pycnidia common and apothecia uncommon; spores 10-15 x 7-9 µm.

Chemistry: Medulla containing salazinic acid with or without lobaric acid, consalazinic acid, and lichesterinic acid (K+ yellow changing to red, P+ orange). Also rarely with accessory galbinic acid, fumarprotocetraric acid, or protocetraric acid and several unidentified fatty acids.



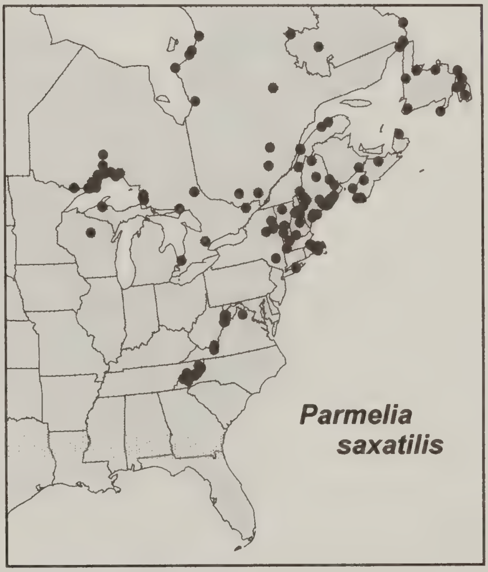
Distribution: (map based on 124 sites: CUP, DUKE, HINDS, LADD, MAINE, MIN, NY, NYS, SCHMITT, US, Ahti 1964, Brodo 1984, Dey 1978, Gowan & Brodo 1988, Hale 1959, Lamb 1954, McQueen 1988, Skult 1987, Thomson 1984 [Canada only], 1993): Locally common on rocks in boreal and arctic Northern Hemisphere; in eNA found only in boreal habitats near Lake Superior and in the Appalachians northward. Skult (1987) reported a specimen from Cleveland, Ohio of W. Mudd (from "Aylon Moor"), but that specimen probably was from Cleveland, England.

Remarks: *P. omphalodes* is treated here as a morphologically variable species that includes small-lobed, marginally pseudocyphellate specimens that are found sparingly in eNA (known sites: alpine region of New Hampshire, Thunder Bay district of Ontario, and Labrador region of Newfoundland). This treatment follows Hale (1987) in not recognizing the small-lobed forms as subsp. *pinnatifida* (Kurok.) Skult. The presence of forms intermediate between broad-lobed and narrow-lobed forms as well as the lack of a consistent correlation between chemistry (the presence or absence of lobaric acid) and morphology (wide-lobed, laminally pseudocyphellate vs. narrow-lobed, marginally pseudocyphellate) [Skult 1987] makes it difficult to support a specific or subspecific status for the small-lobed morphotype.

**Parmelia saxatilis** (L.) Ach., Meth. Lich.: 204 (1803). *Lichen saxatilis* L., Spec. Plant.: 1142 (1753). Type collection (Hale 1987): Sweden (LINN, sheet 127361, lectotype). Syn: *P. kerguelensis* A. Wilson (Stenroos 1991).

Morphology: Thallus adnate to loosely adnate on rocks, less commonly on trees, rarely on soil and moss (US; Sirois et al. 1988), greenish mineral gray to brownish (especially at the lobe ends), with contiguous to crowded lobes, 1-4 mm wide. Upper surface reticulate-foveolate with laminal and marginal pseudocyphellae often forming a reticulate network; isidia cylindrical, simple to sparsely branched and up to 0.5 mm tall and becoming very dense in the older central part of the thallus. Rhizines simple to furcate, rarely subsquarrosely branched. Pycnidia and apothecia uncommon; spores 16-18 x 9-11µm.

Chemistry: Medulla containing salazinic acid and accessory lobaric acid with or without protolichesterinic acid (K+ yellow changing to red, P+ orange). The percentage of specimens with lobaric acid in eNA is about 16%, considerably less than in Europe.



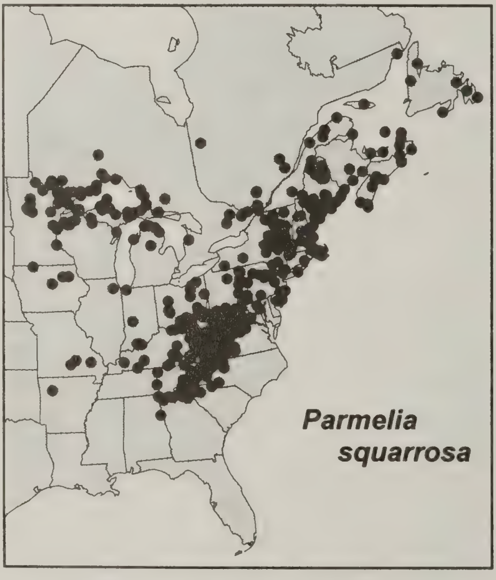
Distribution: (map based on 217 sites: CUP, DUKE, HINDS, LAY, MAINE, MIN, NY, US, Crowe 1994, Dey 1978, Gowan & Brodo 1988, Harris et al. 1988, Thomson 1984 [Canada only], Wong & Brodo 1992): *P. saxatilis* is common in boreal and arctic regions of the Northern Hemisphere and is also found in South America, Africa, and New Zealand; in eNA it has a distribution like *P. omphalodes* but has been found slightly farther south, in Wisconsin (MIN), southern Ontario (Wong & Brodo 1992), eastern Massachusetts (MIN, LAY), and Long Island (NY).

Remarks: Morphologically, *P. saxatilis* closely resembles *P. pseudosulcata* Gyelnik of the Pacific Northwest (=*P. kerguelensis* auct., not A. Wilson), but the latter is said to have more closely appressed, less overlapping lobes and more frequently forked rhizines (Goward et al. 1994). It differs more clearly in its chemistry, having salazinic acid instead of protocetraric acid.

**Parmelia squarrosa** Hale, Phytologia 22: 29 (1971). Type collection (Hale 1987): USA, Virginia, Shenandoah National Park (US, *Hale 36494*, holotype).

Morphology: Thallus adnate to loosely adnate on trees, less commonly on rocks, rarely on moss (LAY, US), greenish to whitish mineral gray, with divaricate, contiguous, or imbricate lobes 1-5 mm wide. Upper surface plane to foveolate with laminal and marginal pseudocyphellae often forming a reticulate network; isidia cylindrical, up to 0.5 mm tall and becoming dense in the older, central part of the thallus. Rhizines squarrosely branched (simple at the lobe margins). Pycnidia and apothecia uncommon; spores 13-15 x 8-9 μm.

Chemistry: Medulla contains salazinic and consalazinic acid (K+ yellow changing to red, P+ orange); lobaric acid has not been reported.

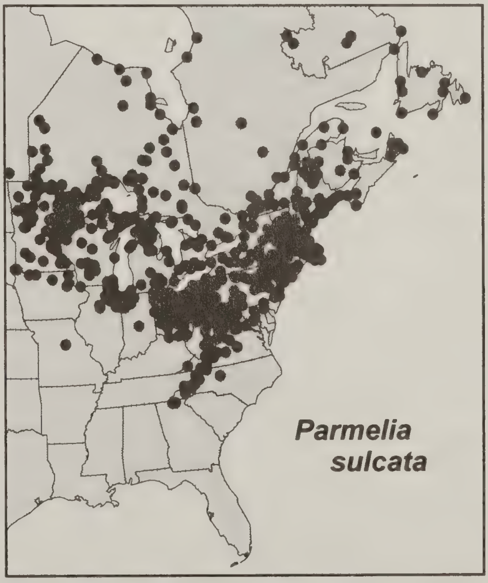


Distribution: (map based on 909 sites: CUP, DIRIG, DUKE, HINDS, LADD, LAY, MAINE, MIN, NY, NYS, SCHMITT, US, Crowe 1994, Dey 1978, Flenniken & Showman 1990, Gowan & Brodo 1988, Harris 1988, Harris et al. 1988, Ladd 1991, Selva 1988, 1989, Thomson 1984 [Canada only], Wetmore 1988, Wilhelm 1995, Wong & Brodo 1992): *P. squarrosa* is common in eNA, especially in the Great Lakes-Appalachian region and is also found in eastern Asia and rarely in western Europe (Hyvönen 1985) and western NA. It has a more southern, temperate distribution than *P. saxatilis*, extending south to Arkansas, Alabama, and South Carolina, but overlaps with *P. saxatilis* from the Great Lakes through New York and New England to Quebec and Newfoundland. In the southern Appalachians the range of *P. squarrosa* extends into the lower foothills, unlike *P. saxatilis*, and generally *P. sulcata*, which are restricted to the high mountain areas.

Remarks: *P. squarrosa* can generally be clearly distinguished from *P. saxatilis* by its squarrosely branched rhizines (simple and furcately branched in *P. saxatilis*). With very small specimens, however, or specimens where the rhizines are not well developed (Dey 1978), identification may be more difficult and require scraping of the lower surface with a scalpel or razor blade to detach the rhizines onto white paper to visualize them clearly.

**Parmelia sulcata** Taylor, in Mackay, Flora Hibernica: 145 (1836). Type collection (Hale 1987): Ireland (FH, lectotype); Syn: *P. rosiformis* (Ach.) Gyelnik.

Morphology: Thallus adnate to loosely adnate on trees and rock, rarely on soil (DIRIG; Sirois et al. 1988), greenish to whitish mineral gray, with divaricate to imbricate lobes 1-5 mm wide. Upper surface plane to foveolate with laminal and marginal pseudocyphellae; soralia laminal and marginal, circular to elongate, eroding, containing granular soredia. Rhizines simple to squarrosely branched. Pycnidia and apothecia rare; spores 11-14 x 6-8 µm.



Chemistry: Medulla contains salazinic and consalazinic acid (K+ yellow changing to red, P+ orange); also accessory lobaric acid in specimens from southern Appalachian mountains. (Dey 1978).

Distribution: (map based on 1449 sites: CUP, DIRIG, DUKE, HINDS, LADD, LAY, MAINE, MIN, NY, US, Ahti 1964, Ahti & Jørgensen 1971, Brodo 1967, 1968, Crichton 1994, Dey 1978, Evans & Meyrowitz 1926, Giardini 1922, Gowan & Brodo 1988, Harris et al. 1988, Hedrick 1940, Henry & Hampton 1974, Hyerczyk 1996; Ladd et al. 1994, Lamb 1954, LeBlanc & De Sloover 1970, LeGallo 1952, McCune 1988, McQueen 1988, Merrill 1926, Mozingo 1948, Newberry 1974, Nimis 1985, Rao & LeBlanc 1967, Reilly 1972, Selva 1988, 1989, Sirois et al. 1988, Taylor 1967, Thomson 1984 [Canada only], Thomson &

Weber 1992, Wilhelm 1995, Will-Wolf 1980, Wong & Brodo 1992): *P. sulcata* is an abundant worldwide species found on all continents; in eNA it is common in the Great Lakes-Appalachian region northward and also the Midwest region from Ohio to northern Iowa and southern Minnesota. It has also been reported from central Missouri (Ladd et al. 1994), but unlike *P. squarrosa*, not from the Ozark Plateau region, or the southern Appalachian foothills of Tennessee, Alabama, Georgia, or South Carolina.

Remarks: *P. sulcata* is an abundant, even weedy, species that more often than the other *Parmelia* species of eNA can be found in highly disturbed sites, such as extensive agricultural lands.

## Acknowledgments

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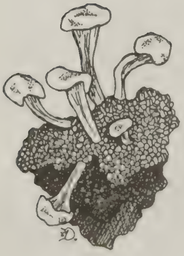

The **Pink Earth Lichen** [*Dibaeis baeomyces* (L. *f.*) Rambold & Hertel, Baeomycetaceae], formerly known as *Baeomyces roseus* Pers. and *B. fungoides* (Sw.) Ach., is widespread and familiar in eastern North America, usually occurring on sunlit eroding clayey or shaly soils. The whitish pseudopodetia grow from a greenish-grey custose primary thallus, reaching 0.25 inch (6 mm) in height, and are capped with pink apothecia. This lichen can spread in such large mats that its pink color is visible along road banks from inside a passing automobile. Drawn from specimens from the Catskill Mountains, New York, by Robert Dirig.

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# LICHEN FLORA OF EASTERN NORTH AMERICA: THE GENUS *GOMPHILLUS* (GOMPHILLACEAE)

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Abstract. *Gomphillus* Nyl. (Gomphillaceae) is reviewed for eastern North America. Two species are recognized, *G. americanus* Essl. in the southeastern and Ozarkian United States, and *G. calycioides* (Duby) Nyl., newly reported for North America from two collections in Macon County, North Carolina. *Gomphillus americanus* possesses hyphophores and capitate-stipitate apothecia, whereas *G. calycioides* lacks hyphophores and has sessile, turbinate apothecia. *Gomphillus caribaeus* is described as new from the Greater Antilles.

*Gomphillus* is probably of as much interest to bryologists as it is to lichenologists because it overgrows bryophytes. Certainly that was my initial fascination. In North America it is truly one of the most spectacular crustose lichens with its relatively large hyphophores that look like little, stalked starbursts. Subsequent study has demonstrated that our common North American species is unique in the genus in this regard and may even deserve generic segregation. In the meantime, though, the genus can be recognized by the thin, gelatinous, glossy thallus (like most members of the Gomphillaceae), hyphophores (when present) stalked and peltate, and linear, multiseptate ascospores.

*Gomphillus* Nyl., Bot. Notiser 1853: 165. 1853. [Etymology: Latin *gomphus* from Greek γόμφος, a bolt, nail or peg + *-illus*, a suffix indicating diminutive]

Type species: *Gomphillus calycioides* (Duby) Nyl.

References: Esslinger 1975; Kalb & Vězda 1988; Vězda & Poelt 1987.

Illustrations: Black and white photograph: Esslinger 1975, p. 191 (*americanus*); drawings: Vězda & Poelt 1987, p. 189 (*americanus*), Kalb & Vězda 1988, pl. 14 (*calycioides*, *ophiosporus*), Ozenda & Clauzade 1970, p. 435 (*calycioides*).

Thallus crustose, thin, gelatinous; photobiont chlorococcoid. Ascomata apothecia, sessile and pseudostipitate or stipitate, blackish above, pale below; exciple well developed, sometimes becoming a pseudostipe, brownish; epithecium red-brown, nongranular; hamathecium of numerous, anastomosing paraphyses, less than 1 μm wide, the apices not swollen; asci 8-spored, narrowly cylindrical, with an apical tholus, I−; ascospores very long, thread-like, multiseptate, hyaline. Conidiomata pycnidia or hyphophores; pycnospores minute, ellipsoid; hyphophore conidia elongate, branched, multiseptate. Chemistry none.

*Gomphillus* is recognized by its grayish-green, thin, shiny thallus, typically growing over bryophytes, in conjunction with thread-like, multiseptate, hyaline ascospores. There are but three species currently described in the genus, two of which are in our flora. The third, *G. ophiosporus* Kalb & Vězda, is much like *G. calycioides*, but differs by a neotropical distribution and ascospores spirally twisted within the ascus. It was described from Ecuador with an additional specimen cited from Costa Rica. I have seen additional material at NY from Puerto Rico, Dominican Republic, Jamaica, and Brazil (Goiás and Rio de Janeiro). There is a fourth, undescribed species in the Caribbean[1]. *Gomphillus americanus*, the widespread species in eastern North America, is significantly different from these other three species in having large, distinctive hyphophores and stipitate apothecia. However, the ascospores are similar in all species.

The genus occurs in westernmost Europe from Portugal to Norway, including the British Isles, Macaronesia, eastern North America, tropical America, and Hawaii, almost always growing over bryophytes.

1. Hyphophores present; apothecia, at least when mature, stipitate, appearing pruinose; widespread in the Southeast and the Ozarks . . . . . . . . *G. americanus*
1. Hyphophores absent; apothecia narrowed below and thus pseudostipitate, not truly stipitate, not pruinose; rare and local in Macon County, North Carolina . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *G. calycioides*

*Gomphillus americanus* Esslinger, Mycotaxon 1: 189. 1975. Type: U.S.A. North Carolina. Wake County: ca. 5 mi SE of the town of Wake Forest in the vicinity of a large granite outcrop along the Cedar Fork of the Little River, *Esslinger 3184A* (holotype US!, isotype DUKE!).

FIGURE 1A–C

Thallus thin, shiny, gray to pale green, typically growing over bryophytes and seemingly killing them. Apothecia sessile when young, becoming stipitate and

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[1] ***Gomphillus caribaeus*** W. R. Buck, n.sp. *Gomphillum calycioidem* et *G. ophiosporum* ob ascomata turbinata et hyphophorum nullum aemulans, sed thallo minore minute granuloso, excipulo fusco tomentuloso crystallofero, ascosporis in asco rectis ca. 300–350 × 5–7 μm incrassatis, cellulisque 2.5–4 μm longis differt. Typus: CUBA. SANTIAGO DE CUBA: La Gran Piedra, near summit, ca. 1200 m, growing over *Phyllogonium fulgens*, 4 April 1982, *W. R. Buck 7642* (holotypus NY, isotypus HAC). Additional specimens: Puerto Rico. Reserva Forestal Toro Negro, along trail beside stream of watershed of Salto Inabón, from Hwy 143 at Km 18.6 at Monte Jayuya, ca. 18°10'N, 66°38'W, 1210–1265 m, humid palm brake, 9 Jan 1992, *R. C. Harris 27269* (NY). Dominican Republic. Prov. Pedernales: 6 km N of Los Arroyos, 5200 ft, very moist broadleaf forest, 6 May 1982, *W. R. Buck 8309* (NY).

FIGURE 1. *Gomphillus* spp. A–C: *Gomphillus americanus*. A: Habit. B: Hyphophores. C: Apothecia. D–E: *Gomphillus calycioides*. D: Habit. E. Apothecia.

compound with age, capitate, blackish, appearing pruinose, in section more or less hyaline throughout except brown in basal part of exciple; paraphyses very slender, less than 1 μm wide, laxly anastomosing; asci cylindric, 220–340 μm long, 7–10 μm wide; ascospores seldom seen (usually immature), linear, hyaline, more or less spiral within the ascus, ca. 200 μm long, ca. 2–2.5 μm wide, transversely pluriseptate, the cells mostly 8–9 μm long. Hyphophores stipitate; stipes (0.8–)1–1.2(–2.0) mm tall, mostly single, occasionally branched, white; apical plate peltate, red- to gray-brown, ca. 0.3–0.45 mm in diameter, essentially entire when young but at maturity becoming deeply divided to ca. ½ its radius into 8–38 arms; conidial mass beige to pale brown in mass when dry, white when moist, completely encircling the stipe, strongly and rapidly hygroscopic, when dry the arms of the apical plate extending well beyond the subtending conidia, when moist the conidial mass expanding to almost full diameter of apical plate; conidia densely packed, filiform, irregularly branched, ca. 1.5–2 μm wide, multiseptate, each cell ca. 3–4 μm long. Pycnidia not seen.

ECOLOGY: Growing over mosses, typically *Leucodon*, but also *Entodon*, and hepatics, sometimes extending onto bark, on branches and trunks of trees. Most commonly found growing over *Leucodon* on horizontal branches of *Juniperus* in seasonally dry habitats. Probably common, but seldom collected, on mosses on horizontal branches of trees, often *Quercus*, in the canopy.

DISTRIBUTION: From North Carolina to Florida and around the southern end of the Appalachians to Mississippi, north to Arkansas and Missouri (FIGURE 2–left); a single collection has been seen from southern Brazil (Santa Catarina) with only hyphophores and no apothecia.

*Gomphillus americanus* is easily recognized by its relatively large hyphophores with a peltate apical plate which becomes divided upon maturity and, with a handlens, appears as a small starburst. It is most often seen, sometimes in patches to 10 cm or more in diameter, growing over the moss *Leucodon julaceus* on large, horizontal branches of old-growth *Juniperus*. Apothecia are uncommon, but not rare. They are distinctive in that they proliferate and become more or less compound, and when mature sit atop a short stipe. In *G. calycioides* the apothecia are turbinate and not truly stipitate. In *G. americanus* mature apothecia appear pruinose (although no crystals could be detected), and thus somewhat grayish. However, in *G. calycioides* the apothecia remain black with no hint of pruina. In *G. americanus* the ascospores are more or less spirally twisted within the ascus, whereas in *G. calycioides* they are straight or irregularly and laxly twisted. Considering the fact that *G. americanus* is the only species in the genus with hyphophores and that the apothecia are capitate-stipitate rather than turbinate, it would not be surprising if eventually it were to be recognized as a new genus.

*Gomphillus calycioides* (Duby) Nyl., Bot. Notiser 1853: 165. 1853; *Baeomyces calycioides* Delise *ex* Duby, Bot. Gall. 2: 636. 1830; *Mycetodium calycioides* (Duby) Massal., Flora 39: 285. 1856 & Sched. Crit. 3: 63. 1856; *Gomphillus calycioides* var. *polycephalus* Nyl., Syn. Meth. Lich. 1(2): 175. 1860, *nom. illeg.* Type: France, "super muscos quos incrustat in sylvâ Briquebec [Manche] detexit cl. Despréaux" (holotype G, *n.v.*, isotype H-Nyl, *n.v.*). FIGURE 1D–E

*Baeomyces microcephalus* Tayl. *in* J. Mackay, Fl. Hibern. 2: 78. 1836; *Gomphillus calycioides* var. *microcephalus* (Tayl.) Nyl., Syn. Meth. Lich. 1(2): 175. 1860; *Gomphillus calycioides* fo. *microcephalus* (Tayl.) Nyl. *ex* Crombie, Monogr. Lich. 1: 108. 1894. Type: Ireland. "On the surface of *Hypnum* [*Isothecium*] *myosuroides*, on Carig mountain, County of Kerry: also on *Jungermannia* [*Frullania*] *dilatata*," 26 Dec 1834, *Taylor* (holotype FH!, isotype H-Nyl, *n.v.*).

Thallus thin, shiny, gray to pale green, typically growing over bryophytes and seemingly killing them. Apothecia sessile, turbinate and thus pseudostipitate, black, not pruinose, in section more or less hyaline above, brown in extensive basal area of exciple; paraphyses very slender, less than 1 $\mu$m wide, laxly anastomosing; asci cylindric, 290–380 $\mu$m long, 9–11 $\mu$m wide; ascospores linear, hyaline, straight or laxly twisted within the ascus, ca. 200 $\mu$m long, ca. 2.5–3 $\mu$m wide, transversely pluriseptate, the cells mostly 3–4 $\mu$m long. Hyphophores none. Pycnidia not seen in North American material, reportedly (James & Brightman 1992) black above, pale below; conidia ellipsoid, 2–4 × 0.5–0.7 $\mu$m.

ECOLOGY: Growing over bryophytes in moist hardwood forests at ca. 1600 m.

DISTRIBUTION: Known in North America from two collections made in September 1989 in the Nantahala National Forest in Macon County, North Carolina, on Wayah Bald (*Buck 17642*) and Wine Spring Bald (*Buck 17667*, both NY) (FIGURE 2-right). Also known from westernmost Europe, including the British Isles, Italy, Macaronesia, Hawaii, and Chile.

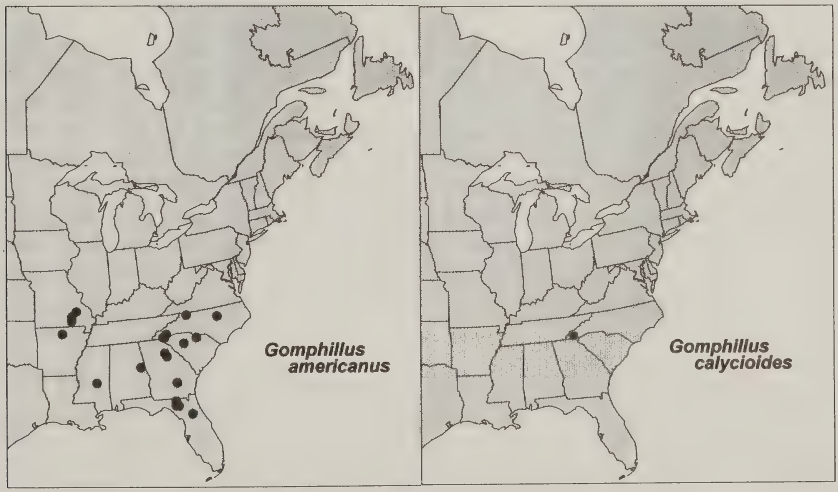

FIGURE 2. Distribution of *Gomphillus* in eastern North America.

ACKNOWLEDGMENTS: First and foremost I thank Richard C. Harris for nurturing my interest in lichens and for assisting at every step of the way. Tor Tønsberg reviewed my manuscript. Bobbi Angell made the illustration. Jim Hinds generously made my distribution maps. Finally, I thank the curators of DUKE, FH, and US for the loan of specimens.

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# LICHEN FLORA OF EASTERN NORTH AMERICA

## THE GENUS *OPHIOPARMA* NORMAN

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**Abstract**: Descriptions, keys, illustrations, and distribution maps are provided for the two species of *Ophioparma* Norman found in eastern North America (eNA), both saxicolous. *O. lapponica*, with simple to one-septate ellipsoidal spores less than 30 µ in length, is known from only one locality in the Flora area. The divaricatic/usnic chemotype of *O. ventosa* is found in alpine and boreal settings as far south as New England and New York. Occasional eNA specimens of *O. ventosa* contain psoromic acid, salazinic acid, atranorin, zeorin, or other triterpenes as accessory compounds.

**Keywords**: Ophioparma / ventosa / lapponica / North America / key

This paper on the lichen genus *Ophioparma* Norman is another in the series of generic reviews by various authors for the Flora of eastern North America (eNA). The Flora covers the part of the continent bordered by the Gulf of Mexico, the Atlantic Ocean, the 97°W meridian, and the 54°N parallel. The 97°W meridian was chosen as the approximate boundary between the midgrass and tallgrass prairies. The 54°N parallel was chosen as the approximate southern boundary of the arctic floristic zone.

The present paper is based on a detailed study of *Ophioparma lapponica* (May 1997) in which 470 mostly North American, mostly saxicolous *Ophioparma* specimens from CANL, COLO, FH, F, H, US, AMNH, and NY were examined. Since then, all eNA specimens at WIS and DUKE have also been examined. A total of 70 specimens from eNA were found among these collections. The species descriptions are based on these eNA specimens, supplemented by other NA specimens in the case of *O. lapponica*. The description of the genus, on the other hand, is based on published data (Printzen & Rambold 1996; Kalb & Staiger 1995; Rogers and Hafellner 1988;

Ekman 1993; Staiger and Kalb 1995; May 1997), with additional specimen-based information provided for eNA.

Previously published distribution maps (Thomson 1968, 1997) and discussions of saxicolous *Ophioparma* in NA (Culberson 1963) confound the two morphological species now known to be on the continent (May 1997). The distribution maps presented here are based on examination of the specimens mentioned previously. The synonyms listed later for *O. ventosa* represent only a subset of the many found in Zahbruckner (1928), namely those commonly encountered on NA herbarium specimens and in the literature of the last century.

**OPHIOPARMA** Norman, Nytt Mag. Naturv. 7:230-231, 1853.

ETYMOLOGY: from the Greek noun *ophis*, snake (combined form, *ophio-*); and the Latin noun *parma*, small round (military) shield. The meaning of the name is unclear, but perhaps has something to do with the sinuous shape of the spores in *O. ventosa* when seen in the ascus.

TYPE SPECIES: *Ophioparma ventosa* (L.) Norman (Hafellner 1984).

KEY REFERENCES for NA: May 1997; Kalb & Staiger 1995; Rogers & Hafellner 1988; for Europe, South America, and Asia: (Kalb and Staiger 1995; Printzen & Rambold 1996; Leukert and Meinel 1981; May 1997; Skult 1997).

SELECTED PREVIOUS ILLUSTRATIONS: Illustrations in the literature have not distinguished between the two morphological saxicolous *Ophioparma* species now known and thus may not be identified correctly at the species level. However, they can be used to get a sense of what the genus looks like.

Color illustrations of the thallus: Wirth 1995, p. 630 (almost certainly *O. ventosa*, based on the locality); Hansen & Andersen 1995, p. 91. Black and white illustrations of thallus: Dopson 1992, p. 220 (probably *O. ventosa*); Thomson 1997, p. 440 (definitely *O. lapponica*, based on recent reexamination of the actual specimen). Drawings showing anatomical characters of the genus: Rogers and Hafellner 1988, p. 170; Staiger and Kalb 1995, p. 15.

HISTORY OF GENUS: Presently six species are known, four of which are corticolous, two saxicolous. Until recently the saxicolous species of *Ophioparma* were included in *Haematomma* as the "*ventosum* group" (Culberson 1963). In segregating the *ventosum* group, Rogers & Hafellner (1988) revived the 1853 generic name *Ophioparma* Norman. Since 1988, four corticolous species--not present in eNA--have been transferred from other genera to *Ophioparma* (Kalb and Staiger 1995; Printzen and Rambold 1996; Ekman 1996). In the process, the definition of the genus was emended to include simple-spored taxa (Printzen & Rambold 1996). Until recently, species concepts for saxicolous *Ophioparma* were primarily based on chemistry. May (1997) and Skult (1997) re-examined saxicolous *Ophioparma* and found there was little basis for erecting taxa based on chemistry, but that two saxicolous species existed based on spore type. May (1997) realigned the names *O. ventosa* and *O. lapponica* to refer to these morphological species. (Previously, *O. lapponica* had been used in NA and elsewhere as the name for the divaricatic/usnic chemical strain of *O. ventosa*.)

VEGETATIVE STRUCTURES: Thallus crustose, dispersed areolate, rimose-areolate, granular, or subsquamulose, up to 15 cm in diameter, ochre, orange brown, gray, gray-olive, or greenish yellow (in eNA usually gray-olive to greenish yellow). Thallus 0.2 mm to 8 mm thick. Photobiont trebouxiod.

REPRODUCTIVE STRUCTURES: Apothecia sessile to 3 mm in diameter, proper exciple well developed, thalline exciple (with algae) present or not (lacking in eNA specimens), hypothecium hyaline, hymenium of mostly simple, strongly agglutinated, fairly thick paraphyses. Epihymenium encrusted with haemoventosin, appearing deep red from above, K+ deep blue, then violet, and finally dissolving.

Asci of the "*Ophioparma*-type" sensu Rogers and Hafellner (1988), that is, with an amyloid tholus lacking axial mass, ring structure, and ocular chamber (Fig. 7-8). Here the "tholus" means the thickened part of the ascal tip that lies within the ascal wall. There is also a thin coating of KI+ dark blue material on the outside of the top of ascus wall, so that the actual appearance in specimens is of a sandwich of blue separated by the unstained cell wall (Fig. 8). The shape of the KI+ dark blue-stained portion of the tholus varies considerably, from a thin crescent at the top, to a filled-in arch, to a circle with a crescent removed from the bottom A late-developing blue-hyaline-blue sandwich completely within the tholus, as described by Ekman (1993), is seen only rarely.

Spores eight, hyaline, simple to transversely multiseptate, 3.5-9 μm wide and 9-70 μm long, with a length-to-width ratio of 2.2 to 18, irregularly ellipsoid to asymmetrically bi-fusiform, sometimes become spatulate at one end (having a "tail"), lacking a gelatinous epispore.

Conidiomata immersed, having a green or red pigment in the ostiole. Conidiophores similar to type VI sensu Vobis (1980). Conidia bacilliform, 7-11 x ca. 1 μm.

CHEMISTRY: Haemoventosin, usually granular, as an epihymenial, hymenial, and sometimes excipular pigment and, for one Asian species, also present in the ostioles of the conidiomata. For most species the ostioles of the conidiomata contain an unidentified green pigment. In the thallus, one or more of the following: usnic acid, divaricatic acid, siphulin, lecanoric acid, thamnolic acid, hypothamnolic acid, various B-orcinol depsidones, atranorin, zeorin and other triterpenes, and various fatty acids. The two species occurring in eNA always have usnic and divaricatic acid. They may also have accessory compounds (see the species descriptions).

DISTRIBUTION AND SUBSTRATES: *Ophioparma* grows on wood, bark, and silicic rock, but only on rock in eNA. All *Ophioparma* species but one have a north temperate to arctic distribution. *O. araucariae* grows in the temperate forests of Chile and Argentina.

LICHENICOLOUS FUNGI: *Muellerella* and *Sphinctrina* (Staiger & Kalb 1995).

RELATED GENERA: *Haematomma* has the following generic characters that differ from *Ophioparma* (Staiger & Kalb 1995): The ascus has both an axial mass and a distinct ocular chamber. The red pigment in the hymenium is not haemoventosin; it reacts KOH+ red or KOH-. The proper exciple of the apothecia is thin; a thick thalline margin is always present (but may be aspicilioid). The paraphyses are thin, individually covered with a gelatinous layer, and highly branched and anastomosed. The conidiomata lack a green pigment. The conidiophores are Vobis (1980) Type V. Some species are sorediate. Specimens are seldom found on rock. Most species have atranorin, sphaerophorin, or placodialic acid as major constituents. The thalli host different lichenicolous fungi than *Ophioparma*.

*Loxospora* has the following generic characters that differ from *Ophioparma* (Staiger & Kalb 1995): The ascus has a wide axial mass. The pigment in the hymenium is not haemoventosin; it reacts KOH+ yellow. The paraphyses are more frequently anastomosed, but are not stuck together with hymenial gelatin. The spores gain their traverse septation only in old age. The conidiomata lack a green pigment. The conidiophores are Vobis (1980) Type V. Many species are sorediate or isidiate. Specimens are rarely found on rock. Most species have thamnolic acid as the main constituent, whereas only one species of *Ophioparma* sometimes contains this compound. The thalli host different lichenicolous fungi than *Ophioparma*.

*Ropalospora* has the following generic characters that differ from *Ophioparma* (Ekman 1996): The full KI blue staining of the mature ascal tholus develops early. The apothecial disks are brown or black and lack haemoventosin. A dark prothallus is usually present around the thallus or

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SPECIMEN AND STAINING INFORMATION FOR FIGURES 1-8: All sections in KOH→water→phloxine unless indicated. Fig. 1: USA, *W. G. Farlow*, Sept., 1894 (FH). Fig. 2: USA, *J. Dunbar*, (COLO S-3004A). Fig. 3: USA, *Ahti 25135* (H). Fig 5: CANADA, *G.W. Scotter 1666* (CANL). Fig. 4, 6, & 7: CANADA, *H. Heikkila* (CANL 24360), Fig 7 KOH→water→Lugol's solution with water replaced by lactic acid Fig 8. JAPAN, *Kurokawa, Lich. Rar. 222*, (COLO), KOH→2% acetic acid→1.5% IKI.

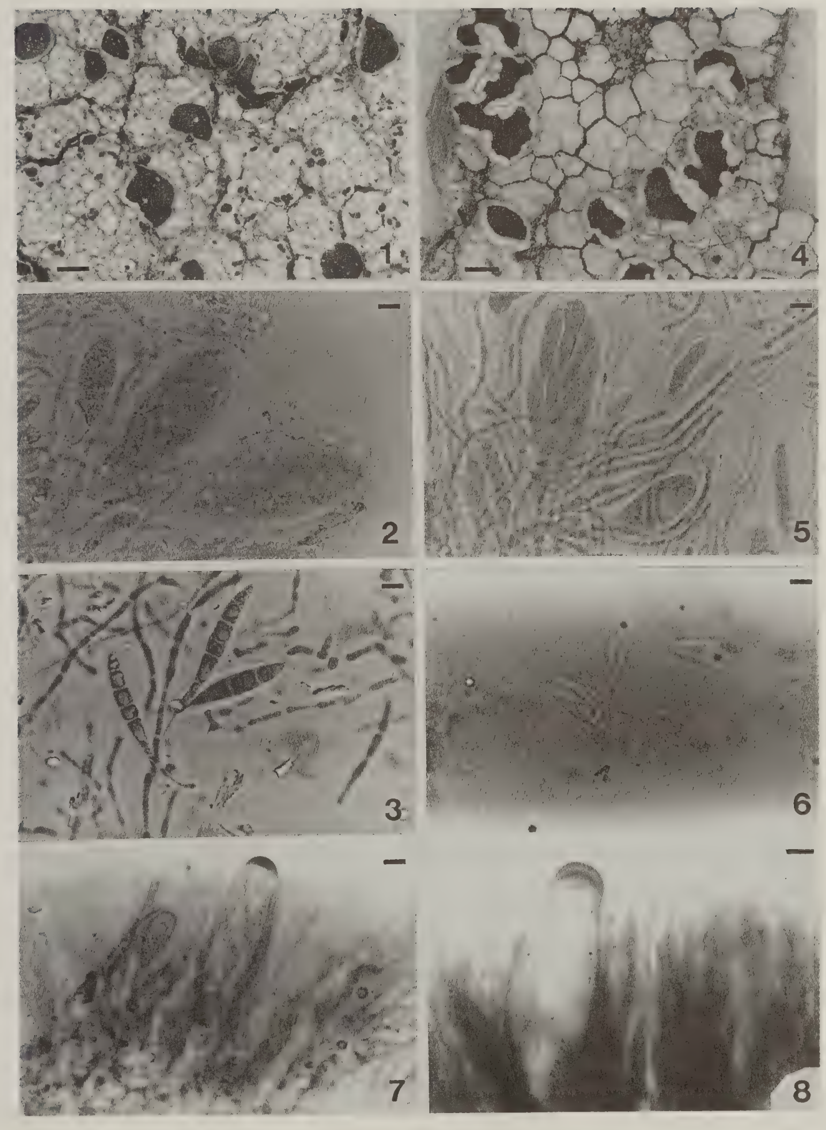


FIG. 1-3. *Ophioparma ventosa*: 1. Thallus. 2. Spores spirally arranged in ascus. 3. Mature spores. FIG. 4-8. *Ophioparma lapponica*: 4. Thallus. 5. Spores irregularly packed in ascus. 6. Mature spores—some are singly septate (arrow). 7-8. *Ophioparma*-type asci. All bars = 5 μm except that for Fig. 1 and 4 bar = 1 mm.

between the areoles. Species usually contain perlatolic acid, gyrophoric acid, usnic acid, atranorin, and/or parietin as major constituents.

## KEY TO SPECIES OF *OPHIOPARMA* IN EASTERN NORTH AMERICA

1a. Spores 3-7 septate at maturity, more than 30 µm long (even when immature), with a length-to-width ratio greater than 6:1, asymmetrically tapered, with one end blunt or fusiform and one end subulate (broadly acicular) to acicular, or sometimes becoming narrowly spatulate (i.e., with a "tail"), often helically arranged in the ascus, but also often arranged subparallel to the long axis of the ascus........................................*O. ventosa*

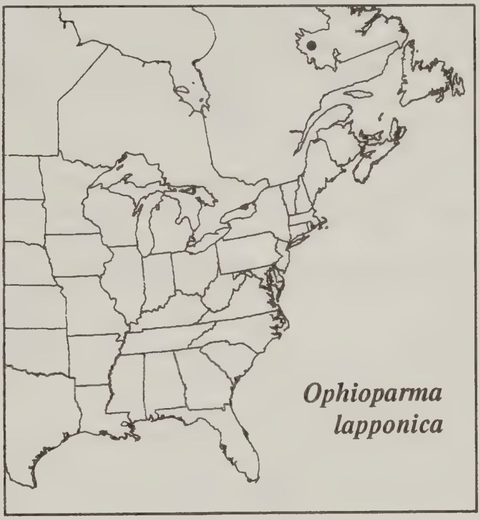
1b. Spores simple to one-septate at maturity, less than 30 µm long, with a length-to-width ratio less than 6:1, narrowly ellipsoid to subfusiform (when immature sometimes asymmetrically tapered, irregular, or curved), arranged sub-parallel or diagonally to the long axis of the ascus.................*O. lapponica*

**Ophioparma lapponica** (Räs.) Hafellner & R. W. Rogers, *Lichenologist* 20: 173. 1988.

*Haematomma lapponicum* Räs., *Ann. Acad. Sci. Fenn, Series A*, 34(4): 67. 1931. TYPE: Finland, Ob. Alkkula (Ylitornio), Aavasksa, Kvartsiitilla, 20 VII 1915, *Veli Räsänen* (H, lectotype, designated by May, 1997) [chemistry: usnic and divaricatic acids, haemoventosin].

**Thallus:** crustose, pale yellow to pale green-yellow or gray green-yellow, rimose-areolate, occasionally with a few dispersed areoles at the margin, evenly thickened to quite variable in thickness within a single thallus, to 7 mm thick (including the hypothallus) where groups of areoles form convex heaps, but more typically 2-5 mm thick. Areoles usually moderately convex, sometimes almost flat, to 2.5 mm across, corticate partway into the cracks, generally matte in luster, with a smooth, finely verruculose (0.1 mm) or micro-rugulose surface. Areoles sometimes resting directly on the substrate, especially near the thallus margin; but more typically areoles and mounds of areoles resting on a thin to thick layer of fungal tissue (which might be considered a hypothallus), often incorporating grains of rock. Hypothallus and the lowest part of the areoles white to dark gray where exposed.

**Apothecia:** sessile, attached over entire diameter or partly to mostly constricted at base, to 3.2 mm in longest dimension, round when solitary, but often crowded together, then slightly compressed to highly irregular in shape, sometimes partially subdivided. Disks plane to moderately convex, deep red brown to very deep red. Margin 100-500 µm thick, sometimes raised, smooth to finely rugose, often strongly flexuose, shiny to matte, pale-yellow to orange-yellow, almost thalline-appearing, or occasionally the same color as the thallus. Margin, however, lacking algae at every stage of development except occasionally a few in the outer basal area of mature apothecia where the margin meets the thallus, usually separated from these algae by a small infold of cortex. A blue-green pigment (same as that in the ostioles of conidiomata) sometimes present in the margin of apothecia, giving the false impression of an algal layer. The interior part of the margin sometimes covered with red pigment, and the outer part of the hymenium sometimes with very few asci, giving the false impression of a two-layered margin.



**Hymenium** and epihymenium together 60-80 µm high, inspersed at the surface and part or all the way down with crystals of deep orange pigment, strongly agglutinated, hyaline and I+ blue in the lower part. Subhymenium hyaline, 60-95 µm thick, I+ blue. **Hypothecium:** hyaline, I-, continuous with and grading into the thick fungal layer (hypothallus) in some specimens; but in other specimens, more compact than the thick fungal layer and separated from it by cortex. **Exciple** of radiating, highly branched, ± anastomosing hyphae originating from the hypothecium, cells 7-12 × 3 µm, the outer, shorter cells forming a compact gelatinous cortical layer interspersed with granules, algae generally lacking. **Paraphyses:** ± simple above, moderately branched halfway down, slightly anastomosing, uniformly thickened to somewhat beaded, multiseptate, cells 7-13 × 1-2 µm, not or slightly swollen at the tips. **Asci**: clavate, 50-65 x 14-18 µm, tholus of *Ophioparma*-type, containing 8 spores **Ascospores:** hyaline, simple to one-septate, not ornamented, lacking a halo, very narrowly ellipsoid, or slightly asymmetrically subfusiform, less commonly fusiform or teardrop shaped, occasionally slightly bent, always lacking a tail, 12-25 × 4-6.7 µm, frequently found immature, but with a few mature spores almost always present, arranged longitudinally to diagonally in the ascus.

**Conidiomata:** immersed pycnidia, of variable shape, often forming in compact groups with up to 20 or more closely adjacent ostioles, the group sometimes occurring in distinctive tubercles up to 2.5 mm in diameter, sometimes occurring in "disks" which resemble apothecia, sometimes in concave hollows; lateral and basal walls of pycnidia hardly pigmented or pigmented strong brown to medium red brown, intensifying in KOH; ostioles pigmented dark green (KOH intensifying, 50% $HNO_3$+ strong red brown), appearing black from above, the groups of ostioles often forming circular or lengthwise elongated gray to black patches on the surface of areoles, also pigmented dark green, lacking algae. **Conidiophores:** similar to Vobis (1980) Type VI, i.e., highly branched with both terminal and lateral conidiogenous cells. **Conidia:** bacilliform, straight to slightly curved, 7-9 (-11) × 1.0-1.4 µm.

**Chemistry:** the only eNA specimen has usnic acid and divaricatic acid by TLC. Elsewhere in NA occasional single specimens have been found with psoromic acid, stictic acid, norstictic acid, or atranorin as accessory compounds. Hymenial pigment (haemoventosin) deep orange in section, KOH+ strong blue, slowly becoming strong purple. Spot tests for eNA: cortex and medulla KOH-, C-, Pd-. Medulla UV+ whitish.

**Ecology and distribution:** Saxicolous, holarctic or subarctic in NA, barely extending south into the eNA floristic area at 53.85 N in Labrador.

**Remarks**: See the remarks under *O. ventosa*.

**Ophioparma ventosa** (L.) Norman, *Nytt Mag. Naturv.* 7:230-231, 1853.

*Lichen ventosus* L., *Sp. pl.* 2, 1753, p. 1141. TYPE: locality apparently unknown (LINN 1273:15, Ehrhart exs. 30, neotype, designated by Jorgensen et. al., 1994) [chemistry: usnic, divaricatic, thamnolic, gyrophoric (tr.) and ?psoromic acids, haemoventosin].

*Parmelia ventosa* Ach., *Methodus*, 1803, p. 166.

*Lecanora ventosa* Ach., *Lichenogr. universalis*, 1810, p. 399.

*Haematomma ventosum* Mass., *Ric. auton. lich. cost.*, 1852, p. 33.

**Thallus:** crustose, light gray-yellow, medium green-yellow, or gray-olive (to gray or brown in European specimens), usually rimose-areolate, sometimes plicate-areolate (i.e., having strongly convex ridges with cracks in between), typically quite variable in thickness within a single thallus, to 8 mm thick (including the hypothallus) where groups of areoles form convex heaps, but more typically 2-5 mm thick; the larger areoles usually moderately convex, but sometime flat, 2-6 mm across, corticate partway down into the cracks, sometimes subumbilicate, generally shiny in luster, verrucose, microsquamulose, or cracked within, the verrucae sometime subdivided into verrucules; the areoles and mounds of areoles typically resting on a thin to thick layer of fungal tissue (which might be considered a hypothallus), which often incorporates grains of rock. Hypothallus and the lowest part of the areoles white to dark gray where exposed. Thallus occasionally partly (near the margin) or entirely of dispersed areoles resting directly on the substrate, then as thin as 0.2 mm and lacking a hypothallus.

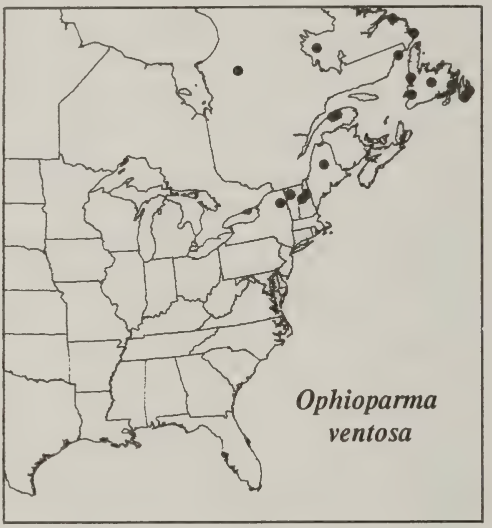
**Apothecia:** sessile, usually attached over most of its diameter, to 3 mm in longest dimension, sub-round to more typically highly irregular in shape, sometimes partially subdivided. Disks gently concave to gently convex, often undulate, deep red brown to very deep red. Margin ca. 100 µm wide parallel to the excipular hyphae, and up to 400 µm thick perpendicular to the hyphae, generally not raised, smooth to finely rugose, often strongly flexuose, shiny to matte, pale-yellow to orange-yellow, almost thalline-appearing, or sometimes pigmented the same color as the disk. Margin, however, lacking algae at every stage of development except occasionally a few in the outer basal area of mature apothecia where the margin meets the thallus, usually separated from these algae by a small infold of cortex. A blue-green pigment (same as that in the ostioles of conidiomata) sometimes present in the margin of apothecia, giving the false impression of an algal layer. An excipular cortex of gelatinized cells present, 7-12 µm thick. **Hymenium** and epihymenium together 35-90 µm high, strongly agglutinated, inspersed at the surface and part or all the way down with crystals of deep orange pigment, hyaline, I+ blue in lower part. Subhymenium hyaline, 15-105 µm thick, I+ blue. **Hypothecium:** hyaline, I-, continuous with and grading into the thick fungal layer (hypothallus) in some specimens; but in other specimens, more compact than the thick fungal layer and separated from it by cortex. **Exciple** of radiating, highly branched, ± anastomosing hyphae originating from the hypothecium, the outer cells forming a compact gelatinous cortical layer, algae generally lacking in NA specimens. **Paraphyses:** ± simple above, sometimes moderately branched halfway down, slightly anastomosing, multiseptate, cells 5-13 × ca. 2.5 µm, mostly uniformly thickened, not or slightly swollen at the tips (to 4.5 µm). **Asci**: clavate, 45-60 x 14-22 µm, tholus of *Ophioparma*-type, containing 8-spores. **Ascospores:** hyaline, 3-7 septate at maturity, 35-61 x 3.3-6.1 µm, (more than 30 µm long even when immature), asymmetrically tapered, with one end blunt or fusiform and one end subulate (broadly acicular) to acicular, or sometimes becoming narrowly spatulate (i.e., with a "tail"), often helically arranged in the ascus, but also often arranged subparallel to the long axis of the ascus.

**Conidiomata:** immersed or often partly raised above the thallus, of variable shape, the ostioles obvious, the exposed part up to 0.3 mm in diameter, sometimes resembling black apothecia with a thalline margin, often in loose groups with up to eight adjacent conidiomata; lateral and basal walls of conidiomata not pigmented, ostioles pigmented dark green in thin section (KOH intensifying, 50% $HNO_3$+ strong red brown), lacking alga. **Conidiophores:** similar to Vobis (1980) Type VI, i.e., highly branched with both terminal and lateral conidiogenous cells. **Conidia:** bacilliform, 6-9 × 1 µm.

**Chemistry:** all specimens with usnic acid and divaricatic acid by TLC (one or the other may occasionally be present only in trace amounts); three eNA specimens also with psoromic acid, one with salazinic acid, three with atranorin, one with zeorin, five with unidentified triterpenes. Hypothamnolic, stictic, and norstictic acid have not been found yet in eNA, but do occur in other parts of the continent (May 1997). Hymenial pigment (haemoventosin) deep orange in section, KOH+ strong blue, slowly becoming strong purple. Spot tests: cortex and medulla KOH-, C-, Pd- (or if accessory compounds are present: KOH+ yellow or orange-yellow and/or Pd+ yellow or orange). Medulla UV+ whitish.

**Ecology and distribution:** Saxicolous; arctic, subarctic-boreal, and alpine in NA, in eNA extending south into alpine regions of northern New England and northern New York.

The southern limit of the species is supported by published and unpublished data that is partially independent of the herbarium collections studied. *O. ventosa* has not been reported for the southern Appalachian Mountains (Degelius 1941; Ciegler 1997) or for the Ozarks of Missouri (Ladd 1996); and it has been found neither in the highest Berkshire Hills of Massachusetts nor the Catskills of New York (first and second Tuckerman Workshops, unpublished lists of species).



**Remarks**: *O. ventosa* and *O. lapponica* are similar species, differing mainly in spore type. Although there are differences in thalline and apothecial characters, these are not always easy to use nor completely reliable. However, *O. ventosa* is more variable than *O. lapponica*. Some variants—for example, those with relatively dark thalli, sub-squamulose areoles, or thin apothecial disks—are different from any NA specimen of *O. lapponica* and therefore can, with experience, be identified on sight.

In NA, *O. lapponica* appears not to occur as far south as *O. ventosa (May 1997)*. If this proves correct, specimens from all but the most northern localities in the eNA Flora region will prove to be *O. ventosa*.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
IN HONOR OF JOHN W. THOMSON.
EDS: M. G. GLENN, R. C. HARRIS, R. DIRIG & M. S. COLE.
MYCOTAXON LTD., ITHACA, NY. 1998.

# THE LICHEN GENUS *PERTUSARIA* IN ILLINOIS AND MISSOURI

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## Abstract

A treatment is presented for the seventeen species of the lichen genus *Pertusaria* documented from Illinois and Missouri. Included are taxonomic keys and a species-by-species evaluation of morphology, chemistry, phytogeography, field identification characters, local ecology and substrate affinities, and distribution maps and specimen data. The region is important for developing an understanding of *Pertusaria* in North America because many of the species are at or near the edge of their range here, and locally most species of *Pertusaria* display strong affinities to areas of remnant natural quality. The fungus *Minutoexcipula tuckerae*, parasitic on *Pertusaria texana*, is reported for the first time from Missouri and Arkansas.

## Introduction

This paper provides an account of the seventeen species of *Pertusaria* documented from Illinois and Missouri. It includes taxonomic keys and information about the morphology, chemistry, ecology, field identification characters, and local abundance and distribution of each taxon. The only previous systematic treatment of the genus to cover the region was Dibben (1980), but this work includes all North American taxa of *Pertusaria*, so the keys are cumbersome and difficult to use. Additionally, the local distribution, habitats, and substrate preferences for several species differ from the generalizations provided by Dibben for the entire North American ranges of each species. Few of the specimens cited here were cited by Dibben, and recent collecting activity has revealed several species previously unknown from the region. Since Missouri and Illinois appear to be near the edge of the range for many species of *Pertusaria*, detailed distributional data from the region is helpful in resolving the range limits.

Illinois and Missouri are located in midcontinental North America and encompass a diverse array of physiography, geology, landscapes, vegetation, and habitat types. The two states extend from the eastern portion of the Great Plains eastward into the western outliers of the eastern deciduous woodlands. The northern portion of Illinois includes a southern extension of boreal forest vegetation associated with the Great Lakes, while the southeasternmost portion of Missouri lies at the northern end of the Gulf Coastal Plain Embayment, with strong biological affinities to the southeastern states.

All of Illinois except the extreme southern portions, as well as the half of Missouri north of the Missouri River, were covered with glacial ice sheets during one or more of the four major Pleistocene glaciation periods. Much of this landscape was dominated by tallgrass prairie vegetation prior to European settlement. Most of the southern portion of Missouri is part of the Ozark region of the Interior Highlands, and is characterized by a highly dissected, rocky landscape of great geological diversity. This is an ancient, unglaciated landscape that includes areas that have been continuously available for terrestrial life forms since the late Paleozoic. The Ozark region, and the similar landscape of the Shawnee Hills of Southern Illinois, are characterized by a predominately woodland vegetation with a preponderance of *Quercus*. Since European settlement, many of the once open woodlands and savannas of the region have been cleared, and surviving woodlands have become closed in and overgrown, with changes in species composition.

Lichen vegetation in Illinois and Missouri reflects the impacts associated with more than two centuries of post-European settlement anthropogenics. Large areas of the glaciated portions of our region have been converted to intensive agriculture, and virtually no tallgrass prairie survives in our glaciated landscapes. Lichen vegetation is often depauperate in these areas, even in remnant woodlands that appear capable of supporting a diverse lichen flora. Several taxa routinely collected in central Illinois as recently as the 1950's, such as *Ramalina* and *Parmotrema*, are now absent from much of the region. Lichen diversity and abundance are greater in our timbered, unglaciated landscapes, although these too show evidence of deleterious impacts in many areas

Species of *Pertusaria* are common on boles of hardwoods in mature timbered uplands in the unglaciated portions of our region, particularly the Ozark region of southern Missouri and the Shawnee Hills of extreme southern Illinois. In the Missouri Ozarks, species of *Pertusaria* can be dominant components of the corticolous lichen vegetation. For instance, in an oak-dominated flatwoods in the northern Ozark region, Ladd (1996a) found *P. paratuberculifera* to have the second highest importance value of all 48 species comprising the mid-bole lichen vegetation, occurring on 56% of the trees sampled. In the glaciated portions of Illinois and Missouri, particularly in the agricultural districts, *Pertusaria* is rare; large areas of central Illinois have no modern records of any *Pertusaria.*

Although several species of *Pertusaria* have been documented locally on lightly shaded siliceous rocks in rare instances, all but two of our taxa are essentially confined to corticolous substrates. *Pertusaria plittiana* is restricted to lightly shaded, well-drained siliceous rocks in timbered uplands, occurring on sandstone and igneous rocks. *Pertusaria globularis*, known in our area from only two records, occurs on mosses over rocks and trees. Most of our taxa occur on hardwood trees, although several occasionally grow on *Juniperus*. In our region, *Pertusaria tetrathalamia* shows a marked preference for *Juniperus*, although Dibben (1980) says that this is species of hardwoods that occurs rarely on conifers. *Pertusaria hypothamnolica,* although predominately occurring on hardwoods, also regularly occurs on *Juniperus.*

Most corticolous species of *Pertusaria* typically occur on lower and mid-boles of trees in wooded uplands where at least some of the timber exceeds 40 years old. *Pertusaria neoscotica* occurs on lignin and mossy logs as well as on tree boles. *Pertusaria texana* occasionally occurs on mid-boles of trees in woodlands, but more typically grows on the upper boles, large branches, and smaller-diameter substrates along woodland edges. The species most frequently found on upper branches of canopy trees, and on trees in more open sites, are *P. propinqua* and especially *P. pustulata,* which sometimes colonizes small upper branches of large trees.

With the exception of *P. pustulata*, all of our local species are associated with landscapes having significant natural integrity, that is, areas displaying strong affinities with presettlement character and conditions. Species such as *P. propinqua*, whose range extends westward into the eastern Great Plains, sometimes occur on trees in exposed sites such as in fencerows or bordering prairies and pastures.

According to Dibben (1980), half of the North American species of *Pertusaria* are endemic. Locally, twelve of our seventeen taxa (71%) are endemic to North America. Several of these taxa, including *Pertusaria globularis, P. ostiolata,* and *P. valliculata,* display a characteristic Ozark/Appalachian distribution. Most of the other endemic taxa, such as *P. neoscotica,* display phytogeographic affinities to the deciduous woodlands of eastern North America. Several of these taxa with distributional affinities to the eastern deciduous woodlands have a markedly southeastern distribution, including *P. hypothamnolica, P. paratuberculifera,* and *P. subpertusa.*

Characteristics useful for identification of local *Pertusaria* species include thallus morphology and color—especially the size, shape, and spacing of the fruiting bodies (warts), as well as chemistry, and ornamentation and number of spores. Chemical information necessary for accurate identification of local species can be obtained through a combination of spot and UV tests. With experience, most species of *Pertusaria* can be reliably determined in the field, although certain groups require spore or chemical data for accurate identification.

The following key relies on thallus morphology, standard chemical spot tests, fluorescence under ultraviolet light, and spore number and ornamentation. Color reactions from chemical tests are often localized. For instance, the C+ yellow reaction characteristic of *P. texana* and certain other taxa often is visible only around the ostioles, and can take up to two minutes to develop. Several K− taxa occasionally can react K+ weakly dingy yellow, which should not be confused with the clearly K+ yellow reaction produced by compounds such as stictic and thamnolic acids. In our key, fluorescent reactions under long-wave ultraviolet light (~360 nm) are characterized as either UV− (no xanthones), UV+ yellow (lichexanthone), or UV+ pinkish to orange (various other xanthones). Spores are either single-walled and 1-2 per ascus in the disciform-fruited subgenus *Pionospora* or 2, 4, or 8 double-walled spores per ascus in the poriform-fruited subgenus *Pertusaria*. Some species, particularly in subgenus *Pionospora*, commonly have aborted or undeveloped asci and rarely produce spores. Some of the four-spored species, notably *P. tetrathalamia,* often produce 2-3 or sometimes 5 spores per ascus, and a single ascoma may have asci with different numbers of spores. Spores are either smooth, as in most taxa, or appear strongly ornamented because of a regular series of radial grooves in the inner wall, as in *P. macounii, P. tetrathalamia,* and *P. valliculata.* A few other species, such as *P. neoscotica, P. plittiana,* and *P. subpertusa*, are characterized by Dibben (1980) as having ornamented spores, but in local population the level of ornamentation is insignificant and the spores appear essentially smooth.

Following the key are alphabetically arranged accounts for each species. These accounts discuss abundance, habitats, distribution, identification features, and confusable similar species. Maps showing species distribution by county accompany the text for each species account. Specimens examined by the authors are marked with solid dots on the maps and supersede literature reports, which are designated with an open dot. Most of the literature reports are from Dibben (1980).

Diagnostic chemical constituents are listed in brackets at the end of each account and summarized in table 1. Note that chemical information is based largely on material from Missouri, Illinois, and adjacent portions of the Midwest. Dibben (1980) notes that individual specimens of certain species may lack certain characteristic chemicals, such as specimens of *P. hypothamnolica* that lack lichexanthone. In instances where we have seen these anomalies in local material, they are discussed in the species accounts.

### Key to the Species of *Pertusaria* in Illinois and Missouri

1. Thallus isidiate, muscicolous . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***P. globularis***

1. Thallus not isidiate, rarely muscicolous.

  2. Fruiting bodies disciform, the warts lecanorate, pruinose, or sorediate; spores 1-2 per ascus or aborted or undeveloped, the walls single (subg. *Pionospora*).

    3. Wart C+ red (lecanoric acid); warts lecanorate . . . . . . . . . . . . ***P. velata***

    3. Wart C-; warts not lecanorate.

      4. Cortex UV+ yellow (lichexanthone) . . . . . . . . . . ***P. hypothamnolica***

      4. Cortex UV− or UV+ pinkish.

        5. Wart K+ deep yellow (thamnolic acid) . . . . . . . . ***P. trachythallina***

        5. Wart K− or K+ weak yellow turning reddish or brownish.

          6. Wart KC+ violet (picrolichenic acid) . . . . . . . . . . . ***P. amara***

          6. Wart KC− . . . . . . . . . . . . . . . . . . . . . . ***P. multipunctoides***

  2. Fruiting bodies poriform, the warts mostly corticate and lacking pruina or soredia (often appearing lecanorate and pruinose in *P. propinqua*); spores 2-8/ascus, the walls double (subg. *Pertusaria*).

    7. Spores prevailingly 5-8/ascus, the inner wall smooth.

      8. Cortex UV+ yellow (lichexanthone) . . . . . . . . . ***P. paratuberculifera***

      8. Cortex UV− or UV+ pinkish to orange.

        9. Cortex, especially near the ostioles, C+ yellow (thiophaninic acid); thallus characteristically with tints of yellow, UV+ brilliant orange . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . ***P. texana***

        9. Cortex C− throughout; thallus without yellowish tints, UV− or UV+ weakly pink.

          10. Medulla K+ yellow turning red (norstictic acid); cortex UV−; warts open and appearing lecanorate, often white in the center . . .

. . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. propinqua**

10. Medulla K−; cortex UV+ pinkish (unknown xanthone), though often weakly so; warts poriform, never lecanorate . . . **P. ostiolata**

7. Spores 2-4/ascus, the inner wall smooth or ornamented.

11. Cortex UV+ yellow (lichexanthone) . . . . . . . . . . . . . **P. valliculata**

11. Cortex UV− or UV+ pinkish to orange.

12. Spores prevailingly 3 or 4/ascus.

13. Medulla K−; spores smooth; very rare . . . . . . . **P. globularis**

13. Medulla K+ yellow (stictic acid); spores walls rough; occasional . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. tetrathalamia**

12. Spores 2/ascus.

14. Medulla K+ yellow turning red (norstictic acid); cortex UV−.

15. Thallus saxicolous; many warts more than 1 mm in diameter . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. plittiana**

15. Thallus corticolous or lignicolous; warts commonly fused, but individual ones notably less than 1 mm in diameter . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. neoscotica**

14. Medulla K− or K+ yellow; cortex UV+ orange to pink (rarely UV−).

16. Ostioles black, often solitary at the apex of a wart, and almost always less than 5/wart, usually >0.2 mm wide; warts prevailingly <0.6 mm broad; cortex C+ yellow, especially around the ostioles . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **P. pustulata**

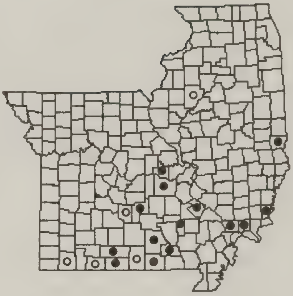
16. Ostioles brownish, usually more than 5/wart, usually <0.12 mm wide; warts prevailingly >0.6 mm broad; cortex C−.

17. Spores smooth to slightly ornamented; medulla P+ orange-red (fumarprotocetraric acid) . . . . . . . . . . . **P. subpertusa**

17. Spores with conspicuous ornamentation; medulla P+ yellow to orange (stictic acid)

18. Inner side of inner spore wall sculpted with +/− broadly rounded ridges; lumen and spore walls often K+ pale violet; warts often with broad, flat to slightly concave apices . . . . . . . . . . . . . . . . . . . . . . . . **P. macounii**

18. Outer (and sometimes also inner) side of inner spore wall finely and densely sculpted with reticulate ridges; lumen and spore walls K−; warts usually with rounded apices . . . . . . . . . . . . . . . . . . . . . . . **P. tetrathalamia**



**Pertusaria amara** (Ach.) Nyl. An occasional species in the Ozarks and Shawnee Hills, growing on shaded tree trunks in remnant woodlands, and very rarely on shaded siliceous rocks in wooded uplands that have substantial corticolous populations of *P. amara*. It occurs mostly on *Carya* and *Quercus*. Although essentially confined to the unglaciated districts in our area, it is common in the northern Great Lakes area to our north.

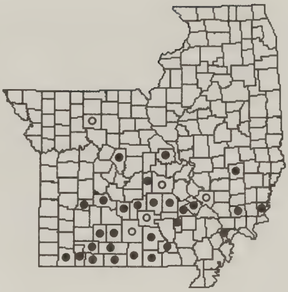
*Pertusaria amara* is quite variable in the size of the warts and disposition of pruina, but locally it is easily recognized in the field by the abundant, minute, punctiform, densely pruinose warts, which appear quite white in contrast to the gray to greenish or brownish cortex. In young thalli, the developing warts appear almost pseudocyphellate. The cortex is darker than that of other local members of subgenus *Pionospora*. North of our area, particularly on coniferous trees, the warts of *P. amara* tend to fuse into larger, irregularly rounded, sorediate-appearing masses, and the thallus is uniformly pale gray. The only local specimen with this morphology is from an old-growth *Juniperus virginiana* at a sandstone barren in Johnson County, Illinois. Almost all local populations lack protocetraric acid and react P−, although forms with protocetraric acid (P+ red) do occur. Based on midwestern material we have seen, the morphology with larger, irregularly massed warts, including the Union County, Illinois specimen discussed above, is more likely to contain protocetraric acid. [picrolichenic acid, ± protocetraric acid]

**Pertusaria globularis** (Ach.) Tuck. Very rare in our area, where it is significantly disjunct from its otherwise eastern distribution. Known only from Pope County, Illinois, as cited by Dibben (1980), and from a collection on mossy chert in an extensive woodland in Oregon County. Its habitat is on mosses over rocks, soil, or tree boles. Endemic to the eastern United States.

This is the only isidiate *Pertusaria* in our area. Dibben (1980) mentions that sterile specimens are highly isidiate, but that fertile specimens frequently lack isidia. The Oregon County specimen is not isidiate. *Loxospora pustulata* (Brodo & W. L. Culb.) R. C. Harris, a locally common sterile lichen with granular to pustular isidia and a K+ bright yellow thallus (thamnolic acid) resembles a *Pertusaria;* it grows mostly on shaded rocks and trees. *Ochrolechia yasudae* Vain. is a rare lichen of siliceous rocks in the Ozarks and Shawnee Hills. It has an isidiate, C+ red, sometimes sterile thallus, and could also be mistaken for a *Pertusaria*. *Pertusaria globularis* has a K− and C− thallus. [2'-O-methylperlatolic acid, xanthone]

**Pertusaria hypothamnolica** Dibben Frequent in timbered uplands on a variety of trees, particularly *Quercus velutina, Q. stellata,* and *Juniperus virginiana,* and infrequently on shaded sandstone. This North American endemic is known from the Interior Highlands and low plateaus of the southeastern United States, and in our area is rare north of the

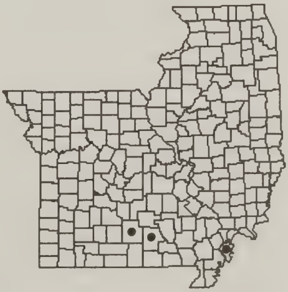
Ozark border and southern Illinois. The type collection for this species is from Randolph County, Illinois (*Skorepa 4244* DUKE).



This species is fairly distinctive in that the warts appear white, but not powdery, with the rims mostly well defined. Although all of our material contains lichexanthone and reacts UV+ bright yellow, Dibben (1980) mentions that some specimens are UV−. Some of our specimens display very localized areas of thallus fluorescence. [hypothamnolic acid, lichexanthone (rarely lacking?)]

**Pertusaria macounii** (I. M. Lamb) Dibben This endemic of eastern North America is rare on hardwoods, usually *Quercus*, in mature woodlands in the Ozark region. There is also a specimen from Cook County, Illinois that was collected in 1898. Although Dibben (1980) did not cite the Cook County specimen, it appears to match his description of *Pertusaria macounii*, in that it was collected on a hardwood tree and that the warts are quite crowded and even in "mutually deformed groups". The warts of this species are typically broad and often slightly concave at the summit.

The only other species that sometimes has two strongly ornamented spores per ascus, *P. tetrathalamia,* usually has more diffuse, rounded warts and often grows on *Juniperus.* The two species are disturbingly similar in appearance, and the only sure character for problematical specimens is spore ornamentation. *P. macounii* has spores with rounded grooves on the inside of the inner wall, while *P. tetrathalamia* has spores with conspicuous, fine reticulate sculpting on the outside of the inner wall, as well as sometimes on the inside of the inner wall. Spores of *P. macounii*, especially when young, are often K+ pale violet, while spores of *P. tetrathalamia* are K−. Older specimens of *P. macounii* are said to have tinted or darkening spores, but this character appears to us to be subtle and inconsistent. Reports of this species by Ladd et al. (1994) are referable to *P. tetrathalamia.* [stictic acid, xanthones]



**Pertusaria multipunctoides** Dibben Apparently rare in our region, but possibly under-collected due to its superficial resemblance to the more common *Pertusaria hypothamnolica.* Our only specimens are from hardwoods in southeastern Missouri. Dibben (1980) also maps a record from extreme southeastern Illinois, but no specimen is cited. Endemic to eastern North America.

While it resembles *Pertusaria hypothamnolica, P. multipunctoides* is readily distinguished by its UV−, P+ red reaction. A similar species that would key here, *P.*

*rhexostoma* Nyl. *ex* Hue, was reported from Menard County by Dibben (1980), based solely on a specimen collected by Elihu Hall, which is presumed to have been collected in Illinois since "Athens" is in Menard County. Problems associated with Hall's collection locality data are well known, as discussed by McKnight (1985). According to Dibben (1980) the nearest populations are several hundred miles from our area, in central Pennsylvania and northern Minnesota. In light of the lack of corroborating data or specimens, this record is excluded from the flora. *Pertusaria multipunctoides* has a P+ orange medullary reaction, spore walls that are K−, and sessile warts; *P. rhexostoma* has a P- medullary reaction (fumarprotocetraric acid absent), K+ violet spore walls, and embedded warts. [fumarprotocetraric acid]

**Pertusaria neoscotica** I. M. Lamb An uncommon species of shaded hardwood boles and mossy lignin in wooded uplands. Endemic to eastern North America.

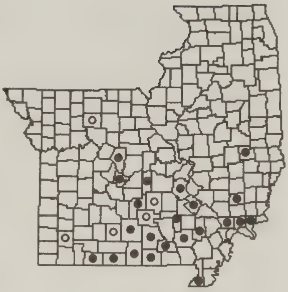
In this species the warts are abundant, irregularly shaped, and commonly fused, with the individual warts usually less than 1 mm in diameter. The thallus surface is usually quite rugulose with numerous small bumps that appear to be incipient warts. This species and *P. propinqua* are our only corticolous species with norstictic acid and a strong K+ yellow turning red reaction, but *P. propinqua* has eight spores per ascus and broad, lecanorate-appearing warts usually exceeding 1 mm in diameter. [norstictic acid]

**Pertusaria ostiolata** Dibben A narrowly endemic species of Appalachian/Ozark distribution, this species grows on a variety of trees, often among mosses on the lower trunks. It is generally uncommon in southernmost portions of Missouri and Illinois; although in the Lower Ozark region along the Current River drainage in Missouri it is locally common in mature woodlands. Our populations are the northwesternmost extension of the range of this species.

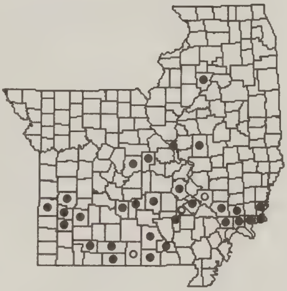
The thallus is characteristically bordered by a pale thin zone, which surrounds tightly aggregated but mostly distinct, more or less papilliform warts that bear one to few tiny ostioles. The warts are notably more cylindrical than those of other local taxa, and average 0.5-0.7 mm in diameter, although they often fuse into larger aggregations. When separate, each wart usually has a single dark ostiole at the apex, with the ostiole averaging 0.1 mm in diameter. [xanthone]

**Pertusaria paratuberculifera** Dibben An endemic of the southeastern United States, this species is common on a wide variety of trees in mature woodlands, but most frequent on *Quercus velutina* and *Q. stellata,* extending well up on shaded boles. It occurs throughout the Ozarks and unglaciated portions of southern Illinois, and rarely northward in glaciated areas.

The warts of this species are relatively large, mostly more than 1 mm in diameter, and appear more as loosely aggregated, elevated mounds, typically with several small, brownish-pellucid ostioles per wart. Without looking at spores, *Pertusaria paratuberculifera* would be impossible to discriminate from the less common *Pertusaria valliculata,* which differs in having 4 ornamented spores per ascus rather than 8 smooth spores. [lichexanthone]

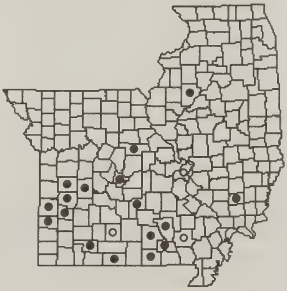


**Pertusaria plittiana** Erichsen An endemic of the eastern United States, this species is frequent on lightly shaded, massive siliceous rock, especially sandstone. It is far more common in the unglaciated portions of our area, probably because that is where large exposure of suitable substrate are available.

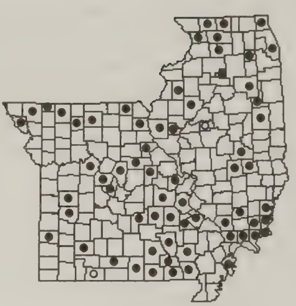


This is the only regularly saxicolous species in the local *Pertusaria* flora. It typically forms large patches, with the thallus often appearing partly endolithic and sometimes with entire portions exfoliating. Small, dark-green thalli of *Buellia vernicoma* (Tuck.) Tuck. frequently grow on or adjacent to *Pertusaria plittiana.* Another gray saxicolous crustose lichen that contains norstictic acid is *Phlyctis argena* (Spreng.) Flot., which is usually sterile with a smooth, thicker, paler gray thallus, and often with scattered eruptions of soredia. [norstictic acid]

**Pertusaria propinqua** Müll. Arg. Endemic to eastern North America, this species is occasional on open-grown trees, commonly hickories, in more exposed situations than most other *Pertusariae.* Habitats include woodland edges, fencerows, pastured woodlands, prairies, savanna remnants, and wooded uplands in the Ozarks. In all of these habitats, *P. propinqua* often occurs on smaller branches as well as the boles, and often occurs higher on the bole than most other *Pertusaria* species. This species shows a phytogeographic affinity to the prairie regions of southern midcontinental North America. While most of our *Pertusaria* species have populations in the Appalachian mountains and piedmont, *Pertusaria propinqua* is nearly absent there, with most of the populations occurring from our area southward and westward (Dibben 1980). In our area, *P. propinqua* is most common in the western Ozarks and Osage Plains of southwestern Missouri.



This species is easily identified by the thick-rimmed, expanded warts often up to 1.5 mm across, many of which at first glance are evocative of lecanorine apothecia. [norstictic acid]



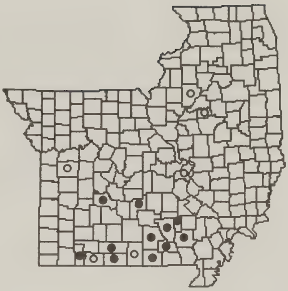
***Pertusaria pustulata*** (Ach.) Duby This is our most common and disturbance tolerant *Pertusaria*. It is frequent throughout our area, growing on the boles and branches of a wide variety of hardwood trees in a diversity of wooded habitats. It frequently occurs on young, smooth-barked trees and branches, especially on *Carya*. Although common in lightly shaded areas, it appears to be intolerant of the shading levels conducive to the growth of other species of *Pertusaria*, such as *P. amara, P. hypothamnolica,* and *P. paratuberculifera*. Grazed woodlands with lightly shaded stands of *Carya ovata* are sometimes characterized by extensive, nearly continuous colonies of *P. pustulata* on the lower boles.

This species is characterized by a thin, pale grayish or yellowish gray thallus with numerous, small, low, rounded, distinct to loosely aggregated warts averaging 0.4-0.7 mm in diameter and tipped with one to a few black or darkening ostioles. The ostioles are larger than ostioles of many *Pertusaria* species, and almost always exceed 0.15 mm in diameter. The spore walls are smooth and unornamented. A closely related species, *Pertusaria xanthodes* Müll. Arg., occurs in adjacent Arkansas and southward, with a distribution mostly confined to the Atlantic and Gulf coastal plains. It differs in having ornamented spore walls and pale ostioles. [stictic acid, xanthone]

***Pertusaria subpertusa*** Brodo Local populations are at the northwesternmost edge of the range of this species, which is endemic to the mid-Atlantic and southeastern United States. In our area, it is confined to the southeastern Ozarks of Missouri, in the watershed of the Current and Eleven Point rivers, where it occurs on the lower trunks of hardwoods in extensive woodlands with remnant natural integrity; one local collection is from old growth *Juniperus*.

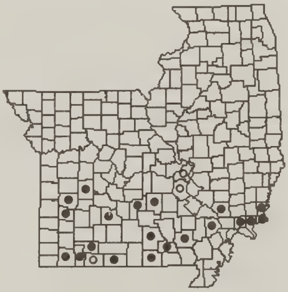
The thallus is dull gray to greenish gray, with abundant, broad, usually well-separated warts typically 0.6-1 mm broad, with numerous tiny ostioles per wart. Each ostiole is about 0.1 mm in diameter. Our specimens are UV+ pinkish, at least on the warts. The two spores per ascus, P+ orange-red thallus reaction, and C− ostioles are diagnostic. Although Dibben (1980) describes spores of this species as radially grooved, local populations have spores that appear almost smooth, with no conspicuous ornamentation. *Pertusaria pustulata* also has two spores per ascus and a P+ yellow to orange medullary reaction, but is a much smaller lichen, with smaller warts with fewer and larger, dark ostioles that react C+ yellow. *Pertusaria macounii* and *P. tetrathalamia* have similar morphology and can have two spores per ascus, but both of these taxa have strongly ornamented spores and react P+ yellow to orange. [fumarprotocetraric acid, xanthone]

***Pertusaria tetrathalamia*** (Fee) Nyl. Occasional, mostly on *Juniperus*, in natural areas. Dibben (1980), on the other hand, notes that over the whole of its range *Pertusaria tetrathalamia* is prevailingly found on hardwoods. Endemic to the eastern United States.



This species is characterized by its pale gray, commonly distinct warts typically about 1 mm broad, with several small brownish ostioles per wart. This species can be confusingly similar to *P. macounii*, as discussed in the entry for that species. Two other species that are similar in appearance, *Pertusaria paratuberculifera* and *P. valliculata,* are both UV+ yellow, as opposed to *P. tetrathalamia,* which is UV+ pinkish orange. The only other species with strongly ornamented spores in our region are *P. macounii* and *P. valliculata.* Many populations from the Ozarks have only 2 spores per ascus, although asci with 3, 4, and even 5 spores also occur, sometimes in the same ascoma. Locally, populations growing on *Juniperus* typically have two spores per ascus, while those on hardwoods are more likely to have three or four spores per ascus. [stictic acid, xanthones]

*Pertusaria leioplaca* DC. [=*P. leucostoma* (Bernh.) A. Massal.] would key here; it has smooth spore walls. It was reported from Jefferson County by Berry (1937) and Taney County by Wetmore (1992). The Taney County record is apparently based on *Wetmore 68977* (MIN), which is *P. paratuberculifera*. No supporting vouchers have been seen to substantiate the Jefferson County report, but Ladd (1996b) discusses some of the problems and uncertainties associated with Berry's work. The nearest records of *P. leioplaca* cited by Dibben (1980) are from south central Arkansas, southeastern Kentucky, and northeastern Iowa.



**Pertusaria texana** Müll. Arg. Occasional to locally frequent in the unglaciated districts of our area, where it grows on a wide variety of hardwood trees, as well as *Juniperus.* Populations in Missouri are at the northwestern limit of the range of this endemic, southeastern species.

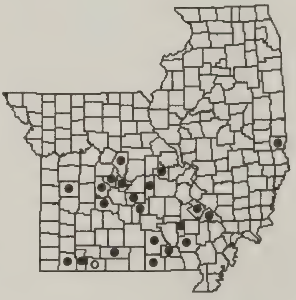
*Pertusaria texana* is characterized by relatively small thalli, with tinctures of green or yellow, and the area around the ostioles is regularly yellow. Areas of the cortex, particularly around the ostioles, react C+ yellow. Occasional specimens of *Pertusaria pustulata* may have yellowish tints, but the ostiole area will be black or dark colored, rather than yellow. Most local specimens of *P. texana* fluoresce UV+ brilliant orange, in a far more intense display than our other UV+ pinkish to orange taxa. [stictic acid, thiophaninic acid]

*Minutoexcipula tuckerae* V. Atienza & D. Hawksw., a small lichenicolous deuteromycete with two celled, brown conidiospores, parasitizes *P. texana*. It was previously known only from Louisiana (Atienza and Hawksworth 1994), but occurs on *P. texana* at several locations in and around our region: ARKANSAS Howard Co.: *Ladd 19683;* MISSOURI Ozark Co. *Harris 40633A* (NY); St. Clair Co. *Harris 21296A* (NY); Stone Co.: *Ladd 12366.*

**Pertusaria trachythallina** Erichsen This species has an Appalachian-Great Lakes distribution with outliers in the Ozarks and the Gulf coastal plain. It is rare in our area, but apparently more common to the south: Dibben (1980) cites specimens from seven counties in northwestern Arkansas. Locally, *P. trachythallina* is known from a few collections in the southern Ozarks, mostly from the Current River drainage of the Lower Ozark region. One collection was from the shaded trunk of an old growth *Carpinus caroliniana* along a stream and most others are from lightly shaded canopy branches of oak trees in mesic areas.

This species somewhat resembles *P. hypothamnolica*, but the latter species has larger, more thickly corticate-margined warts and is UV+ yellow and K− to K+ pale yellow or weakly violet (lichexanthone and hypothamnolic acid), as opposed to the smaller, more thinly corticate-margined warts and UV−, K+ rapidly deep yellow thallus (thamnolic acid but no cortical xanthones) of *P. trachythallina*. *Pertusaria multipunctoides,* which can resemble P. *trachythallina,* also has a UV− thallus but reacts K−. The warts of *P. trachythallina* appear more coarsely granular-pruinose than the warts of *P. hypothamnolica* or *P. multipunctoides*. [thamnolic acid]

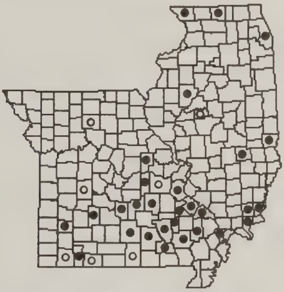
**Pertusaria valliculata** Dibben This is an endemic species with a range essentially confined to the Interior Highlands and southern Appalachian region. In the Ozark region of Missouri and adjacent portions of Arkansas, it typically occurs on the lower and mid-boles of trees in wooded uplands, growing on a wide variety of hardwoods and occasionally on *Juniperus virginiana.*



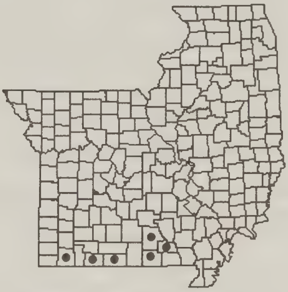
*Pertusaria valliculata* is morphologically and ecologically similar to *P. paratuberculifera,* which is common in the region. Both taxa contain lichexanthone and react UV+ yellow, but *P. paratuberculifera* has 8 smooth-walled spores per ascus, while *P. valliculata* has 4 (rarely 3) strongly ornamented spores per ascus, with strong radial groves on the inside of the inner spore wall. *Pertusaria macounii* and *P. tetrathalamia* have ornamented spores and can resemble *P. valliculata,* but *P. macounii* and *P. tetrathalamia* fluoresce UV+ pinkish. Additionally, local populations of *P. tetrathalamia* display a strong predilection for *Juniperus*. A specimen from Oregon County, Missouri, *Harris 21689* (NY), appears to have the lichexanthone restricted to the warts and contains stictic acid, but otherwise resembles *P. valliculata*. [lichexanthone]

**Pertusaria velata** (Turner) Nyl. Widespread in temperate and tropical regions, locally this is a common species of wooded uplands in the Interior Highlands, in both the Missouri Ozarks and Shawnee Hills of extreme southern Illinois. This species is rare elsewhere in our region. *Pertusaria velata* commonly occurs on lower and mid-boles of hardwood trees, especially oaks, and less commonly on *Juniperus*, in extensive woodlands under moderate to light shading.

The pale gray thallus with abundant, closely spaced, powdery pruinose warts is distinctive. The thallus of *P. velata* often has a narrow, pale margin. Most of our material lacks lichexanthone and is UV−, but in extreme southern Missouri southward into Arkansas, populations that contain lichexanthone and fluoresce UV+ yellow are occasional to locally common. The lichexanthone-containing element was described as *P. pulchella* Malme. Harris (1990) reported this element from North America, and noted that species with depside/depsidone chemistry commonly have lichexanthone-containing chemotypes in the subtropics or the tropics. Archer and Messuti (1997) consider both chemotypes to be referable to *P. velata*. Local populations of *P. velata* differ from specimens we have seen from Florida in that midwestern material tends to be more diffusely warty, with more of the individual warts expanded into powdery patches. [lecanoric acid, ±lichexanthone]



*P. velata* - lecanoric acid only



*P. velata*- lecanoric acid &
lichexanthone

## Acknowledgments

Appreciation is extended to Richard Harris and Irwin Brodo for their review and advice, and to Ron Oesch and Blane Heumann for their assistance. Much of this paper is based on work conducted in association with the Missouri Ozark Forest Ecosystem Project, supported by the Missouri Department of Conservation.

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## Specimens Cited

One representative specimen is cited for each county, with counties listed in alphabetical order under their respective states. The letter "L" denotes Ladd collections and "W" denotes Wilhelm collections. Unless indicated by a standard herbarium acronym, all specimens are deposited at the Morton Arboretum herbarium (MOR), Lisle, Illinois, including Ladd specimens intended for eventual deposition at MOR.

**Pertusaria amara** ILLINOIS. Clark: *Whiteside s.n. 22 May 1971;* Gallatin: *W 8715*; Johnson: *L 13963;* Union: *Earle s.n., n.d.* (NY). MISSOURI. Carter: *L 20285;* Douglas: *Buck 32082* (NY); Franklin: *L 13872;* Iron: *Harris 31114* NY); Oregon: *L 7544;* Ozark: *L 17133;* Phelps: *L 17531;* Ste. Genevieve: *W 22687;* Shannon: *L 14108;* Warren: *L 10623.*

**Pertusaria globularis** MISSOURI. Oregon: *Buck 15903A* (NY).

**Pertusaria hypothamnolica** ILLINOIS. Alexander: *Fried s.n. 28 Sep 1978;* Gallatin: *W 16914;* Marion: *Nyboer s.n. 27 Sep 1975;* Williamson: *Basinger 9288.* MISSOURI. Barry: *L 14625;* Boone: *L 15871;* Camden: *Jones 13* (MCJ); Carter *L 20570;* Christian: *L 9170;* Crawford: *W 20009;* Douglas *L 21194;* Gasconade: *W 17659;* Hickory: *L 7712;* Howell: *L 1738;* Iron: *Harris 31117* (NY); Lincoln: *L 19393;* Oregon: *Harris 40545* (NY); Ozark: *L 20206;* Phelps: *L 16305;* Pulaski: *L 12564;* St. Francois: *Harris 25476* (NY); Ste. Genevieve: *W 22689;* Shannon: *L 19596;* Stone: *W 15660;* Taney: *Harris 40687* (NY); Washington: *L 13455;* Webster: *L 8019;* Wright: *L 15017.*

**Pertusaria macounii** ILLINOIS. Cook: *Calkins 78* (NY). MISSOURI. Douglas: *Buck 32074* (NY); Maries: *Summers 3940;* Shannon: *Harris 25817* (NY).

**Pertusaria multipunctoides** MISSOURI. Mississippi: *W 13375;* Shannon: *L 20720;* Texas: *L 16287.*

**Pertusaria neoscotica** ILLINOIS. Fulton: *Wolf s.n. 1888* (NY). MISSOURI. Carter: *Buck 31809* (NY); Phelps: *L 17956;* Stone: *L 12412.*

**Pertusaria ostiolata** ILLINOIS. Johnson: *W 19044;* Pope: *Harris 31362* (NY); Saline: *W 16775;* Union: *Basinger 9163a;* MISSOURI. Bollinger: *L 12888;* Butler: *L 14185;* Carter: *L 19716;* Christian: *L 9171;* Iron: *Harris 31140* (NY); Oregon: *Harris 21704* (NY); Reynolds: *Buck 24210* (NY); Ripley: *L 18391;* Shannon *L 19599*; Taney *Harris 40649* (NY).

**Pertusaria paratuberculifera** ILLINOIS. Effingham: *W 18045;* Franklin: *W 22224a;* Johnson: *W 19049;* Pope: *W 22142;* Union: *Basinger 9163b.* MISSOURI. Bollinger: *L 12921;* Boone: *Berry 304c* (UMO); Carter: *L 20291;* Cole *L 12802;* Dunklin: *L 14174;* Gasconade: *W 17636;* Howell: *L 11861;* Iron: *Harris 31169* (NY); Jefferson: *L 12660;* Oregon: *Harris 21692* (NY); Ozark: *L 17139;* Phelps: *L 17513;* Shannon: *L 8659;* Ste. Genevieve: *L 19166;* Taney: *Buck 32044* (NY); Texas: *L 16286;* Wayne: *L 11750.*

**Pertusaria plittiana** ILLINOIS. Calhoun: *Jones 2311;* Gallatin: *W 13705;* Hardin: *W 16801;* Jackson: *Harris 31273* (NY); Johnson: *W 22110;* Macoupin: *McClain 129;* Peoria: *W 18614;* Pope: *W 17783;* Union: *Earle s.n. 1880* (NY); Williamson: *W 19182.* MISSOURI. Callaway: *L 11140;* Carter: *L 11794;* Cedar: *L 6497;* Christian: *L 9113;* Crawford: *W 20000;* Dade: *L 12078;* Douglas: *L 21093;* Iron: *L 14425;* Jefferson: *L 17937;* Montgomery: *L 10631;* Oregon *L 20141;* Ozark: *L 17115;* Phelps: *L 17517;* Polk: *L 6776;* Pulaski: *L 16272;* St. Clair: *L 17740;* Ste. Genevieve: *W 22674;* Shannon *L 20666;* Vernon: *L 13145.*

**Pertusaria propinqua** ILLINOIS. Franklin: *W 22212;* Fulton: *Haines s.n. n.d.* (NY); MISSOURI. Audrain: *L 9946;* Barton: *L 19784;* Benton: *L 13524;* Carter *L 20544;* Cedar: *L 19777;* Christian: *L 12036;* Cole: *L 12817;* Henry: *Forbes 2104;* Oregon: *Buck 31924* (NY); Ozark *L 20213;* Phelps: *L 17545;* Reynolds *L 21023;* St. Clair: *L 17736;* Shannon *L 19587;* Vernon: *L 16213.*

**Pertusaria pustulata** ILLINOIS. Adams: *Jones 2067;* Brown: *Jones 2046c;* Carroll: *Jones 2689;* Champaign: *W 18015;* Cook: *Calkins 79;* Effingham: *W 18043;* Fayette: *W 17100;* Ford: *Hyerczyk 1075;* Franklin: *W 22209;* Fulton: *Haines s.n. n.d.* (NY); Gallatin: *W 13681;* Hardin: *W 17892;* Jackson: *Harris 31298* (NY); Johnson: *W 19048;* Kendall: *W 13956;* Lake: *W 14225;* Lee: *Jones 2856;* Livingston: *Hyerczyk 881;* Ogle: *Jones 1719;* Pope: *W 17767;* Putnam: *Jones 3939;* Saline: *W 16560;* Shelby: *Harris 21810;* Stephenson: *Jones 1308;* Union: *Harris 31413* (NY); Warren: *W 19657;* White: *W 22356;* Winnebago *Jones 2435.* MISSOURI: Audrain: *L 17033;* Barton: *L 19783;* Boone: *L 15848;* Butler: *Summers 3139;* Carter: *L 19519;* Cooper: *Nee 11092;* Crawford *L 11939;* Douglas: *L 15500;* Franklin: *Harris 31112* (NY); Greene: *Summers 1720;* Grundy *W 16121;* Harrison *W 15880;* Henry *L 13920;* Holt *W 15951;* Howell *Summers 2308;* Jefferson: *L 14241;* Lewis: *L 13538;* Mississippi: *W 13384;* Moniteau: *W 15749;* Montgomery: *Darigo 2798;* Nodaway: *W 15913;* Oregon: *L 20105;* Phelps: *W 15585;* Ralls: *W 15554;* Reynolds: *L 14118;* Ripley: *Summers 3126;* Saline: *L 13950;* St. Charles: *L 12723;* St. Clair: *Buck 15728* (NY); St. Francois: *L 12103;* Ste. Genevieve: *L 11375;* Scotland: *L 17210;* Shannon *L 20725;* Sullivan: *L 14361;* Washington: *L 13429;* Wayne: *L 11756;* Worth: *W 15906.*

**Pertusaria subpertusa** MISSOURI. Carter: *L 19739;* Oregon: *L 20148;* Shannon *L 20689.*

**Pertusaria tetrathalamia** MISSOURI. Camden: *L 6931;* Carter: *L 19529;* Douglas *Harris 40716* (NY); Iron: *L 17667;* Oregon: *Harris 40528* (NY); Ozark *Harris 40640* (NY); Phelps: *L 17851;* Reynolds: *Harris 31236* (NY); Shannon: *L 19662;* Stone: *W 15623;* Wayne: *L 17089.*

**Pertusaria texana** ILLINOIS. Gallatin: *W 16927;* Hardin: *W 18758;* Jackson: *Harris 31297* (NY); Johnson: *W 19081;* Pope: *W 17932.* MISSOURI. Barry: *L 13099;* Benton: *L 13526;* Cape Girardeau: *L 16195;* Carter: *L 20307;* Cedar: *L 19778;* Christian: *L 12037;* Crawford: *W 20011;* Laclede: *L 13406;* Oregon: *L 21050;* Ozark *L 20198;* Phelps: *L 17753;* St. Clair: *Harris 21295* (NY); Shannon: *L 17199;* Stone: *L 12366;* Wayne: *L 17095.*

**Pertusaria trachythallina** MISSOURI. Carter: *Harris 25642* (NY); Shannon: *L 14109.*

**Pertusaria valliculata** ILLINOIS. Clark: *McKnight 1056.* MISSOURI. Barry: *L 13111;* Boone: *L 15879;* Camden: *Dewey 4;* Carter: *L 19709;* Cole: *L 11990;* Douglas *Harris 40717* (NY); Gasconade: *W 17690;* Henry: *L 13915;* Iron: *Harris 31175* (NY); Maries: *L 8560;* Moniteau: *L 12484;* Morgan: *L 9997;* Oregon: *Harris 21721* (NY); Perry: *Demetrio 18* (NY); Phelps: *L 8389;* Ste. Genevieve *Harris 25971* (NY); Shannon: *L 18709;* Stone: *L 12418;* Warren: *L 10617;* Wayne: *L 17105.*

**Pertusaria velata** [lichexanthone lacking] ILLINOIS. Alexander: *Basinger 9197;* Clark: *McKnight 857;* Cook: *Calkins 80;* Effingham: *W 16454;* Fulton: *Haines s.n. n.d.* (NY); Gallatin: *W 8735;* JoDaviess: *Jones 2950;* Pope: *Hatcher 1334s;* Saline: *W 16764;* Winnebago: *Jones 2606.* MISSOURI. Bollinger: *L 12922;* Carter: *L 20313;* Crawford: *W 20013;* Dade: *L 12057;* Dallas: *L 9988;* Gasconade: *W 17588;* Iron *Harris 31121* (NY); Jefferson: *L 17921;* Montgomery *L 8146;* Perry *Demetrio s.n. April 1886* (NY); Phelps *L 17528;* Pulaski *L 8165;* Reynolds *Apfelbaum 266b;* St. Francois: *Harris 40744* (NY); Ste. Genevieve *W 13641;* Shannon *L 13644;* Stone *W 15659;* Texas *L 16285;* Wayne *Summers 3162.*

**Pertusaria velata** [with lichexanthone] MISSOURI. Barry: *L 13101;* Carter: *Harris 25696* (NY); Oregon: *Harris 21705* (NY); Ozark: *L 17120;* Shannon: *L 19416;* Taney: *Harris 40666* (NY).

**Table 1: Diagnostic Characters for *Pertusaria*[1]** [modified from Dibben (1980)]

| Species | UV | K | C | KC | P | Spores |
|---|---|---|---|---|---|---|
| *amara* |  | ± yellow →red$^{m}$ |  | + violet$^{m}$ | ± yellow →orange$^{m}$ | 1 |
| *globularis* | ± weak yellow-pink |  |  |  |  | 2 or 4 |
| *hypothamnolica* | + yellow | ± yellow →violet$^{m}$ |  | + rose/violet$^{m}$ |  | 1 |
| *macounii* | ± pink/orange | + yellow$^{m}$ |  | ± weak yellow | + yellow →orange$^{m}$ | 1-2 (3-4)° |
| *multipunctoides* |  | ± yellow →brown$^{m}$ |  |  | + yellow →red$^{m}$ | 1 |
| *neoscotica* |  | + yellow →red$^{m}$ |  |  | + yellow →orange$^{m}$ | (1) 2 |
| *ostiolata* | ± weak orange-pink |  |  |  |  | 8 |
| *paratuberculifera* | + yellow | ± weak yellow |  | ± weak yellow |  | 8 |
| *plittiana* |  | + yellow →red$^{m}$ |  |  | ± yellow →orange$^{m}$ | 0-2 |
| *propinqua* |  | + yellow →red$^{m}$ |  |  | + yellow →orange$^{m}$ | (4 or 6) 8 |
| *pustulata* | + pinkish orange | + yellow$^{m}$ | + yellow | + yellow-orange | + yellow →orange$^{m}$ | (1) 2 (3) |
| *subpertusa* | ± weak pinkish | ± yellow →red$^{m}$ |  |  | + yellow →red$^{m}$ | (1) 2 |
| *tetrathalamia* | ± weak orange-pink | + weak yellow$^{m}$ |  | ± weak yellow | + yellow →orange$^{m}$ | 2-5° |
| *texana* | + orange-red | ± yellow | + yellow | + yellow-orange | ± yellow →orange$^{m}$ | (6) 8 |
| *trachythallina* |  | + deep yellow$^{m}$ |  |  | + yellow →orange$^{m}$ | 0-2 |
| *valliculata* | + yellow | ± weak yellow |  | ± weak yellow |  | 2-5° |
| *velata* | ± yellow |  | + red$^{m}$ | + red$^{m}$ |  | 1 (2) |

[1] description applies to cortex unless superscripted by an "m", for medulla

° denotes notable ornamentation on the inner spore wall

*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
IN HONOR OF JOHN W. THOMSON.
EDS: M. G. GLENN, R. C. HARRIS, R. DIRIG & M. S. COLE.
MYCOTAXON LTD., ITHACA, NY. 1998.

# A MONOGRAPH OF *LECANORA* SUBG. *PLACODIUM* SECT. *ARCTOXANTHAE* (LICHENIZED ASCOMYCOTINA)

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**ABSTRACT:** The systematics of the known species of *Lecanora* subg. *Placodium* sect. *Arctoxanthae* Ryan, characterized by rosulate to lobate thalli containing only xanthones and occurring on Arctic or boreal coasts, are treated. Chemotypes of *L. straminea* with an *O*-methylated trichloronorlichexanthone (granulosin) as a major substance (plus or minus non-*O*-methylated xanthones) appear to be restricted to Pacific regions, while the typical chemotype, with arthothelin as the major substance and lacking *O*-methylated xanthones, occurs in both Atlantic and Pacific areas. The species is reported here for the first time from Japan. Rare chemotypes of *L. straminea* containing thiophanic acid as a major substance from the Pacific coast of North America are also reported in this article. The considerable variability in *L. straminea* shows only partial correlations with chemistry and distribution. *Lecanora perconcinna,* from Japan, contains thiophanic acid as the major substance. *Lecanora microbola*, originally described from eastern Canada, differs from *L. perconcinna* especially in having more extensive and irregular thalli with a strongly maculate surface, somewhat narrower paraphyses, and containing arthothelin as the major substance. Collections of *L. microbola* other than the holotype differ from it especially in having rather irregular and scattered thalli.

## INTRODUCTION

*Lecanora* sect. *Arctoxanthae* Ryan was described in Ryan & Nash (1997) for rosulate to lobate species containing only xanthones and found on Arctic to boreal coasts. The purposes of the present treatment are to give detailed information on the morphology, chemistry and distribution of three species, their variability, and their similarities and differences.

This article is dedicated to Dr. John W. Thomson, who has encouraged and aided me since I first began research on lichens over two decades ago, and who has contributed greatly to our knowledge of the lichens of Arctic and other regions.

## METHODS AND TERMINOLOGY

Unless noted otherwise, the methods and terminology used in this paper are as described by Ryan (1989a, 1989b). Colors (followed by numbers in parentheses), as viewed through a dissecting scope with fiber optic lighting, refer to the system of Kelly

(1965). Scanning electron microscopy (SEM) of *L. straminea* and the Waghorne 107 collection of *L. microbola* was done at the Smithsonian Institution (results mentioned in the text but not illustrated).

To be consistent with my previous articles, I have retained the terminology originally recommended to me by the late professor Poelt, but to avoid confusion it is especially important to remember that in these articles "hypothecium" = excipular tissue below hymenium, while "subhymenium" = the ascogenous layer.

Chemical analyses of most specimens were made by the author using standard thin-layer chromatographic (TLC) method of Culberson (1972) modified as described by Ryan (1989a). Selected specimens were analyzed by C. Leuckert using both TLC (including spraying of solvent system C plates with anisoaldehyde-sulphuric acid, and two additional solvent systems: chloroform: acetone 4:1 sprayed with P, and chloroform: methyl ethylketone 3:1, sprayed with water), and mass spectroscopy. In most cases, co-chromatography with specimens analyzed by Leuckert was used by the author for identifying at least the major xanthones in the other specimens.

In the specimen citations, specimens are on rock unless noted otherwise; * = TLC'd by Ryan; ** = analyzed by TLC and mass spectroscopy by Leuckert; unless noted otherwise, other specimens were not analyzed chemically.

## SYSTEMATIC TREATMENT OF KNOWN SPECIES

***LECANORA* SECT. *ARCTOXANTHAE* Ryan in Ryan & Nash, Nova Hedwigia 64: 115 (1997). Type Species:** *Lecanora straminea* Ach.

**THALLUS** rosulate to lobate; **lobes** distinct, radiating or irregular; **upper surface** usually ± yellowish brown, epruinose or sometimes pruinose, often pale maculate; **upper cortex** ± irregular and interrupted, composed of rather conglutinate hyphae, usually forming thick bundles that penetrate deeply into the algal layer and connecting with the medulla, with occasional scattered dead algal cells, at least the upper part inspersed with fine yellowish granules soluble in C and K; **algal layer** loose, interrupted, often penetrating fairly deeply into medulla; **medulla** whitish to yellowish, sometimes brownish towards base, moderately loose to rather dense (as seen in SEM, ± uniform in consistency, hyphae distinct, sometimes rather strongly interwoven, but not conglutinate), with or without yellowish granules (soluble in K) or grayish granules (insoluble in K); **lower cortex** developed at least towards lobe tips, similar to upper one but thinner and more uniform.

**APOTHECIA** adnate to sessile or substipitate; **discs** mostly various shades of brown, to brownish black, epruinose to densely pruinose, pruina fine, ± whitish; **thalline margins** usually ± persistent; **proper margins** often visible between disc and thalline margin; **cortex** thicker at base, hyphae conglutinate; **algal layer** ± well developed in margin and below hypothecium, uneven, interrupted; **medulla** sometimes with yellowish granules; **parathecium** sometimes differentiated, of ± parallel hyphae; **hypothecium** hyaline to yellowish or orangish, bowl-shaped to broadly conical, of variously oriented, strongly conglutinate hyphae, lumina rounded to elongated, 0.5-1 μm wide; **subhymenium** hyaline to yellowish or brownish; **hymenium** hyaline; **epihymenium** brown, not inspersed, but sometimes with surface granules; **paraphyses** ± coherent in water, free in K, simple to furcate, septate, with cylindrical cells, with one or two apical cells clavate to globose, tips brownish; **asci** clavate, typical *Lecanora*-type, with amyloid apical dome, moderately wide non-amyloid axial mass, and (at least when immature) ocular chamber; **spores** ± ellipsoid, wall c. 0.75 μm thick.

**SPERMOGONIA** immersed (sometimes in small bumps); **spermatia** filiform, ± curved, over 12 µm long; **fulcra** acrogenous.

**SPOT TESTS:** Thallus P-; **cortices** K± yellow, C+ yellow to orange, KC+ orange to reddish orange; **medulla** K± yellow or K-, C-, KC-, or C+ yellowish orange, KC+ reddish orange.

**CHEMISTRY:** Containing xanthones (chlorinated norlichexanthones, sometimes *O*-methylated) as the only lichen substances. Thin-layer chromatography data for the section are given in Table 1.

**ECOLOGY AND DISTRIBUTION:** On rocks (usually non-calcareous), nitrophilous, in coastal areas, Arctic to boreal.

**DISCUSSION:** The apparently very few and disjunct specimens of members of *Lecanora* sect. *Arctoxanthae* in NE Asia and NE Canada (both rather distant from the main centers of distribution in Europe [including Iceland and Greenland] and NW North America) may be relicts from pre-Pleistocene times, and the lack of recent collections (since at least the 1940's) suggests that the section (and perhaps the two rare species) may be extinct in those outlying areas. However, collections of crustose lichens from seashore rocks at least in many parts of North America appear to be rather few (or perhaps not yet curated or identified and therefore not easily seen in herbaria), and so far I have had the opportunity to examine only a very few collections from Japan.

The section appears to be a natural one, which may well eventually deserve to be recognized at the genus level. However, I feel that, as with other groups of placodioid *Lecanorae*, such segregation is premature at this stage.

## Key to Known Species of *Lecanora* sect. *Arctoxanthae*

1. Thallus to 1-3(-5) mm thick in center, often ± loosely attached; main lobes 0.5-1.5 mm wide (but branches sometimes less than 0.5 mm wide); upper cortex inspersed only in upper parts, hyphae ± anticlinally oriented and long-celled even near surface; medulla ± loose, without yellowish granules, C-; lower cortex usually extensive. Apothecia to 1.5-2.5(-4) mm diam.; hypothecium often ≥ 100 µm thick, yellowish to yellow-orange. Circumarctic with boreal-oceanic extensions, common. .................... 1. *L. STRAMINEA*

1. Thallus to 0.5(-1) mm thick, tightly attached; main lobes 0.2-0.5 mm wide; upper cortex inspersed throughout, hyphae ± irregularly oriented and short-celled well below surface; medulla dense, with yellowish granules, C+ orange; lower cortex present only near lobe tips. Apothecia to 0.5-1 mm diam.; hypothecium mostly ≤ 80 µm thick, ± hyaline. Boreal-oceanic, very rare. .......................................................................................... 2

    2. Thallus to c. 1.5 cm across, forming regular rosettes; center of angular areoles; upper surface at most weakly maculate; upper cortex 40-80 µm thick, with epinecral layer. Apothecia ± numerous; parathecium to 30 µm thick; paraphyses 2-2.5 µm thick below; spores mostly 5-6 µm wide. With thiophanic acid as the major substance. Japan. .................................................... 2. *L. PERCONCINNA*

    2. Thallus to 2-4 cm or more across, often irregular or scattered; center of tiny roundish granules grouped into larger units; upper surface ± strongly maculate; upper cortex 15-40 µm thick; epinecral layer absent. Apothecia very rare; parathecium absent or ≤ 10 µm thick; paraphyses 1.2-1.5 µm thick below; spores mostly 4-5 µm wide. Containing arthothelin as the major substance. Eastern Canada and southern Alaska. ............................................... 3. *L. MICROBOLA*

Table 1. Thin-layer chromatography (TLC) data for identified secondary metabolic products (xanthones) in *Lecanora* sect. *Arctoxanthae* (in **bold**) and standard control substances (in normal type and in brackets). $R_F$ classes (with + or - to indicate relative position within those classes) in solvent systems A, B', and C are given (with absolute $R_F$ values, when known, given below them in parentheses). * = after spraying with acid and heating. UV = fluorescence in long wavelength ultraviolet (color given only when distinctive); UV* = fluorescence in long wavelength ultraviolet after spraying and heating. Data come from Elix, et al. (1989, 1991), and Elix & Crook (1992). For some of the substances, the fluorescence after spraying and heating may differ from that given here, due to factors such as concentration of the substance (in particular, in my TLC arthothelin appeared to be UV*+ red to orange, sometimes with a greenish outer ring); in the case of xanthones fluorescence prior to spraying is more critical (Leuckert & Knoph, 1992).

| SUBSTANCE | SOLVENT SYSTEMS | | | CHARACTERISTICS |
|---|---|---|---|---|
| | A | B' | C | |
| [atranorin] | 7<br>(75) | 7<br>(73) | 7<br>(79) | orange*, UV+, UV*+ orange |
| **granulosin** (4,5,7-trichloro-6-*O*-methylnorlichexanthone) | 6-<br>(63) | 5-6<br>(56) | 6-<br>(60) | red-brown*, UV+ red, UV*+ dull orangish, C+ red-orange |
| **thiophanic acid** (2,4,5,7-tetrachloronorlichexanthone | 5+<br>(55) | 5-6<br>(52) | 5+<br>(49) | pale brown*, UV+ orange-red, UV*+ pale brown |
| **arthothelin** (2,4,5-trichloronorlichexanthone) | 5-<br>(43) | 5<br>(40) | 5<br>(37) | orange*, UV+ orange, UV*+ green |
| **4,5-dichloronorlichxanthone** | 5-<br>(44) | 5+<br>(48) | 4-5<br>(33) | pale orange*, UV+, UV*+ green |
| **2,4-dichloronorlichexanthone** | 5<br>(49) | 5<br>(43) | 4<br>(30) | pale yellow*, UV+, UV*+ green, C+ pale red |
| [norstictic acid] | 4<br>(40) | 4<br>(32) | 4<br>(30) | yellow*, UV+, UV*+ yellow |
| **5-chloronornorlichexanthone** | 4<br>(40) | 5<br>(46) | 3<br>(25) | pale yellow*, UV+, UV*+ green, C- |
| **4-chloronorlichexanthone** | 3-4<br>(38) | 5-<br>(43) | 3<br>(23) | yellow*, UV+, UV*+ green, C+ pale red |
| **norlichexanthone** | 3+<br>(35) | 5<br>(40) | 2<br>(11) | pale yellow, UV+, UV*+ bright blue |

**1. *LECANORA STRAMINEA* Ach.**, Lichenogr. Univers. 432 (1810) (α; excl. ß [which = *Dimelaena oreina*]) (Figs. 1-8 in present article).

**TYPE:** (from protologue): "ad saxa in summo cacumine alpium Septentrionalium juxta Mare glaciale. [on rock on top of northern mountain near the Arctic sea]. *Wahlenberg.*". **NORWAY: Finnmark:** "Nord Kap" (= Nordkapp), 1802, G. Wahlenberg, lectotype (chosen here) (H-ACH 1017!*).

[*Parmelia straminea* Wahlenb. in Ach., Meth. Lich. Suppl. 47 (1803), nom. inval. pro. syn.--*Lichen stramineus* ("Wahlenb.") Wahlenb., Flora Lappon. 417 (1812)--*Lichen peltatus* * *Lecanora straminea* ("Wahlenb.") Lam., Encycl. Method. Bot. Suppl., Vol. III, 133 (1813)--*Squamaria straminea* ("Wahlenb.") Nyl., Annal. Scienc. Nat. Bot., ser. 4, vol. II: 153 (1855); *Placodium stramineum* ("Wahlenb.") Th. Fr., Nova Acta Reg. Soc. Scient. Upsal., ser. 3, vol. 3, 185 (1860)--*Placolecanora straminea* ("Wahlenb.") Räsänen, Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo, 18: 29 (1943)].

*Parmelia stramineum* ("Wahlenb.") Th. Fr. f. *glaucescens* Branth, Medd. Grønl. 3: 476 (1887). **TYPE** (from protologue): **GREENLAND:** "Godthåbs-Fjord" (not seen).

**THALLUS** usually rosetted, to (1-)2-5(-9) cm across, sometimes dying in center, often coalescing, firmly to loosely attached; **thallus center** (0.3-)1-3(-0.5) mm thick, of verrucae c. 0.5-1 mm across, uneven, verruculose, knotted or finely divided, sometimes forming ascending and overlapping lobes; **lobes** usually radiating, contiguous and separated by steep-sided cracks, to overlapping or discrete and divergent, usually highly convex to terete, to 2-7(-14) mm long, 0.5-1.5 mm wide, (0.3-)0.5-0.8(-1) mm thick, often with transverse cracks, towards tips often dilated and somewhat flattened, sometimes crenate or divided dichotomously or palmately to less often pinnately, branches ± parallel and straight-sided, 0.5-2 x (0.3-)0.5-1 mm; **upper surface** mostly finely warted, pitted, or corrugate, at least toward center usually rather strongly maculate, often scabrid or crystalline-pruinose (salt crystals also sometimes present), matt to slightly shiny; central parts usually pale greenish yellow (104) to grayish yellow (90) or pale yellow (89), in herbarium becoming moderate yellow (87), yellowish brown (74-80), or orangish yellow (71-73), or sometimes partly olive brown (94-96), dark grayish olive (111), olive gray (113), brownish gray (64), dark reddish gray (23), or dark gray (266), when maculae or pruina abundant appearing light orangish yellow (70), pale yellow (89), yellowish gray (93), yellowish white (92), grayish blue (185-187), or dark bluish gray (187); maculae 0.1-0.2 mm across, roundish to oblong or irregular, plane or slightly elevated, appearing to be associated with thin areas of the cortex, pale orangish yellow (73), pale yellow (89), yellowish white (92), or light bluish gray (190), or sometimes strong yellowish brown (74); peripheral parts often light or moderate yellow (86-87), in herbarium becoming yellowish brown (75, 77-78, 80-81), strong or moderate brown (55, 58), light olive brown (94), grayish reddish orange (39), or brownish orange (54); lobe tips sometimes dark brown (59); **lower surface** brownish black (65) to brownish orange (54), near edge yellowish brown (74-75) or paler; **upper cortex** very irregular, (20-)50-100(-150) μm thick, hyphae ± anticlinal and long-celled throughout, especially towards base with elongated lumina c. 1 μm wide, forming distinct bundles extending to 200 μm or more and partly connecting with medulla; upper 25-65 μm inspersed with yellowish granules, lumina near surface partly shorter and to 1.5-2 μm wide, epinecral layer 5-15(-30) μm thick; **algal layer** strongly interrupted, (50-)100-150(-200) μm thick, algae (6-)10-15 μm; **medulla** ± loose, without yellowish granules, hyphae variously oriented, 2-4(-7) μm thick, lower part decaying; **lower cortex** usually extensive, to 25(-50) um thick, ± dark brown.

**APOTHECIA** few and scattered to often numerous and loosely aggregated or crowded, adnate to constricted sessile or substipitate, to 1.5-2.5(-4) mm diam., mostly in thallus center, primordia tuberculate, often common even when mature apothecia lacking; **discs** usually concave then ± plane, often corrugated and scabrid/roughened or with radiating reticulate cracks, matt to shiny, moderate to reddish orange (37-38), reddish brown (40, 43-44), brown (55-56, 58, 59, 62), brownish black (65), or deep yellowish brown (75), sometimes with thin to dense, whitish, yellowish, or bluish pruina especially towards center or when fairly young, appearing light brownish grey (63), when wet paler, brownish orange (54) or deep reddish brown (41); **thalline margin** (0.1-)0.2- 0.5(-0.7) mm wide, often ± raised and inflexed at least when young, entire to flexuous and undulate, striate to crenulate, irregularly crenate (especially towards inside), or sublobate or interrupted, usually thinner and lower with age but ± persistent, concolorous with thallus or darker when young, dark grayish yellowish brown (81), pale yellow (89) to light orangish yellow (70), matt, often with maculae; **proper margin** narrow to moderately wide, moderate- or dark grayish- yellowish brown (77, 81), light olive brown (94), or light reddish brown (42); **cortex** ± uneven, laterally (20-)35-50 µm thick, with epinecral layer in upper part, outer part inspersed with yellowish granules, lower part to 50-100(-200) µm thick, outermost 5-10 µm grayish brown; **algal layer** strongly interrupted, to 180-300 µm thick below hypothecium; **medulla** dense near cortex, looser inside; **parathecium** to 60 µm thick in margin, intergrading with cortex, yellowish-orangish; **hypothecium** (50-)150-250(-400) µm thick; upper part pale yellowish, lower part yellow-orange; **subhymenium** (40-)60-75(-90) µm thick; **hymenium** (50-)60-80(-90) µm high; **epihymenium** 15-20 µm thick, often with granular surface layer to 5-10 µm thick (partly soluble in K, insoluble in $HNO_3$); **paraphyses** ± contorted, 1.5-2(-2.5) µm thick below; tips to 2.5-4(-6) µm thick, ± yellow-brown, K+ paler; **asci** (45-)60 x 10-15(-20) µm; apical wall c. 5-6 µm thick; **spores** (8-)10-12(-14) x (4.5-)5.5-6.5(-8) µm, ± ellipsoid, L:W = (1.4-)1.6-2.2(-2.6).

**SPERMOGONIA** often very numerous and conspicuous, immersed in somewhat raised bumps; **ostiole** moderate reddish brown (43) to brownish black (65); **cavity** 130-175 µm deep, 80-150 µm wide; **spermatia** (15-)20-25(-30) µm long; **fulcra** occasionally branched; basal cells oblong, 7-14 µm long, 2.5 µm wide, spore-bearing cells oblong, c. 7-12 µm long and 1-1.5 µm wide.

**SPOT TESTS:** Thallus P-; **cortices** K± pale yellow, C+ yellow to orange, KC+ orange; **medulla** K± pale yellow, C-, KC- [Note: occasional apparently positive medullary reactions are probably due to rapid diffusion of the cortical reactions through rather thin thalli, or possibly to abnormal pigment distribution in thalli regenerating from damage].

**CHEMISTRY:** The chemistry of this species in Europe was discussed by Eigler & Poelt (1965), Santesson, 1967, 1969-a,-b,-c,-d,-e), and Sundholm (1979). Xanthones reported for this species include arthothelin, 4,5- and 2,4-dichloronorlichexanthones, 4- and 5-chloronorlichexanthones, norlichexanthone, and thiophanic acid (2,4,5,7-tetrachloronorlichexanthone).

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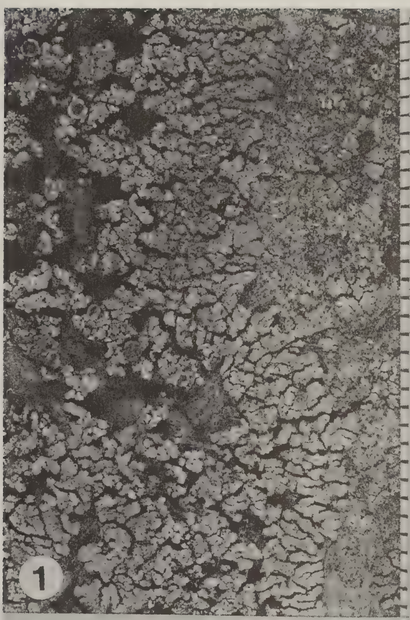
Figures 1-4. *Lecanora straminea.* 1. Part of lectotype, from Norway (H-ACH 1017). 2. A specimen from Alaska (arthothelin major) (Viereck & Bucknell 4124, ALA). 3. Another specimen from Alaska (granulosin major, arthothelin trace) (Nash 13485, ASU). 4. A specimen from British Columbia (granulosin and arthothelin both major) (Brodo 11539, CANL). Scale (Figs. 1-4) = mm.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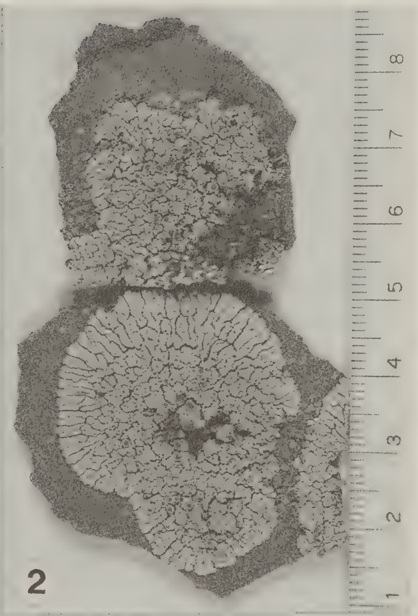
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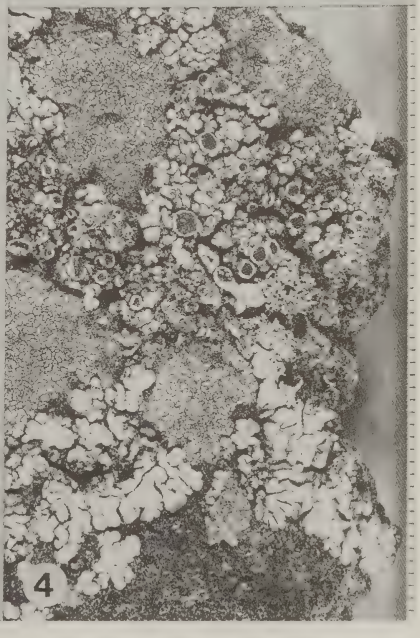

4

In the present study, two additional substances were found by Leuckert, in material from western North America: granulosin (2,4,5-trichloro-6-*O*-methylnorlichexanthone, 6-O-methylarthothelin), and an unidentified O-methyldichloronorlichexanthone. In my own TLC, I also found minor or trace amounts of various unidentified substances (presumably all xanthones, except for contaminants from other lichens, e.g., anthraquinones or pulvinic acid derivatives from associated orange or yellow lichens), which seem to occur sporadically, in some TLC runs and not in others, using the same thallus fragment.

Based on Leuckert's results, the chemical variation worldwide can be classed into three major chemotypes: 1) (typical, i.e., found in the lectotype): arthothelin (major), usually with 4,5- and 2,4-dichloronorlichexanthones (minor or trace), and sometimes thiophanic acid (trace); 2): granulosin (major), arthothelin minor to trace or apparently absent, dichlorinated norlichexanthones and thiophanic absent or rarely in trace amounts; and 3): arthothelin (major), granulosin (major), 4,5- and 2,4-dichloronorlichexanthones (minor or trace).

My own TLC indicates that a few specimens from NW North America belong to additional major chemotypes: 4) thiophanic acid (major), unknown [contaminant?]; 5) thiophanic acid (major), arthothelin (major), 4,5- and 2,4-dichloronorlichexanthones (minor).

**DISTRIBUTION:** The species is circumarctic with oceanic-boreal extensions (Figs. 5-8), from Norway (including Svalbard), to NW Russia, British Isles (at least the Outer Hebrides), Iceland, Greenland, E Canada, Alaska to British Columbia, and NE Asia.

Reports of *Lecanora straminea* from Labrador (Arnold, 1896; Ahti, 1978) and of *L. muralis* v. *garovaglii* from "Labrador or Newfoundland" (Eckfeldt, 1895, Macoun, 1902) are based on Waghorne specimens (no collecting numbers cited), which were identified as *L. straminea* by Arnold. Of the Waghorne specimens seen by me, Waghorne 107 is *L. microbola*, while Waghorne 304 is quite typical *L. straminea.* The positions for these collections on my maps are at best rather rough guesses, but the sites were probably somewhere between the St. Lawrence River in Quebec and the SW tip of Labrador.

**Erroneous or unconfirmed literature reports, not on my maps:** Reports from southern Norway (Østfold: Fredrikstad (SE of Oslo), and Vestfold: "Laurvig" [= Larvik, SW of Oslo)] (Sommerfelt, cited by Fries, 1871, 1874 and Olivier, 1909) are probably erroneous.

Several reports from NE Siberia are not included in my maps because the identifications and chemistry need to be confirmed: [Chukotskiy Poluostrov]: "Konyam Bay, Lich. Fr. Berh. pp. 49 and 49" (Hue, 1892); "Prope Pitlekai: in insula Idlidlja prope pagum Tjapka; hoc loco etiam ade lignum lecta" (Vainio, 1909). Although the area then known as "Pitlekai" (67°7'N, 173°24'W), is rather far inland, the Almquist collection (S) labelled simply "Prope Pitlekai" would have been coastal, probably on Chukotskiy Poluostrov, which he visited during the same time period.

The report from New England (Tuckerman, 1845) cited a specimen from the White Mountains, New Hampshire (well inland, undoubtedly misidentified). Although Tuckerman mentioned that he had also seen the species "on the coast", the species was not mentioned later by Tuckerman (1882), nor by Fink (1935). The locality for a Willey collection that is indeed *L. straminea,* from "America septentrionalis" (UPS!) may well have been somewhere near the New England coast where Willey lived, but his report from Colorado (Willey, 1874) is based on a misidentification (Shushan & Anderson, 1969). The report from an inland area of the District of Mackenzie, NW Territories of Canada by (Bird, et al., 1981) is also erroneous, although the earlier report from that District by

Richardson (1823) might be correct if the locality was coastal. The identification of the Scotter collection from Bathurst Inlet, NW Territories (Thomson & Scotter, 1983) also needs confirmation.

**ECOLOGY:** The species usually grows on hard siliceous rocks (andesite, basalt, gneiss, granite, granodiorite, quartzite, schist, etc.), on horizontal to vertical surfaces of boulders, fractured and weathered bedrock, etc., less often on limestone, rarely on wood (e.g., Neher specimen from Alaska) or mosses. It usually occurs on the seashore, in the supralittoral (aerohaline) to supralittoral fringe (upper hygrohaline) zone, often in Arctic areas where the sea is frozen part of the year, from near sea level, (0-)5-20 m, occasionally up to as much as 210 m, always in clearly maritime areas. *Lecanora straminea* is highly nitrophilous (often on bird rocks, or surfaces exposed to runoff from turf) and quite frequently occurs with *Xanthoria candelaria*, *Amandinea coniops, and Caloplaca verruculifera.* Other lichens sometimes associated with it include *Acarospora smaragdula*, *Caloplaca marina*, *Candelariella arctica, C. crenulata*, *Lecanora muralis* s. l., *L. aleutica* in Alaska, *Physcia caesia*, *P. tenella*, *Rinodina* spp., and *Xanthoria elegans*, or occasionally *Parmelia saxatilis* or *Umbilicaria* spp. (including *U. hyperborea*), or in Europe *Ramalina siliquosa* agg. Another occasional associate is the green alga *Prasiola.* In the British Isles it occurs rarely, in the *Caloplacetum marinum* community (James, et al. 1977). Lichenicolous fungi on *L. straminea* include *Buellia adjuncta.*

**ADDITIONAL LITERATURE REPORTS:** Andreev, et al. (1996); Clauzade & Roux (1985); Degelius (1937); Duncan (1970); Fletcher (1975); Hansen (1978); Hawskworth & Dalby (1992); Kopaczevskaja, et al. (1971); Lettau (1956); Lynge (1921, 1937); Noble (1982); Poelt (1958); Poelt & Romauch (1977--with drawing of thallus anatomy); Poelt & Vězda (1977); Thomson (1955).

**DISCUSSION:** Although *L. straminea* seems to be a well-defined species, it has a difficult nomenclatural history and is quite variable, especially in morphology and external appearance.

**Nomenclature and typification:** The new *Parmelia* names based on Wahlenberg's material from his expedition in 1802 and published in the supplement to Acharius (1803), are generally regarded (e.g., by Santesson, 1993) as being authored by Wahlenberg in Acharius. However, as indicated by Santesson (1993: 105), *Parmelia straminea* Wahlenb. should be rejected as an invalidly published name, i.e., one that does not exist for nomenclatural purposes, because in the publication Acharius (1803: 47) clearly treated it as a synonym [Art. 34.1 (a, c)] of *Parmelia recurva* Ach. [The latter is a superfluous (hence illegitimate) name for *Lichen incurvus* Pers. (= *Arctoparmelia incurva* (Pers.) Hale)]. The Code [Art. 46.3] clearly indicates that Wahlenberg is not to be included in author citation for this species because even though he supplied the specific epithet he did not provide the name (genus + epithet), *Lecanora straminea*, later published by Acharius (1810: 432). One author cannot publish a name for another while simultaneously rejecting it (that would mean publication of two names for the same taxon, which is not allowable under the rules of the Code). Since *P. straminea* Wahlenb. is invalid, combinations citing it as the basionym are illegitimate. As concluded by Santesson (1993), the protologue for *Lecanora straminea* Ach. is Acharius (1810: 432), in which Acharius validly published *L. straminea* as a new (and legitimate) name by separating it from *Parmelia recurva*, which he retained in *Parmelia.* In this protologue, Acharius gave a diagnosis directly under the name *Lecanora straminea*, then cited "Parmelia straminea *Wahlenberg. secundum specimen missum* [second specimen sent] (*Sub Parmelia recurva* in Meth. Lich. Supplem. p. 47)".

Because the only Wahlenberg specimen of *L. straminea* that was undoubtedly seen by Acharius is the one from Nordkapp in Acharius's herbarium (H-ACH-1017), I have chosen it as the lectotype of the species (this specimen was annotated in 1970 by P. James as the lectotype, but that lectoypification was apparently never published). Additional Wahlenberg specimens collected from Finnmark in 1802 (BM!, GZU!) do not give specific localities, and thus should not be regarded as isolectotypes. The Wahlenberg specimen in UPS (also collected in 1802, but from a different locality in Finnmark, Alta), was annotated as the "type" by Motyka in 1969 and cited by Motyka (1996) simply as the "type" (of *Parmelia straminea*, which he treated as the basionym). Since *P. straminea* is invalid, Motyka's choice does not need to be followed for *Lecanora straminea*.

**Variability:** As in most common placodioid taxa, this species is extremely variable in morphology (thickness and adnation of the thallus; orientation, relationships and dimensions of the lobes; width of the apothecial margin) and in the color and pruinosity of the thallus and apothecia. While some of the variation in *L. straminea* is probably determined genetically, much of it is undoubtedly related to environmental conditions, developmental stages, and (in the case of thallus color) age of the collection. Contrasts between extreme variants, especially thick, loose, and coarsely lobed thalli (perhaps associated with exceptionally nutrient-rich conditions) and thin, tight, and narrowly lobed thalli (including young stages) are often very striking. Likewise, differences in thallus color, from pale greenish (many freshly collected specimens, or from shaded sites) to strongly browned (especially in older collections, or from sunny sites) or distinctly bluish (occasional specimens) can be quite noticeable. The thickness and structure of the cortices and hypothecium also appear to be quite variable, but often difficult to determine due to interdigitation with the algal layer. The height of the hymenium also seems quite variable, depending on how it is delimited from the subhymenium, and on the size of the apothecia and position of the sections; however, I saw no sections in which it approached the value of 120 μm given by Poelt (1958).

Mainly because of its rather small lobes and occurrence in Japan, I originally thought that the tiny bits of material included incidentally in some samples of Kurokawa Exs. 225 (see below under chemotype 2) might be *L. perconcinna*. However the material differs from that species in all critical features (including the strongly maculate upper surface, distinctly anticlinal cortical hyphae with inspersion restricted to a rather thin upper layer, and clearly non-inspersed and C- medulla), and is most likely a young or poorly developed form of *L. straminea*, which has not been previously reported from Japan.

The Almquist collections (all in S) are mostly rather anomalous, at least partly due to parasitism or other external factors. I initially annotated Almquist's specimens from "Peninsula Jinretlen", Cape Rykapiy, and Taymyr I. (all in Siberia), and St. Lawrence I. (Alaska) as *L. microbola*, based especially on what appeared to be a C+ orange medulla (see notes above; unfortunately the slides I made of the Almquist specimens have all been treated with C, so I am unable to determine whether yellowish granules were originally present in the medulla). However, on the basis of other considerations (the partly rather broad (0.5-1 mm wide) main lobes with extensive lower cortex, and in the fertile material the thick hypothecium), these specimens seem to fit much better under *L. straminea*. Therefore, except for the Taymyr I. specimen (listed under "chemotype unknown or uncertain"), I have included these specimens on my maps of the distribution of this species.

In the Almquist specimen labelled simply "prope Pitlekai", which has a clearly C- medulla, the large, very numerous apothecia (obscuring most of the thallus) make the specimen somewhat reminiscent of *Arctopeltis thuleana* Poelt. However, in other respects (e.g., lobate rather than peltate thallus, distinct maculae, concave, pruinose discs, and the anatomy) the material seems to fit well within *L. straminea,* and corresponds to chemotype 3, whereas *A. thuleana* contains only an *O*-methyldichloronorlichexanthone (analysis by Leuckert of a Th. Fries specimen in S).

**Relationships among morphology, chemistry, and distribution:** Many of the specimens containing granulosin as a major substance (chemotypes 2 and 3, both restricted to the Pacific coast) have thicker, more loosely attached thalli and broader, longer lobes than those of material without granulosin (mostly chemotype 1, found on the Atlantic as well as the Pacific coast), or show particular variations that are absent or rare in material lacking granulosin. However, many other specimens of chemotypes 2 and 3 are externally quite similar to material of chemotype 1, while specimens of all chemotypes from Alaska and British Columbia tend to have more loosely attached thalli, more frequently pruinose discs, and other variations not found in Europe.

Among the two granulosin chemotypes, thalli of chemotype 2 more frequently have darker upper surfaces than those of chemotype 3, longer lobes, and more often lack apothecia, but these differences are far from absolute. Although chemotype 3 contains a mixture of the substances found in chemotypes 1 and 2, there is no evidence that it is also morphologically intermediate between specimens of those chemotypes. The thiophanic acid chemotypes are ± similar to other material from Alaska or British Columbia.

Even among specimens from the same region and belonging to the same chemotype, various collections can be conspicuously different from each other, but can also appear quite heterogeneous within themselves. In several cases where thalli of different colors occurred in the same collection (e.g., in Krypt. Exs. Vindob. 2459 and Lynge, both from Honningsvåg, Norway), these different thalli were of the same major chemotype but showed different unidentified minor or trace substances. In material from NW North America, thalli tested from different "duplicates" of some collections (including exsiccati), or even within a given packet, were of different major chemotypes.

**REPRESENTATIVE SPECIMENS (unless noted otherwise, specimens were seen by me and are shown in my maps):**

**Chemotype 1 (typical): arthothelin major; granulosin absent; thiophanic acid absent or trace**

**EUROPE. "Lapponia Orientalis"** [= Finnmark, Norway, or Murmansk Oblast, Russia]: 1863, Fellman 102 (BM).

**BJØRNØYA (BEAR I.):** Bustnes (TROM–not seen; cited by Elvebakk & Hertel, 1997).

**DENMARK: Faeroe Islands (Føroyar):** Strømø [= Streymoy]: Tórshavn Strand, VII.1867, Rostrup (O: L-25016*, UPS).

**NORWAY:** "Norvegica Arctica", Collector? (FH*). **Finnmark:** 1802, Wahlenberg (BM*, GZU); ***Alta*:** 1802, Wahlenberg (UPS*); Bosekop, R. Santesson 20089 (US) and Collector? ("Ex hb. M. N. Blytt") (O: L-24860*); Eibydalen i Alten, Collector? (O: L-24864*); ***Båtsfjord*:** Hamningberg, Spira, Timdal 4735 (O*); ***Gamvik*:** Mehavn, på Gorgos Njargga, 22.VIII.1906, Havås (O: L-24863*); ***Gamvik or Lebesby*:** Nordbø pr. Nordkinn, Norman. (BM, FH, O: L-24871*); ***Kvalsund*:** ad Kvaløysund, Norman (O L-24871*); ***Lebesby*:** 1857, Th. Fries (O: L-24862*, US); Brattholmen, near Lebesy, Th. Fries, Lich. Scand. Exs. 7 (BM, S*, US); ***Loppa*:** Øksfjord, 1897, Baur (O: L-24866*); ***Måsøy*:** Th. Fries (M, UPS, US, S); ***Nesseby:*** N side of Varangerfjorden, 7 km E of Karlebotnhøgda, Poelt 1743 (TLC by H. G. Zigler, Berlin) (GZU); Mortensnes E of Nesseby, along road from Varangebotn to Vadsø, R. Santesson 25284 (GZU); ***Nordkapp***: 1802, Wahlenberg (lectotype, H-ACH-1017); 18.VII.1906, Havås (O: L-24859*); Magerøya: Kjelvik hd., Kamøyvær, Vasviken, Degelius 6951 (TLC by Zigler) (GZU), and 14.VII.1959, Degelius (COLO: L-45577*, O: L-24856*); Magerøya: Honningsvåg: Krypt. Exs. Vindob. 2459 (BM: 2 packets, COLO, H*, MIN*, US), 29.VI.1914, Lynge. (BM, FH*, H**: 2 packets, MIN [ABLS 3565]*, O: L-24861*, L-24872*, US); undated, Lynge (O: L-24867*), and 12.VII.1906, Havås (O: L-24868*); ***Sør-Varanger:*** S side of Varangerfjorden, Bugønes, Magnusson exs. 175 (H*); ***Vadsø:*** 1857, Th. Fries (O: L-24857*, UPS--under *Buellia adjuncta*); 1869, Th. Fries (BM*); Norman (O L-24858*); ***Vardø:*** 1864, Th. Fries (BM: 2 specimens [TLC of one by P. James], FH*, O: L-24865*, S, US); Persfjord, Bakkemoltangen, Haugan 3486 (O*). **Nordland:** ***Bodø:*** Grønholmen, VII.1822, Collector? and Strömmen [= Straumen], X.1922, Collector? (O: 2 collections on 1 sheet: L-24849*); Salstrømen, 30.VIII.1906, Havås (O: L-24581*); ***Flakstad:*** Flakstadøy: Ramberg, 6.VII.1960, Degelius (O: L-24834*); ***Hamarøy:*** 10 km N of Skutvik, Buschardt 16614 (GZU); ***Moskenes:*** Moskenesøy: Sørvågen, fågelholmar utanför kyrkan (= bird islets outside the church), 31.VII.1937, Degelius (MIN 660509*, O: L-24833*, L-24844*); Sørvågen, VII.1924, Lynge (O: L-24843*); ***Narvik:*** Beisfjord, Poelt 11823 (GZU); ***Røst:*** Lofoten, Skomvær fyr, 27.VII.1924, Lynge (O: L-24835*, US); Trenyken: 5.VII.1937, Grønlie (O: L-24839*, L-24848*), and (under the old name Breinyken) 28.VII.1937, Grønlie (O: L-24845*, L-24847*); Vedøya: 17.VII.1937, Grønlie (O: L-24841*), 18.VII.1937, Grønlie (O: L-24837*), and 21.VII.1937, Grønlie (O: L-24838*); Vedøya: 28.VII.1924, Lynge (O: L-24836*, L-24840*); Vedøya: Fågelberg, 2.VIII.1937, Degelius (O: L-24842*); Vedøya: Røstlandet, 4.VIII.1925, Du Rietz (US); ***Vågan:*** R. Santesson (FH); Svolvær, 6.VIII.1936, Almborn (COLO L-61627*, S*); Åstrøya pr. Svolvær, Norman (O: L-24850*); ***Værøy:*** Røssnesvågen, 7.VIII.1922, Du Rietz (FH*); ***Vega:*** Dypingan I., Degelius V-2420 (COLO*); Valladamman; Nesjan: Lyngås; and Hestvikfjellet, Degelius (not seen; cited by Degelius, 1982). **Troms:** ***Karlsøy:*** Tromsøy amt, Mikkelvik, 8.VI.1910, Lynge (O: L-24854*, WIS); ***Karlsøy or Tromsøy:*** "Renøe", Collector? ("ex hb. M. N. Blytt") (O: L-24853*); Ringvassøy, Lynge (O: L-24855*); ***Skjervøy:*** ad insulam Hagsten pr. Skjervø, Norman (O: L-24852*). ***Tromsøy:*** Tromsøysund, Kvaløy: Skulsfjord and Rekvik, R. Santesson 20110 (UPS, under *Buellia adjuncta*; not seen; cited by Hafellner, 1979).

**SVALBARD:** (unspecified localities in W part [Spitzbergen]), Nordenskiöld (not seen; cited by Fries, 1860, 1867; Darbishire, 1909).

**UNITED KINGDOM: Scotland: Zetland (Shetland) Islands:** Fair Isle, near South Haven, above the "Gully", IX.1971, Duncan. (BM); Mainland, near Spiggie Hotel, IX.1961, Duncan (not seen; det. by Poelt and cited by James, 1962); **Outer Hebrides:** Eilean Mhór, Flannan Isles, Gilbert (BM); **St. Kilda:** Wathern (BM). **Northumberland South:** Chirdon Burn, Gilbert (small and fragmentary; not on my map) (BM).

**ICELAND.** SW part: "Steinaklettar", 1897, Jønsson (O: L-25028*). **Isafjarðsýsla:** Hnífsðalur, 18.VIII.1939, Lynge (O: L-25026*); Isafjörður, 17.VIII.1939, Lynge (O: L-25018*, L-25024*); Seljalandsðalur, 17.VIII.1939, Lynge (O: L-25021*, L-25022*); **Norður-Múlasýsla:** Langanesströnd Distr., Skeggjastaöir Farm, Kristinsson 17262 (TLC by Zigler) (GZU). **Snæfellsnessýsla:** 1939, Lynge (O). **Vestur-Skaftafellsýsla:** Hjörleifshöfdi, "Bergvorposten in den Mýradalssandur", Henssen 23190-b (ASU*).

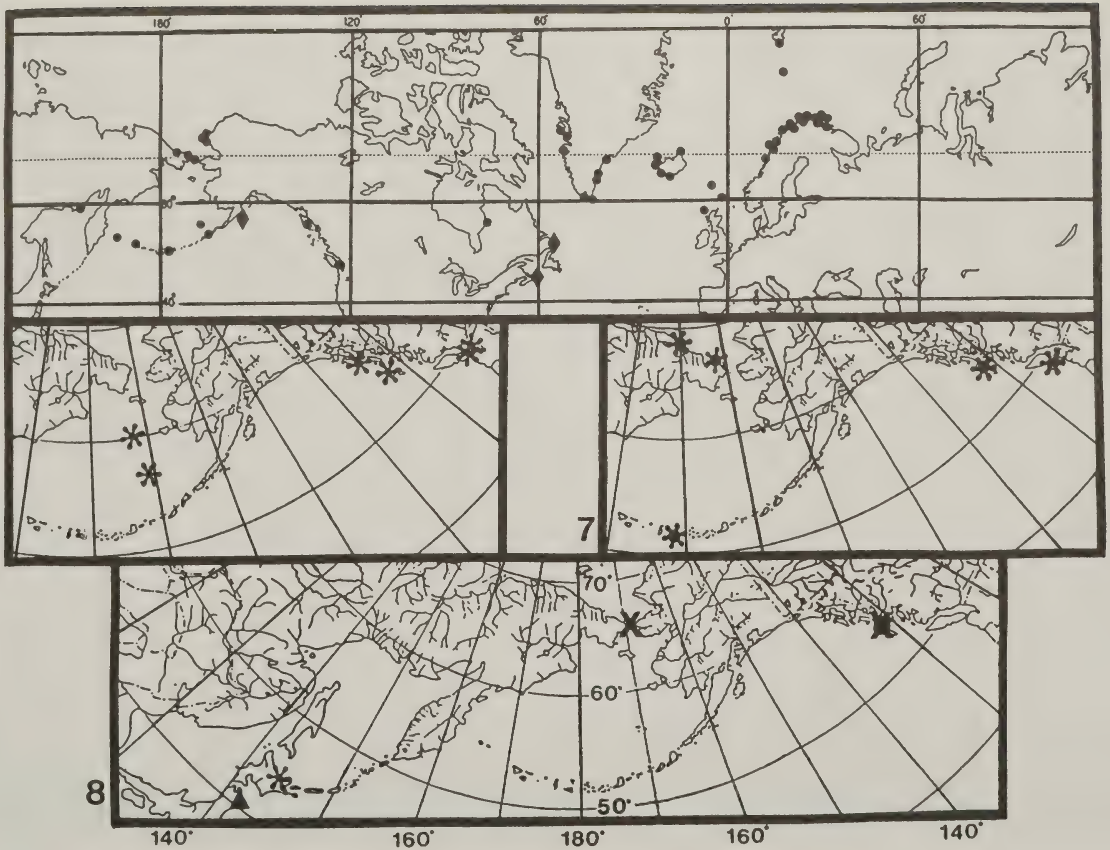
**GREENLAND:** På Klipper ved Havredden" (not seen; cited by Branth, 1887; not on my map). **W. Part: Inanetrok**, 28.VII.1884, Fylla Expedition [probably collected by

Warming and Holm, from "the northernmost part of the Godthaab District and northwards" (Dahl, 1950)] (O*); **Holsteinsborg (Sisimiut):** Kornerup (US); **Isartoq:** *Invarssuaq*, Lich. Groenl. Exs. 250 (ALA, ASU, BM*, C, DUKE**, G, H*, O*, S*, US, WIS); **Disko I.:** gneiss region SW of Godhavn, 28.VII.1983, Poelt & Ullrich (GZU); vicinity of Godhavn, 28.VII.1983, Poelt & Ullrich (GZU: 4 packets); *Malinqiaq*, 7.VI.1871, Th. Fries (C, O*); *Disko Bügt: Rotten (= Numalnaq)*, Gelting 10789 (UPS*), and Lich. Groenl. Exs. 1 (ALA, BM*, C, COLO, DUKE, G, H*, O*, S*, US, WIS); **Brændvinskær**, 69°25'N [on or near Disko I.], 9.VII.1897, Kruuse (O); **S Part: Nanortalik:** III.1885, Eberlin (C, UPS*); V.1885, Eberlin (UPS*); 20.VIII.1885, Eberlin (FH); 4.II.1885, Eberlin (H*), and II.1829, Vahl (UPS*); **Julianehåb [Qaqortoq] Distr.:** Collector? (H-Nyl 28155*); Arpatslvik, Lich. Groenl. Exs. 1147 (BM, C, WIS); Mâjût, Lich. Groenl. Exs.. 60 (ALA, BM*, C, DUKE, G, H*, O*, S*, US, WIS), and Lich. Groenl. Exs. 387 (ALA, BM*, C, DUKE, GZU, UPS*, US); **Kangerdlugssuatsiaq area:** Narsaq Distr.: *Narsaq*, 29.VII.1932, Scholander (O). **SE Part: Angmassalik area:** *Isertoq*: Hansen 1141 (GZU, C); 25.8.1971, Hansen (ASU*, C); **Skjoldungen area:** *Kulusuk (Gerners Øya)*, Hansen (C); *Siorartussoq I.*, Hansen 1545 (C, GZU).

**CANADA. BRITISH COLUMBIA: Vancouver I.:** Discovery I., 3 km E of Oak Bay, Victoria, Crane & Noble 5305 (with trace of thiophanic acid, and with an unknown, probably phenolic, substance [UV+ bright orange after spraying and heating; probably = parietin from *Xanthoria*] (UBC**). **"LABRADOR":** "East of Modeste [Quebec]", Waghorne 304 (US*). **QUEBEC:** Richmond Gulf, E coast of Hudson Bay, island of Wiachewan River, Wiachewan Bay, Marr M-518 (WIS*).

**U.S.A. ALASKA: Arctic coast region (NW part of state, near Chukchi Sea):** *Cape Sabine*, at the Pitmegea River, 13-16.VII.1960, Mårtensson (UPS*); *Cape Dyer*, drainage of Kipaloq and Angowlik Creeks, Viereck & Bucknell 4124 (ALA, COLO*, UAC*, UPS*, US, WIS*); *Ogotoruk Creek*, 30-31.VII.1960, Hultén (S*); Ogotoruk Creek Drainage, on limestone spires on Crowbell Ridge, 210 m, Johnson, Viereck & Melchior 201 (arthothelin, possible traces of a dichloronorlichexanthone and thiophanic acid) (COLO S-26782**) and Johnson, et al. 202 (ALA*, COLO*). **Bering Straits:** *Little Diomede I.*, Porsild & Porsild 1742 (CANL*); *St. Lawrence I.*, 3.VII-2.VIII.1879, Almquist (S*). **St. Matthew's I. (Bering Sea):** 23.VII.1982, Ward (WIS*). **Aleutian Islands:** *Attu I.*: vicinity of Massacre Bay, Casco Cove, Casco Point, Van Schaak 201 (US*); *Kanaga I.*, NW side, Hultén 6489 (UPS*); *Unalaska I.:* Hulten 5592 (UPS*), Hultén 5593 pr. p. (UPS*: one specimen; other one is of chemotype 3); and Hultén 5594 (UPS*); 1880, Bean (US*); VI-VIII.1899, Setchell, et al. (UC 52932*); Dutch Harbor, 27.VI.1976, Neher (WIS*).

**RUSSIA.** "Lapponicum Rossicum" (not seen; cited by Th. Fries, 1860). **Murmansk Oblast: vicinity of Pechenga [formerly Petsamo territory of Finland]:** Vaitolahti [now Vaydaya Guba], 9.VI.1931, Räsänen (H), and 7.IX.1936, Ahlner (S*, UPS**); Kervanto, Maatlivuono, Trifona, Peuravuono, and Iso Heinäsaari [now Ayona I.], Räsänen (not seen; cited by Räsänen, 1943). **Siberia (NE part): Kamtchatkaya Oblast:** *Ostrov Bering [Bering I.]*, E of Kamchatka Peninsula: 14-19.VIII.1879, Almquist (S*). **Magadanskaya Oblast:**. Chukchi A. Okr.: *[Cape] Ryrkaypiy*, 12-13.IX.1878, Almquist pr. p. (one thallus, other one is of chemotype 3) (S*). *"Peninsula Jinretlen" [= Chukotskiy Poluostrov]*: IX.1878-VII.1879, Almquist (S*).


5
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70°
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50°
140°
160°
180°
160°
140°

**Chemotype 2: granulosin major; arthothelin at most minor**

**U.S.A. ALASKA: St. Matthews I. (Bering Sea):** 28.IX.1880, Bean (US*); Bering Sea National Wildlife Refuge, Glory of Russia Cape, 27.VII.1983, Vacca (WIS*), **Pribilof Islands:** *St. Paul's I.*: Hultén 7354 (UPS**); Nash 13485 (ASU*); 9.VII.1899, Trelease & Sanders (US*: 4 packets, including MO 34395 and 30558); *St. George's I.*, on log (wood), Neher (WIS*). **Alexander Archipelago:** *Kuiu I.*: Washington Bay, small rock islet, Eyerdam 1003 (MIN*, G) and Eyerdam 4026 (UPS*, G).

**CANADA. BRITISH COLUMBIA. Gulf Islands:** *S Pender I.*, Gowland Pt., Cursley & Noble 266 (UBC*). **Vancouver I.:** Victoria area, Gauley H-3 (CANL 22463*). **Queen Charlotte Islands:** *Graham I.*, 18 km N of Skidegate Mission and St. Mary's Spring (Lawn Pt.), Lich. Canad. exs. 36 pr. min. p. (specimen in ALA*; specimens in other herbaria analyzed by me are all of chemotype 3).

**ASIA. JAPAN: Hokkaido. Prov. Kitami:** Cliffs along the coast, Shani-Sando, Esashi-guni, 17 Aug. 1970, Kurokawa 70818, Kurokawa, Lichenes Rariores et Critici Exs. 225 (of *Lecanora muralis*, with that species as the main lichen present) (M*, US*).

**Chemotype 3: granulosin and arthothelin both ± major**

**U.S.A. ALASKA: Aleutian Islands:** Amchitka I., beach between Banjo and Crown Reefer Points, Erdman 630-b (with traces of an *O*-methyldichloronorlichexanthone and possible other xanthones) (COLO L-45612**); Unalaska I., Hultén 5593 pr. p. (UPS*: one specimen; other one is of chemotype 1).

**CANADA. BRITISH COLUMBIA: Queen Charlotte Islands:** *Graham I.*: Gudal Bay, Brodo, Shchepanek & Schofield (Brodo 10175) (CANL*), 18 km N of Skidegate Mission and St. Mary's Spring (Lawn Point), Lich. Canad. exs. 36 pr.max. p. (ASU, BM, DUKE, H*, MIN [as Brodo & Shchepanek (Brodo 10050)]*, O*, STU*; specimen in ALA* is of chemotype 2), Seal Inlet in Rennell's Sound, Brodo 10333 (ALA, CANL*); Skidegate Islet, Balch I., (N) entrance of Maude Channel, Brodo & Shchepanek (Brodo 11539) (CANL*, GZU, H**, MIN, WIS*). **Vancouver I.:** Frank I., 10 km S of Tofino, Ohlsson 1098 (ASU*, MSC).

**RUSSIA. Siberia (NE part): Magadanskaya Oblast:** *Chukchi A. Okr.*: [Cape] Ryrkaypiy, 12-,13.IX.1878, Almquist, pr. p. (one thallus; other one is of chemotype 1) (S*); Chukotskiy Poluostrov, "prope "Pitlekai", 28.IX.1878-18.VII.1879, Almquist (S*).

**Chemotype 4: thiophanic acid major; arthothelin absent.**

**U.S.A. ALASKA. Bering Straits:** *Little Diomede I.*, Porsild & Porsild 1743 (CANL*).

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Figures 5-8. Distribution of *Lecanora* sect. *Arctoxanthae.* 1. Chemotype one (arthothelin major) of *L. straminea* (●), and *L. microbola* (◆). 6. Chemotype two (granulosin; arthothelin at most minor) of *L. straminea* (✱). 7. Chemotype three (granulosin and arthothelin both ± major) of *L. straminea* (✱ + ●). 8. Chemotype four (thiophanic acid; without arthothelin) (✖) and five (thiophanic acid and arthothelin both major) (✖ + ●) of *L. straminea*, plus the Japanese collection of chemotype two (✱) of that species, and *L. perconcinna* (▲).

**Chemotype 5: thiophanic acid and arthothelin major**

**CANADA. BRITISH COLUMBIA. Queen Charlotte Islands:** *Graham I.*: Seal Inlet in Rennell's Sound, Brodo & Wong 17409 (CANL*).

**Chemotype Unknown or Uncertain (sites not on my maps):**

**USA: ALASKA: Bering Straits:** *Little Diomede I.*, Porsild & Porsild 1745 (CANL) and Porsild & Porsild 1752 (CANL). **Aleutian Islands:** *Adak I.*: NW coast of Mt. Adagdak, Talbot 637A and S side of Gannet Cove in Expedition Harbor, Talbot 277 (WIS; not seen; cited by Talbot, et al., 1997). **Alexander Archipelago**: *Baranof I.*, 13.VI.1880, Bean (in packet of *L. muralis* s. l.) (US); *Kuiu Is.*: Washington Bay, 4.IX. 1955, Eyerdam 1155 (COLO, G); **Kodiak I.:** 9.VII.1880, Bean (US).

**CANADA. BRITISH COLUMBIA:** Noble 5342 (not seen; cited by Noble, 1982, without specific locality).

**RUSSIA. Siberia (NW part): Krasnoyarskaya Oblast:** *Taymyr (Dolgan-Nenets) A. Okr.*: Ostrov Malyy Taymyr [Taymyr I.], N of Polugstrov Taymyr [Taymyr Peninsula]: "Portius Actiniae" [= Actinia Harbor, 76°19'N, 95°48'E], 14-18.VIII.1878, Almquist (originally annotated by me as *L. microbola*; apparently with unknown xanthones, without arthothelin, granulosin, or thiophanic acid) (S*). **Siberia (NE part): Magadanskaya Oblast:** *Ol'skii region*, c. 4 km SW of Ola, Haugan & Timdal YAK31/07 (O*).

**2. *LECANORA PERCONCINNA* Hue**, Ann. Mycol. 12: 519 (1914) (Figs. 7 and 9-10 in present article).

**TYPE:** (from protologue): **JAPAN. [Honshū: Aomori Prefecture, N end of the island]:** "Hachinohe, April 1899", Faurie 1254, 1290, 1291, syntypes (not seen), Faurie 1245, lectotype (chosen by Ryan & Nash, 1997) (BM!); isolectotype (W!).

**THALLUS** tightly adnate throughout, forming regular rosettes to 1.5 cm wide; **thallus center** areolate or diffract to slightly verrucose but not granular, to 0.3-0.6 mm thick, areoles angular, steep-sided, 0.8-1.2 mm wide, plane to convex or irregular, contiguous but discrete, to rarely dispersed (and then clumped, with rounded elevations); **lobes** tightly crowded, contiguous to subimbricate, 1-1.5(-2) mm long, 0.2-0.3(-0.5) mm wide, to 0.3-0.6 mm thick, weakly to highly convex, towards tips scarcely dilated, rounded, entire to crenate, branching irregular, ± apical, branches 0.2-0.5 x 0.1-0.2 mm; **upper surface** smooth to slightly rugulose, at most faintly maculate near thallus center, slightly shiny, towards center grayish yellow (90) to pale yellow (89), lobes slightly paler than light olive brown (94) or moderate yellow (87), tips dark yellowish brown (78) or dark olive brown (96); **lower surface** yellowish; **upper cortex** somewhat irregular, 40-80 μm thick, rather weakly inspersed throughout with ± scattered clumps of yellowish granules, hyphae in main part irregularly oriented with short cells with lumina 2 μm wide, towards base forming rather few, rather narrow and indistinct hyphal bundles with cells cylindrical, 5-8 μm long, epinecral layer 12-15 μm thick; **algal layer** ± interrupted, c. 30-70(-125) μm thick; algae12-18 μm; **medulla** rather dense, rather weakly inspersed with yellowish granules, hyphae 3-4 μm thick, periclinally oriented but reticulately branched in various directions; **lower cortex** developed near lobe tips, to c. 20 μm thick.

**APOTHECIA** ± numerous, solitary or in groups, 0.5-1 mm diam., constricted sessile; **discs** plane then slightly convex, slightly shiny, bare to weakly pruinose, dark brown (59), brownish black (65), or dark grayish brown (62); **thalline margins** 0.1 mm wide, ± level, entire to somewhat irregular or ± crenulate, slightly shiny, concolorous with thallus, persistent to ± excluded; **proper margins** partly evident, narrow, grayish yellowish brown (80); **cortex** (25-)40 µm thick above, to 40-60 µm thick below, similar to that of thallus, light yellowish brown, not inspersed below; **algal layer** below hypothecium interrupted but rather even, c. 50 µm thick; **medulla** rather dense; **parathecium** to 30 µm thick in margin; **hypothecium** c. 80 µm thick, hyaline, hyphae unoriented to periclinal; **subhymenium** c. 20 µm thick; **hymenium** 60-80 µm high; **epihymenium** c. 15(-20) µm thick, dark brown, covered by thin hyaline layer with surface granules (partly soluble in K, insoluble in $HNO_3$); **paraphyses** straight, 2-2.5 µm thick below, tips capitate, to 4-5 µm wide, yellowish to olive brown, K-, $HNO_3$+ reddish); **asci** 45-50 x 12-14 µm; **spores** (7-)9-11(-13) x (4.5-)5-6.5(-7.5) µm, ellipsoid or occasionally globose, L:W = (1.2-)1.4-2.0(-2.2).

**SPERMOGONIA** sparse, immersed; **ostioles** brownish black (65); **cavity** globose, c. 100 µm diam.; **spermatia** 14-18(-25) x 1 µm; **fulcra** (according to Hue, 1914) "sterigmata" branched, nonseptate, 25-30 x 2-3 µm.

**SPOT TESTS:** Thallus P-; **cortex** K+ yellow, C+ orange, KC+ reddish orange; **medulla** K-?, C+ orange, KC+ reddish orange.

**CHEMISTRY:** Thiophanic acid (major); arthothelin (minor or trace). Although the identification of these xanthones needs to be confirmed by mass spectroscopy, the chemistry of both the lectotype and the isolectotype appears to be identical in TLC, and the isolectotype was co-chromatographed with specimens of other species definitely containing thiophanic acid and arthothelin.

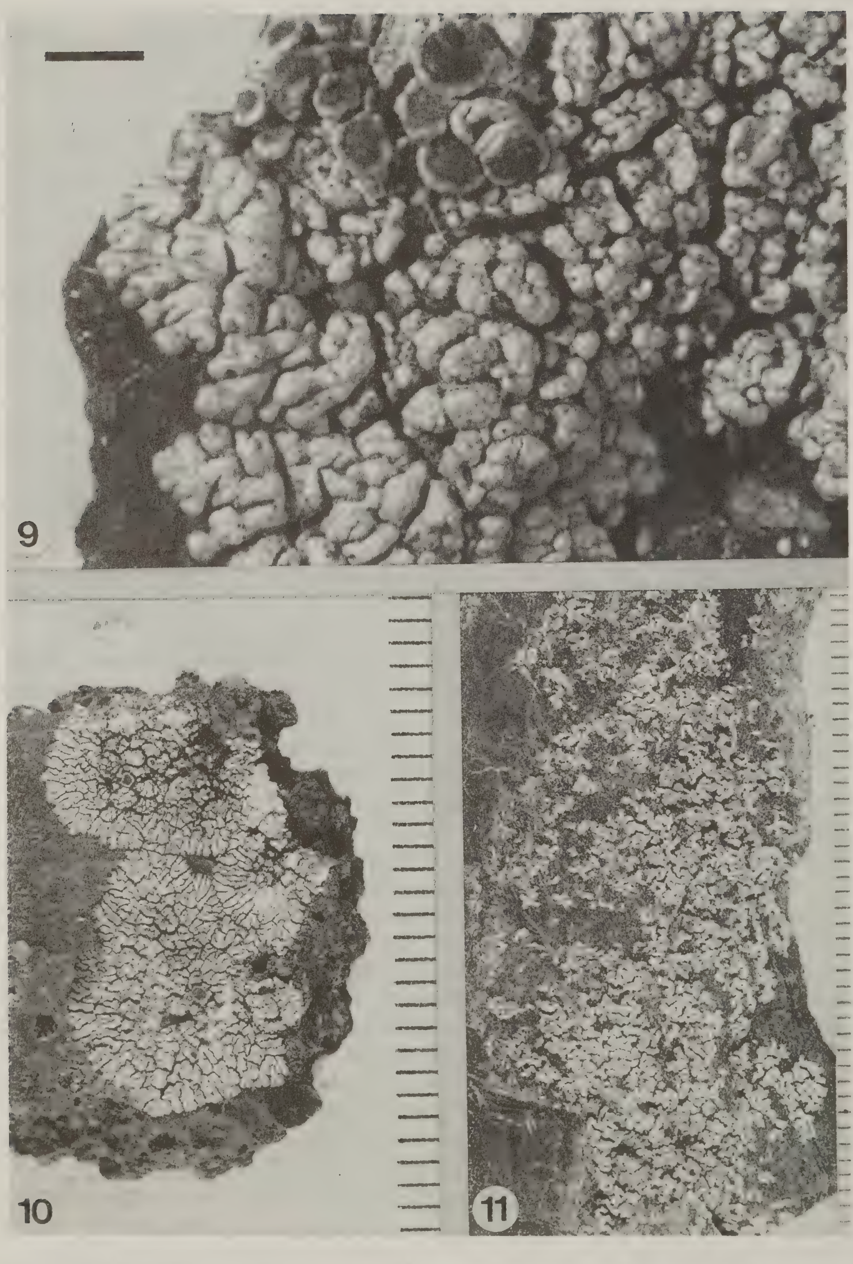
**DISTRIBUTION:** Known only from Japan.

**ECOLOGY:** On noncalcareous rocks on the seashore.

**ADDITIONAL LITERATURE REPORTS:** Poelt (1958).

**DISCUSSION:** Lamb (1977, in a phytogeographical discussion in connection with *Stereocaulon*) mentioned that he had seen the "holotype" of *L. perconcinna* in PC but did not give the specimen number. Although I found a note from Lamb in PC (in the area where specimens determined by Hue are stored) regarding the species, I found none of syntypes. Unless the specimen seen by Lamb was explicitly annotated by Hue as "the" type, it cannot be a holotype. Therefore, unless such a specimen is found, the explicit, published choice of the Faurie 1245 specimens in BM and W (as the lectotype and isolectotype, respectively) by Ryan & Nash (1997) should be followed.

As shown in Table 2, *L. perconcinna* differs from *L. straminea* especially as follows: 1) thallus smaller, thinner, and more tightly attached; 2) thallus center of flatter and more angular areoles; 3) lobes narrower and mostly flatter; 4) thallus center of angular to irregular, often ± plane, areoles; 5) upper surface epruinose and at most weakly maculate; 6) upper cortex thinner, with the hyphae more irregularly oriented and short-celled for some distance below the surface, and ± inspersed throughout; 7) algal layer thinner; 8) medulla denser and inspersed with xanthone granules, C+ orange; 9) apothecia and their tissues smaller; 10) thalline exciple ± level, and becoming ± excluded; 11) hypothecium hyaline; and 12) paraphyses somewhat thicker (though not up to the 3 µm given by Hue). Although the type collection of *L. microbola* is easily distinguished from *L. straminea* externally, the medullary inspersion probably the most critical difference.



Figures 9-11. 9. Close-up of lectotype of *Lecanora perconcinna* (Faurie 1245, BM). 10. Habitus of isolectotype of *L. perconcinna* (W). 11. A specimen of *L. microbola*.from Alaska (Nybakken, US). Bar (Fig. 9 = 1 mm); scale (Figs. 10-11) = mm.

Although I annotated an additional, very small, specimen (Faurie 1589, PC*, from Rishiri-Tō [Rishiri I.]) as *L. perconcinna*, it differs somewhat from the type collection of that species in morphology and color, and apparently also in chemistry (the substances might be granulosin and arthothelin, but appeared to be colorless and UV-, C-, possiibly due to low concentrations or to C reagent that had gone bad). The locality is not shown on my maps, because further material must be studied (and the presence of xanthones confirmed) before conclusive identification is possible. My annotation slip should be removed from the specimen; at present the material is best treated simply as *Lecanora* sp.

**3. *LECANORA MICROBOLA* Lamb**, Natl. Mus. Canada Bull. 132: 291 and plate IV (1954). (Figs. 8, 10 and 11 in present article).

**TYPE: CANADA. NOVA SCOTIA.** Cape Breton Island: Louisbourg, c. 5 m, on a large stone near the seashore, July 19, 1952, Lamb 6897, Holotype (CANL**!).

**THALLUS** tightly attached, forming discrete or confluent, ± orbicular rosettes 2-4 cm or more wide, or ± scattered and irregular; **thallus center** to 0.8-1 mm thick, composed of concrescent granules c. 0.1-0.2 mm wide, irregularly cracked into groups c. 0.5-1 mm across, or partly short lobed; **lobes** radiating, contiguous, not overlapping, to irregularly oriented and divergent, 1.5-3 mm long, 0.2-0.3(-0.5) mm wide, 0.3-0.4 mm thick, ± strongly convex to terete, towards tips not or only slightly broader, rounded, sparingly dichotomously or irregularly branched apically or laterally, branches often sinuous and divergent, 0.2-0.5 x 0.1-0.2 mm; **upper surface** ± even, epruinose, matt or shiny, ± strongly maculate at least towards center, when fresh "sordid stramineous-yellowish", central parts in herbarium grayish olive to olive gray (111-113) or occasionally dark grayish brown (81), or in places dark gray (266) mottled with olive black (114), mostly appearing light yellowish brown (76) due to maculae, or yellow (84, 86-87); maculae slightly raised, pale yellow (89) to yellowish white (92); peripheral parts light to moderate or strong yellow (84, 86-87), moderate yellowish brown (77) or occasionally grayish yellow (90), lobe tips concolorous, or darkened to moderate olive brown (95); **upper cortex** unevenly thickened, basically similar to that of *L. straminea* (as seen in SEM), but the main part mostly 15-40 µm thick, densely inspersed with yellowish granules, hyphae irregularly oriented, short-celled, with lumina 2 µm wide, becoming ± narrowed and anticlinally elongated mainly towards the base, in bundles extending to c. 100 µm deep and partially connecting with the medulla (and sometimes more weakly inspersed in these areas), epinecral layer absent, cells at lobe tips sometimes ± brown-pigmented in outer 6-12 µm; **algal layer** ± interrupted, 65-100(-120) µm thick; algal cells 7-12 µm diam.; **medulla** 65-120(-200) µm thick, rather dense, heavily inspersed with yellowish granules, hyphae variously oriented, 3-4 µm diam.; **lower cortex** developed only near lobe tips, to c. 20 µm thick.

**APOTHECIA:** very rare, 0.2-0.5(-0.8) mm diam., sessile; **discs** plane or slightly concave, epruinose, dark brown (59), brownish black (65), or dark gray (266) or moderate brown (58); **thalline margins** level or slightly raised, to 0.1-0.2 mm wide, smooth, entire or almost, concolorous with thallus, or sometimes pale orangish yellow (73) to yellowish white (92), persistent; **proper margins** absent or narrow, light brown (57); **cortex** similar to that of thallus, 15-25 µm thick above, 25(-70) µm thick below; **algal layer** 25-40(-75) µm thick below hypothecium; **medulla** with fine yellowish granules and sometimes coarse (5-15 µm) crystals (insoluble in K) in lower part; **parathecium** absent or to c. 10 µm thick in margin; **hypothecium** 25-70 (-125) µm thick, ± hyaline; **subhymenium** 20 (-50) µm

Table 2. Comparison of the three species of *Lecanora* sect. *Arctoxanthae* (**bold** = diagnostic features).

| | *L. straminea* | *L. microbola* | *L. perconcinna* |
|---|---|---|---|
| THALLUS | to 2-5 cm or more across, forming rosttes or ± irregular, **often ± loosely attached**. | to 2-4 cm or more across, forming rosettes or ± scattered, tightly attached. | **to 1.5 cm across,** forming regular rosettes, tightly attached. |
| center | strongly convex areoles, verrucae or lobes 0.5-1 mm across, **to 2-3(-5) mm thick.** | granules (0.1-2 mm diam.) or short lobes, concrescent into units 0.5-1 mm across, to 0.3-0.8(-1) mm thick. | **plane to convex, angular areoles** 0.3-0.5 mm across, to 0.3-0.6 mm thick. |
| lobes | 2-7(-14) mm long, **(0.5-)1-1.5 mm wide,** ± strongly convex, branches ± straight sided and parallel, mostly apical, 0.5-2 x (0.3-)0.5-1 mm. | 1.5-3 mm long, 0.2-0.3(-0.5) mm wide. ± strongly convex , branches often sinuous and divergent, often lateral, 0.2-0.5 x 0.1-0.2 mm. | 1-5(-7) mm long, 0.3-0.5 mm wide, plane to ± convex, branches ± straight-sided and parallel, mostly apical, 0.2-0.5 x 0.1-0.2 mm. |
| upper surface | ± strongly maculate, sometimes pruinose. | ± strongly maculate, not pruinose. | **at most weakly maculate,** not pruinose. |
| upper cortex | (20-)50-150(-200) µm thick, **hyphae ± anticlinal ly oriented and ± long-celled, even close to surface, inspersed only in upper parts,** epinecral layer 5-15(-30) µm thick. | 15-40(-100) µm thick, hyphae ± irregularly oriented and ± short-celled well below surface, inspersed ± throughout, **epinecral layer absent**. | 40-80(-150) µm thick, hyphae ± irregularly oriented and ± short-celled well below surface, inspersed ± throughout, epinecral layer 12-15 µm thick. |
| algal layer | (50-)100-150(-200) µm thick. | 65-100(-120) µm thick. | 30-70(-125) µm thick. |
| medulla | **± loose (hyphae very discrete),** without xanthone granules, C-. | rather dense, with xanthone granules, C+ orange. | rather dense, with xanthone granules, C+ orange. |
| lower cortex | **± extensive.** | only near lobe tips. | only near lobe tips. |

Table 2, continued.

| | *L. straminea* | *L. microbola* | *L. perconcinna* |
|---|---|---|---|
| APOTHECIA | rare to often numerous, **1.5-2.5(-4) mm diam.** | very rare, 0.2-0.5(-0.8) mm diam. | ± numerous, 0.5-1(-1.5) mm diam. |
| discs | reddish-, orangish, brownish or blackish, naked to weakly or strongly pruinose, concave then ± plane. | brownish black to moderate brown, naked, slightly concave then plane. | dark brown to brownish black, naked to slightly pruinose, plane then slightly convex. |
| thalline margins | ± crenulate, ± raised when young, ± persistent, often > 0.2 mm wide. | ± entire, ± raised when young, persistent, ≤ 0.2 mm wide. | entire to often crenulate, ± level, persistent to ± excluded, ≤ 0.2 mm wide. |
| proper margins | narrow to moderately wide. | absent or narrow. | ± narrow. |
| apothecial cortex | (20-)35-50 µm thick above, 50-100(-200) µm thick below. | 15-25 µm thick above, 25(-70) µm thick below. | (25-)40 µm thick above, 40-60 µm thick below. |
| parathecium | to 60 µm thick in margin. | absent or to 10 µm thick in margin. | to 30 µm thick in margin. |
| hypothecium | **(50-)150-250(-400) µm thick,** ± yellowish to yellow-orange. | (25-)70(-125) µm thick, ± hyaline. | c. 80 µm thick, hyaline. |
| hymenium | (50-)60-80(-90) µm high. | (50-)60-70(-80) µm high. | 60-80 µm high. |
| paraphyses | 1.5-2(-2.5) µm thick below. | 1.2-1.5 µm thick below. | **2-2.5 µm thick below.** |
| spores | (8-)10-12(-14) x (4.5-)5.5-6.5(-8) µm, L:W = (1.4-)1.6-2.2(-2.6). | (8-)10-11.5 x 4-5(6.5) µm, L:W = (1.4-)1.8-2.3(-2.5). | (7-)9-11(-13) x (4.5-)5-6(-7.5) µm, L:W = (1.2-)1.4-2.0(-2.2). |
| CHEMISTRY | arthothelin, granulosin, or thiophanic acid. | arthothelin (± traces of thiophanic acid). | thiophanic acid (± traces of arthothelin). |

thick; **hymenium** (50-)60-70(-80) µm high; **epihymenium** 6-10(-15) µm thick, reddish brown to dark brown, occasionally with surface granules (insoluble in K); **paraphyses** 1.2-1.5 µm thick below, tips partly capitate, 2-3(-4) µm wide, or embedded in the brown epihymenial gelatin; **asci** 37-45(-55) x 10-12(-14) µm, wall c. 1.5 µm thick; **spores** (8-)10-11.5 x 4-5(-6.5) µm, ± ellipsoid or rarely bean-shaped, L:W = (1.4-)1.8-2.3(-2.5).

**SPERMOGONIA:** immersed, 150-200 µm deep, 100-150 µm wide, ostioles grayish brown (81) or paler; **spermatia** filiform, 15-25 µm long; **fulcra** with spore-bearing cells c. 13 µm long, 1.5-2 µm wide.

**SPOT TESTS:** Thallus P-; **cortices** K± yellow, C+ orange, KC+ reddish orange; **medulla** K-, C+ orange, KC+ reddish orange.

**CHEMISTRY:** The holotype contains arthothelin (major) and a dichloronorlichexanthone, according to TLC and mass spectroscopy by Leuckert. My own TLC showed (in addition to arthothelin as the major substance) traces of both 4,5- and 2,4-dichloronorlichexanthone in the holotype and also in the other collections. In the Nybakken collection I found in addition traces of thiophanic acid and an unknown substance ($R_F$ 2 in solvent systems A, B', and C).

Reports of gyrophoric acid from the holotype (Hale 1956, by microchemical tests; Eigler & Poelt 1965, by paper chromatography) are erroneous. However, I have seen an externally rather similar specimen of what appears to be a *Dimelaena* from the coast of Maine (MSC), containing a C+ red substance that is probably gyrophoric acid, with one small apothecium containing a few brown, 1-septate spores.

**DISTRIBUTION:** The species occurs on boreal coasts of North America (E Canada and S Alaska) and is apparently very rare. In spite of searches for it along the eastern Canadian coast (Brodo, pers. comm., 1986), it has previously been known only from the holotype. I have not yet seen the Talbot 1161 specimen (WIS) from Adak I., Aleutian Islands, Alaska recently cited by Talbot, et al. (1997), and it is not on my map.

**ECOLOGY:** On calcium-free rock near the seashore, without accompanying species, or with *Physcia* cf. *tenella* in Alaskan material.

**DISCUSSION:** Considering the extreme variability exhibited by many placodioid *Lecanorae* (including *L. straminea*), the scarcity and poor development of the material make it rather difficult at present to clearly assess the taxonomic significance of the characters and variations in *L. microbola.* However, until further material of both of the rare taxa is discovered and critically studied, I prefer to treat *L. microbola* as a separate species.

**Relationship to *L. perconcinna*:** *Lecanora microbola* differs from *L. perconcinna* (Table 2) especially as follows: 1) thallus larger, more irregular and sometimes scattered; 2) thallus center of fine, roundish granules or short lobes, forming concrescent masses grouped into areole-like units; 3) lobe branches often sinuous, divergent, and lateral; 4) upper surface ± strongly maculate; 5) upper cortex mostly thinner, and epinecral layer absent; 6) apothecia rarer and smaller, with correspondingly thinner tissues; 7) discs epruinose; 8) thalline exciple entire, somewhat more prominent, persistent; 9) proper margin (parathecium) absent or very thin; 10) paraphyses somewhat thinner; 11) spores more narrowly ellipsoid and somewhat less in width; and 12) containing arthothelin the major substance. Other differences are that in *L. microbola* the lobes tend to be more convex and more discrete (and not overlapping) and the spermogonia (seen in Waghorne 107) have paler ostioles and slightly longer spermatia. In contrast to the statements made by Lamb (1954), *L. microbola* (including the holotype) does have a lower cortex, although it is thin and developed only near the lobe tips.

After seeing "the holotype" of *L. perconcinna* in PC, Lamb later (as mentioned by Lamb, 1977) decided that *L. microbola* was a synonym of that species. It is quite plausible that the two are at least closely related to each other, since (as shown by Culberson, 1972) disjunctive distributions and morphologically or chemically differentiated vicariads of various other lichens between Japan and eastern North America are known, and some species or species pairs occur primarily in those two areas but also in Siberia or Alaska.

*Lecanora microbola* and *L. perconcinna* differ in ways that are mostly subtle or of questionable taxonomic significance, and the geographical gap between them is partly bridged by the Nybakken specimens (discussed below). However, based on the limited amount of material I have seen, the combination of differences in overall dimensions and morphology of the thallus and apothecia, maculation of the thallus (unevenness of the upper cortex), and widths of the paraphyses, in addition to the chemical difference, seems to be sufficient to recognize the two as separate taxa.

**Relationship to *L. straminea*:** This species is distinguished from *L. straminea* (Table 2) primarily by: 1) thallus thinner and more tightly attached; 2) thallus center mostly of fine concrescent granules; 3) lobes and branches shorter and narrower, with the branches often sinuous and divergent, more often arising laterally, 4) upper surface epruinose; 5) upper cortex thinner, with more irregularly oriented and short-celled hyphae well below the surface, ± inspersed throughout, without epinecral layer; 6) algal layer thinner; 7) medulla denser and inspersed with xanthone granules, C+ orange; 8) lower cortex developed only near lobe tips; 9) apothecia and their tissues smaller; 10) discs epruinose; 11) thalline exciple ± entire; 12) hypothecium ± hyaline; and 13) spores narrower.

Most of these features (many of which are shared with *L. perconcinna*) may reflect immature stages or development under certain environmental conditions, rather than the full potential variability of the species. However, taken together they seem to be sufficient to distinguish *L. microbola* from at least the vast majority of specimens of *L. straminea*.

Although occasional mature thalli of *L. straminea* are rather tightly attached, with unusually thin and finely branched lobes (e.g., a Degelius specimen from Flakstad, Norway [O: L-24834]), such thalli are distinctly thickened in the center, with an overall appearance that is rather different from that of *L. microbola*, and often have distinctly larger apothecia. On the other hand, while some specimens of *L. straminea* (including the lectotype and other Wahlenberg collections) include at least a few pieces that are externally rather similar to those of *L. microbola*, those thalli are much smaller than mature thalli of the latter species, and are clearly very young stages, with at most apothecial primordia.

Probably the most critical difference between the two species, which originally led Poelt (1958) to place them in different sections, is the presence or absence of yellowish granules in the medulla (and lower part of the upper cortex), which can be seen clearly even when the distribution of the C reaction is uncertain.

**Variability:** The Waghorne specimens from "Labrador" (see discussion above on the distribution of *L. straminea*) and Nybakken collections from Alaska both differ from the holotype of *L. microbola* in several ways, especially: 1) thallus ± scattered, with lobes more distinctly divergent; 2) upper surface mostly yellowish brown or yellow, with concolorous lobe tips; and 3) apothecia and their tissues somewhat larger.

In addition to the above differences, the Waghorne 107 collection (confirmed as *L. microbola* by Poelt when he saw it in 1987) also differs from the holotype as follows: 1) medulla thicker, becoming brownish in lower part; 2) thalline exciple wider; 3) discs dark gray; and 4) spores slightly wider and more broadly ellipsoid.

The Nybakken material from Alaska is of special interest, because of the considerable disjunction in range (and much closer proximity to Japan). Other features found in this material and not in the holotype include: 1) discs relatively pale brown; 2) thalline exciple partly paler than thallus; 3) proper margin (parathecium) present; and 3) thallus containing an unidentified substance ($R_F$ class 2 in solvents A, B' and C) in addition to arthothelin. However, in most respects the Alaskan material is very similar at least to the Waghorne 107 collection, and the ± scattered thallus and strongly maculate upper surface clearly distinguish it from *L. perconcinna* (at least as seen in the type collection).

**ADDITIONAL SPECIMENS:**

**CANADA: "LABRADOR" (?):** "L'eau Claire", on metamorphic rock, 9.VII.1894, Waghorne 107 (BM, MIN, US*). **U.S.A. ALASKA. Kodiak I.:** Three Saints Bay, 28.VII.1963, Nybakken (BM, US*, WIS).

## EXCLUDED TAXA

*Lecanora straminea* v. *oreina* Ach. = *Dimelaena oreina* (Ach.) Hale & Culb. (Sheard, 1974).

*Lecanora straminea* (Stenh.) Lahm, nom. illeg. (non *L. straminea* Ach.) = *L. symmicta* v. *straminea* (Stenh.) Migula.

*Parmelia saxicola* (Poll.) Ach. *β. plicata* Wallr., Flora Cryptog. German. 3: 486 (1831). This name was listed as a synonym of *L. straminea* by Zahlbruckner (1927-1928), presumably because its protologue listed *"Lecanora straminea* Spreng." as a synonym. However, the description (thallus gray-green, margin plicate-radiate, etc.), and occurrence in Germany, indicate that this is not *L. straminea* Ach.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
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# A PRELIMINARY REVISION OF *PSEUDOPYRENULA* MÜLL ARG. (LICHENIZED ASCOMYCETES, TRYPETHELIACEAE) WITH A REDISPOSITION OF THE NAMES PREVIOUSLY ASSIGNED TO THE GENUS

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## ABSTRACT

The genus *Pseudopyrenula* Müll. Arg. (lichenized ascomycetes, Trypetheliaceae) is revised to consist of four species and one variety. Eighteen names are placed in the synonymy of *P. diluta* (Fée) Müll. Arg. s. lat. Seventy other names previously placed in *Pseudopyrenula* are redisposed necessitating thirteen new combinations: *Arthopyrenia subvelata* (Nyl.) R. C. Harris, *Polymeridium chioneum* (Mont.) R. C. Harris, *Polymeridium sulphurescens* (Müll. Arg.) R. C. Harris, *Pyrenula balia* (Kremp.) R. C. Harris, *Trypethelium basilicum* (Kremp.) R. C. Harris, *T. calosporum* (Müll. Arg.) R. C. Harris, *T. ceratina* (Fée) R. C. Harris, *T. cinereoglaucescens* (Vainio) R. C. Harris, *T. elmeri* (Vainio) R. C. Harris, *T. infossum* (Nyl.) R. C. Harris, *T. pupula* (Ach.) R. C. Harris, *T. trypethelizans* (Nyl.) R. C. Harris and *T. ubianense* (Vainio) R. C. Harris.

The present preliminary treatment of *Pseudopyrenula* Müll. Arg. is another step in clearing the path to a revision of the family Trypetheliaceae. It is an important one in that many of the names ascribed to *Pseudopyrenula* are "lost" here, belonging in other genera of Trypetheliaceae. Further, *Pseudopyrenula diluta* s. lat. has been described many times based on minor variations in the thallus and ascomata, hamathecial pigmentation and ascospore size, resulting in considerable synonymy. At some time in the past twenty years I have seen type material of all but five of the names assigned to *Pseudopyrenula*. These five are tentatively dealt with based on original descriptions or other literature.

*Pseudopyrenula* was described by Müller in 1883 for species that have the dispersed unilocular ascomata of *Pyrenula* Ach. but which have colorless ascospores ("Omnia ut in genere *Pyrenula* sed sporae hyalinae."). Seventeen species were included (only two of which were newly described) but no type species was designated. Nine of these are referable to *Trypethelium* Sprengel as presently constituted, four to *Pseudopyrenula* as accepted here, and one each to *Arthopyrenia* Massal., *Polymeridium* (Müll. Arg.) R. C. Harris, *Pyrenula*

Ach. and *Saccardoella* Speg. In 1885 Müller described *Plagiotrema* believing that it differed from *Pseudopyrenula* in having a laterally positioned ostiole. The type collection is nearly moribund with many ascomata jumbled together growing on top of one another at all angles. While the ostioles are in fact apical, it is easy to understand how Müller might have thought them to be lateral. Vainio (1890) apparently realized, unlike Müller, that based on hamathecial and ascospore characters *Pseudopyrenula* belongs not with *Pyrenula* but with *Trypethelium*. (Also within a single species of *Trypethelium* often there is a continuum from dispersed ascomata to ascomatal complexes included in well developed pseudostromata, i.e., *Trypethelium variolosum* Ach. s. lat.) As a result Vainio synonymized the two genera. Unfortunately he chose the younger name *Pseudopyrenula* for the combined genus which explains why so many of Vainio's names and combinations below have been transferred to *Trypethelium*. Although Vainio chose no type species for *Pseudopyrenula*, it could be argued that his actions should have been considered in selecting a lectotype. However, *Pseudopyrenula* was not formally lectotypified until Clements and Shear (1931) chose *P. diluta* (Fée) Müll. Arg. without discussion or explanation. In consequence the name *Pseudopyrenula* is now applied not in the original "majority" sense = Vainio's sense, but in the sense of a small group of anatomically less complex taxa.

*Pseudopyrenula* is identical in type of hamathecium, ascus and ascospores to most of the rest of the Trypetheliaceae. It differs in having dispersed, simple ascomata (i.e., the pseudostroma is reduced to a single black wall layer) and ecorticate endophloeodal thallus. *Polymeridium* shares these characters but differs in lacking thickened ascospore walls. At this time there is no firm evidence to state positively whether *Pseudopyrenula* and *Polymeridium* are basal or derived (reduced). However, it is my current intuition that the basal groups in the Trypetheliaceae have a very well developed corticate thallus, deeply immersed ascomata (often with lateral or fused ostioles), or ascomata in complex pseudostromata, and large ascospores (often multiseptate). Such taxa seem concentrated in tropical, wet, lowland and premontane forests with the major centers of diversity in Southeast Asia and northern South America. Two groups of Trypetheliaceae have become adapted to dry, tropical-subtropical scrub and forest types. *Pseudopyrenula-Polymeridium* seems to have accomplished this by reduction of presumably moisture- and energy-requiring structures, reducing the thallus to a thin endophloedal layer and the complex pseudostromata to simple, dispersed, unilocular ascomata. The *Trypethelium eluteriae* Sprengel group, often associated with *Pseudopyrenula*, retains well developed pseudostromata and has probably adapted by less visible physiological means. If one were to postulate a taxon basal to *Pseudopyrenula* derived from *Trypethelium*, one would come up with something very near or identical to *T. tropicum* (Ach.) Müll. Arg. which has clustered or scattered, naked ascomata somewhat similar to *Pseudopyrenula* combined with the well developed corticate thallus of *Trypethelium*. For this reason one might wish to merge the genera as Vainio did, but since they are readily separated by the thallus character, I suggest that any action should be delayed until an independent molecular data set is available to test the evolutionary hypothesis suggested above.

The definition of species in *Pseudopyrenula* is based on what I consider to be rather "weak" characters: *Pseudopyrenula saxicola* by its substrate preference, *P. cerei* on a KOH+ yellow pigment in the ascomatal wall, and the other two species, *P. diluta* and *P. endoxantha*, without such "distinctive" characters, on ascospore size. Overlapping ascospore size ranges are a problem throughout the Trypetheliaceae. It is particularly bad in *Polymeridium* (Harris, 1993) where I have recognized complexes of 3–4 taxa with overlapping ascospore sizes. *Pseudopyrenula endoxantha* is treated as a species since its ascospore size seems considerably larger than that of *P. diluta* s. lat. The nasty problem is within *P. diluta* s. lat. I have in the past recognized two species based on ascospore size. There is so much overlap that the sensible solution is to recognize one species with a very broad range. However, this is not an entirely satisfying solution for two reasons, one the combined size range is considerably larger than "normal" and the other is that if one makes a rough graph of ascospore length or width, a broad, vaguely bimodal curve results. Therefore, I have decided to use a new (for me) approach, to treat the ascospore variation at the infraspecific level. This keeps the question of taxonomic status open but also allows any given specimen to be assigned to a species (*P. diluta*) without a great deal of trauma. If one wishes to recognize the smaller spored taxon at the specific level, the correct name is *P. subnudata* Müll. Arg. I suggest that more careful statistical study and correlations with ecology may yet resolve the question.

Occasional specimens of *P. diluta* s. lat. may produce lichexanthone in the thallus. I can see no correlations with any other characters or with geography and feel that lichexanthone is of no taxonomic significance. I have previously likewise abandoned the presence/absence of lichexanthone as a specific character in *Polymeridium* (Harris, 1993) and in *Trypethelium variolosum* Ach. (Harris, 1995.).

Another character which is tempting to use at the species level is the presence or absence of a yellow pigment (KOH+ reddish) in the hamathecium. As with lichexanthone, I can find no correlations and have concluded that is just another variable character within *P. diluta* s. lat. Very rarely the normal colorless hamathecial granules may be lacking. Again I cannot attribute any taxonomic significance to this absence.

## **PSEUDOPYRENULA** Müll. Arg.

Flora 66: 247. 1883. Lectotype (Clements & Shear, 1931): *Pseudopyrenula diluta* (Fée) Müll. Arg.

*Plagiotrema* Müll. Arg., Bot. Jahrb. Syst. 6: 387. 1885. Holotype: *P. cubanum* Müll. Arg. (= *Pseudopyrenula diluta* (Fée) Müll. Arg. var. *degenerans* Vainio).

Thallus not corticate, with *Trentepohlia* in upper layers of disrupted bark cells, mostly UV−, rarely UV+ yellow (lichexanthone). Ascomata perithecioid, uniloculate, solitary or a few "accidentally" fused, with melanized, pseudostromatic wall, on dense bark sometimes extending outward forming a clypeal ring, KOH− or bleeding deep yellow in *P. cerei*. Hymenium trypethelioid, trabeculate pseudoparaphyses (paraphysoids) loosely and regularly anastomosed, mostly inspersed with colorless granules, often with a yellow pigment (KOH+ reddish) throughout or concentrated adjacent to the ascomatal wall. Asci fissitunicate, cylindrical, with a broad, flat apical chamber surrounded by a poorly defined ± refractive ring. Ascospores colorless, distoseptate (median locules ± hexagonal or octagonal in optical section), 4-loculate, not ornamented, with variably developed sheath. Pycnidia subglobose; wall melanized or not. Microconidia rod-shaped, 4–7 × 0.5 μm.

## KEY TO SPECIES

1. Growing on bark or rarely on decorticate wood . . . . . . . . . . . . . . . . . . . 2

2. Ascomatal wall in section KOH− . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3

3. Ascospores 18–35 × 5.5–12 μm; hamathecium yellow pigmented or not; common . . . . . . . . . . . . . . . . . . . . . **_P. diluta_ (Fée) Müll. Arg.**

Ascospores 24–30(–37) × 7–10(–12) μm . . . . . . . . . . . . **var. _diluta_**
Ascospores 18–25 × 5.5–7.5(–8.5) μm . . . **var. _degenerans_ Vainio**

3. Ascospores 37–44 × 10–12 μm; hamathecium yellow pigmented, KOH+ reddish; known only from type collection from Dominica . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . **_P. endoxantha_ Vainio**

2. Ascomatal wall in section bleeding deep yellow in KOH; ascospores 21–32 × 6.5–10 μm; Brazil . . . . . . . . . . . . . . . . . . . . . **_P. cerei_ Vainio**

1. Growing on sandstone; ascomata largely immersed; ascospores 35–45 × 11–13 μm; Brazil . . . . . . . . . . . . . . . . . . . . . . **_P. saxicola_ Malme**

## TAXONOMIC SECTION

***Pseudopyrenula cerei*** Vainio, Étud. Class. Lich. Brésil 2: 212. 1890.
Brazil. Rio de Janeiro, in Cerei, 1885, *Vainio*, Lich. Bras. 121 (holotype TUR Vainio 30815).

Thallus whitish, UV−. Ascomata 0.6–0.9 mm diam., ca. ⅓ immersed, applanate to subglobose; melanized wall entire or lacking below, pigment not obvious but bleeding deep yellow in KOH. Hymenium inspersed, without yellow pigment. Asci cylindrical with eight biseriately arranged spores. Ascospores 4-celled, 23–25 × 6.5–7.5 μm (type collection).

The type collection from Rio de Janeiro and two collections from Santa Catarina have ascospores 21–25 × 6.5–7.5 μm, one from São Paulo and two from Santa Catarina have larger ascospores, 26–32 × 8–10 μm. This parallels the variation in *P. diluta*. I suppose the intelligent thing to do would be to include these specimens in the appropriate variety of *P. diluta* and treat the ascomatal wall pigment as just one more variable character within *P. diluta* s. lat. However, since ascomatal wall pigments are a rare character in the Trypetheliaceae, since there are only six collections known and since there is a name available, I choose to highlight the unresolved questions through maintaining specific status for this Brazilian population.

Additional specimens. Brazil. (Smaller ascospores) Santa Catarina: Ilha de Santa Catarina, Praia do Santinho, 1 May 1980, *Kalb*, Cachoeira Bom Jesus, 3 May 1980, *Kalb*. (Larger ascospores) Santa Catarina: Ilha de Santa Catarina, Restinga am Canal DNOS, 1 May 1980, *Kalb*, Cachoeira Bom Jesus, 3 May 1980, *Kalb* (all hb. Kalb).

***Pseudopyrenula diluta*** (Fée) Müll. Arg. var. ***diluta***

*Verrucaria diluta* Fée, Suppl. Essai Crypt. Écorc. Off. 85, pl. 41, f. 2. 1837.
  *Pseudopyrenula diluta* (Fée) Müll. Arg., Flora 66: 249. 1883.
  Ad cortices Cinchonarum (lectotype G; isolectotype G).
*Verrucaria diremta* Nyl., Ann. Soc. Sci. Fenn. 7: 492. 1863.
  *Pseudopyrenula diremta* (Nyl.) Müll. Arg., Flora 66: 249. 1883.
  Colombia. Villeta, 2000 m, *Lindig 2827* (holotype H-NYL 1033; isotypes BM, FH-Tuck 4086, H-NYL p.m. 7333, M).
*Pseudopyrenula albonitens* Müll. Arg., Flora 66: 271. 1883.
  Brazil. Apiahy, July 1879, *Puiggari 497* (holotype G). See comments below.
*Plagiotrema cubanum* Müll. Arg., Bot. Jahrb. Syst. 6: 387. 1885.
  Cuba. *Wright*, Verr. Cub. 62 (isosyntypes, FH-Tuck 3948, US), Verr. Cub. 65 (isosyntypes, FH-Tuck 3948, H-NYL 1022, US).
*Pseudopyrenula superans* Müll. Arg., Bot. Jahrb. Syst. 6: 408. 1885.
  Cuba. *Wright*, Verr. Cub. 71 (isotypes, FH-Tuck 4090, UPS, US). [Lichexanthone present.] See comments below.
*Pseudopyrenula atroalba* Vainio, Étud. Class. Lich. Brésil 2: 211. 1890.
  Brazil. Minas Gerais, Carassa (1400 m), 1885, *Vainio*, Lich. Bras. 1402 (isotypes BM). (This name is omitted in Zahlbruckner's *Catalogus*.)
*Pseudopyrenula sitiana* Vainio, Étud. Class. Lich. Brésil 2: 213. 1890.
  Brazil. Sitio, 1000 m, 1885, *Vainio*, Lich. Bras. 1089 (isotypes BM).
*Pseudopyrenula erumpens* Müll. Arg., Bull. Soc. Bot. Belg. 32: 170. 1893.
  Costa Rica. Boruca, *Pittier 6300*. See comments below.
*Pseudopyrenula dubia* Vainio, Ann. Acad. Sci. Fenn. ser. A, 6: 354. 1921.
  Guadeloupe. Savane-aux-Ananas, 900–1000 m, *Duss 1496* (holotype TUR Vainio 30831).
*Pseudopyrenula oahuensis* H. Magn., Ark. Bot. ser. 2, 3(10): 234. 1956.
  Hawaiian Islands. Oahu, 1852, *N. J. Andersson* (holotype U).

Thallus normally whitish or grayish, rarely appearing yellowish to tan when the bark is relatively unaltered, ecorticate, UV− (three collections UV+ yellow, lichexanthone). Ascomata highly variable (probably related to substrate density and age), 0.3–1.0 mm diam., immersed to almost entirely exposed, applanate to subglobose; melanized wall entire or lacking below (subglobose ascomata on less dense barks tend to be entire, applanate ascomata on denser barks tend to be open below). Hymenium inspersed, rarely not inspersed, with or without yellow pigment, KOH+ reddish. Asci cylindrical with eight biseriately arranged spores. Ascospores 4-celled, 24–30(–37) × 7–10(–12) μm.

A few anomalous specimens have been tentatively included in *P. diluta* var. *diluta*. Three collections are known lacking hymenial inspersion: Brazil, *Puiggari 1388*; Guyana, *Sipman & Aptroot 18699, 19117*. Three collections produce lichexanthone in the thallus: Cuba, *Wright*, Verr. Cub. 71 (type collection of *P. superans*), *Buck 23359*; Jamaica, *Imshaug 15779* (distributed by MSC as *P. antillarum* sp. nov. [nom. nud.], isotype). Several collections have large ascospores whose size falls between that of *P. diluta* var. *diluta* and *P. endoxantha*: Guadeloupe, *Duss 1496* (type collection of *P. dubia*); Dominica, *Imshaug 33224*; Tobago, *Imshaug 31279A*; Brazil, Sep 1901, *Schiffner*. They are included here pending further study.

*Pseudopyrenula diluta* var. *diluta* is common in the Neotropics at low and moderate elevations from the Greater Antilles to Paraguay. (Although var. *degenerans* occurs in the southern United States, var. *diluta* has not been found in North America.) It is known from a relatively few collections from the Paleotropics and Macaronesia. Specimens have been seen from Cuba, Hispaniola, Jamaica, Puerto Rico, Nevis, St. Lucia, Guadeloupe, Dominica, Martinique, Tobago, Honduras, Costa Rica, Colombia, Venezuela, Guyana, French Guiana, Brazil, Paraguay, Cameroon, Guinea, Ivory Coast, India, Sarawak, New Caledonia, Hawaiian Islands and Azores.

### var. **degenerans** Vainio

*Pseudopyrenula* (subg. *Heterothecium* sect. 3 *Hemithecium*) *diluta* var. *degenerans* Vainio in Schmidt, Bot. Tidsskr. 29: 148. 1909.
Thailand. Koh Chang, Gulf of Siam, 1900, *Schmidt X* (TUR Vainio 30823).
*Pseudopyrenula subnudata* Müll. Arg., Flora 66: 272. 1883.
Brazil. Apiahy, Mar 1880, *Puiggari 138.b* pr. p. (holotype G).
*Pseudopyrenula elliptica* Müll. Arg., Bot. Jahrb. Syst. 6: 409. 1885.
Cuba. *Wright*, e miscellanea segreg. (holotype G).
*Pseudopyrenula flavicans* Müll. Arg., Bot. Jahrb. Syst. 6: 408. 1885.
Cuba. *Wright*, Lich. Cub. II.650 (isotypes BM, FH-Tuck 4090, TUR Vainio 30817, UPS, US, W).
*Pseudopyrenula subgregaria* Müll. Arg., Bot. Jahrb. Syst. 6: 408. 1885.
Cuba. *Wright*, Verr. Cub. 80 (isotypes BM, FH-Tuck 4090, H-NYL 1024, UPS, US, W).
*Pseudopyrenula araucariae* Vainio, Étud. Class. Lich. Brésil 2: 212. 1890.
Brazil. Minas Gerais, Carassa, 1885, *Vainio*, Lich. Bras. 1461 (holotype TUR Vainio 30775).
*Arthopyrenia minutissima* Vainio, Étud. Class. Lich. Brésil 2: 234. 1885.
Brazil. Minas Gerais, Lafayette, 1885, *Vainio*, Lich. Bras. 323 (holotype TUR Vainio 32106).
*Pseudopyrenula endoxanthoides* Vainio, Hedwigia 46: 180. 1907.
Thailand. Gulf of Siam, Koh Chang, 1900, *Schmidt XVI* (holotype TUR Vainio 30829).
*Pseudopyrenula confluens* G. K. Merrill *ex* Hedrick, Mycologia 22: 247. 1930.

Puerto Rico. Near Aibonito, 4 Jan 1916, *Fink 1856* (holotype MICH, isotype FH).

Thallus whitish or grayish, UV− (a few collections UV+ yellow, lichexanthone). Ascomata highly variable (probably related to substrate density and age), 0.3–0.7 mm diam., immersed to almost entirely exposed, applanate to subglobose; melanized wall entire or lacking below (subglobose ascomata on less dense barks tend to be entire, applanate ascomata on denser barks tend to be open below). Hymenium inspersed, with or without yellow pigment, KOH+ reddish. Asci cylindrical with eight biseriately arranged spores. Ascospores 4-celled, 18–25 × 5.5–7.5(–8.5) µm.

As in var. *diluta*, var. *degenerans* may also have occasional thalli that produce lichexanthone, seemingly restricted to the Guianas: French Guiana, *Montfoort & Ek 385*; Surinam, *Zielman 1307*.

The distribution of var. *degenerans* is virtually the same as that of var. *diluta*. Perhaps the only notable difference being its occurrence in the southernmost United States. My perception is that it tolerates drier habitats. It is occasionally even collected growing on cacti. Specimens have been seen from Florida, Louisiana, Texas, Cuba, Cayman Islands, Hispaniola, Jamaica, Puerto Rico, St. Eustatius, Nevis, Dominica, Trinidad, Guatemala, Honduras, Costa Rica, Colombia, Venezuela, French Guiana, Guyana, Surinam, Brazil, Ecuador, Bolivia, Cameroon, Sierra Leone, Zaire, India, Thailand, Sarawak, Malaysia, Hong Kong, Philippine Islands and Hawaiian Islands.

***Pseudopyrenula endoxantha*** Vainio, J. Bot. 34: 292. 1896.
Dominica. Morne Anglais, 15 July 1892, *Elliott* (holotype TUR Vainio 30821; isotype BM).

Thallus whitish, ecorticate, UV−. Ascomata 0.5–0.6 mm, ⅓–⅔ immersed, conical; melanized wall entire. Hymenium inspersed, yellow pigmented, KOH+ reddish. Asci cylindrical with eight, biseriately arranged spores. Ascospores 37–44 × 10–12 µm.

Although the variation in ascospore size within a "species" of *Pseudopyrenula* is considerable, *P. endoxantha* seems far enough out of the normal variation that it deserves recognition. It perhaps should also be included in *P. diluta* as a variety but since it is known from only a single collection and has an available name, it seems overkill to give it a new status at this time.

***Pseudopyrenula saxicola*** Malme, Ark. Bot. 22A(6): 8. 1928.
Brazil. Minas Gerais, São João d'el Rey, 31 Aug 1892, *Malme*, Regn. lich. 239 (lectotype, selected here, S; isolectotype S); Mato Grosso, Serra da Chapada, Bocca da Serra, 18 Mar 1894, *Malme*, Regn. lich. 2553C (syntype, S); Mato Grosso, Serra da Chapada, pr. São Jerenymo, 3 Jun 1894, *Malme*, Regn. lich. 2759 (syntype, S).

Thallus endolithic, a few tiny whitish areas visible between large grains of the sandstone, UV−. Ascomata 0.5–1.0 mm in diam., immersed to weakly emergent, subglobose; melanized wall entire, thick, 75–150 µm. Hymenium inspersed, weakly inspersed or not inspersed. Asci cylindrical with eight, biseriately arranged spores. Ascospores 4-celled, 35–45 × 11–13 µm.

This is the only saxicolous species in the genus and one of the very few saxicolous species in the entire family. The thick ascomatal wall may be a response to the unusual habitat.

In addition to the three localities above, *P. saxicola* is known from two additional stations: Mato Grosso, Serra da Chapada, Buriti, 22 Jun 1894, *Malme s.n.* (S); Mato Grosso do Sul, Serra da Maracaju, zwischen São Gabriel d'Oeste und Rio Verde do Mato Grosso, 430 m, 28 Jun 1980, *Kalb s.n.* (hb. Kalb).

## NAMES ASSIGNED TO *PSEUDOPYRENULA* AND THEIR DISPOSITION
(Accepted names in boldface)

aenea (Eschw.) Vainio, Étud. Class. Lich. Brésil 2: 207. 1890.
    *Verrucaria aenea* Eschw. *in* Mart., Icon. Pl. Cryptog. 15, pl. 8, f. 3. 1828. Brazil. Bahia, Caetité, *Martius* (holotype M).
    ≡ **Trypethelium aeneum (Eschw.) Zahlbr.**
albonitens Müll. Arg. = **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**
    Müller in the original description also described conidia which he attributed to the *Pseudopyrenula*. They are a different collection (*Puiggari 250* in G, WU) and are macroconidia of a *Strigula*. *Pseudopyrenula* is not known to produce macroconidia. *Puiggari 497* (WU, ex hb. Puiggari) with same data as holotype is *Anisomeridium excaecariae* (Müll. Arg.) R. C. Harris.
annularis (Fée) Müll. Arg., Flora 68: 331. 1885.
    *Pyrenula annularis* Fée, Essai Crypt. Écorc. 73. 1824.
    "Habitat in America, ad cortices annosas Cinchona lancifoliae" (isotype? M).
    ≡ **Trypethelium annulare (Fée) Mont.**
annularis var. tuberculosa Vainio, Ann. Acad. Sci. Fenn. ser. A, 6(7): 196. 1915.
    Guadeloupe. Safraga, on *Inga laurina*, *Duss 1415* (holotype TUR Vainio 30778).
    ≡ **Trypethelium tuberculosum (Vainio) R. C. Harris**
antoniae (Krempelh.) Zahlbr., Cat. Lich. Univ. 1: 354. 1922.
    *Verrucaria* (*Pyrenula*) *antoniae* Krempelh., Nuovo Giorn. Bot. Ital. 7: 51, pl. 1, f. 15. 1875. Sarawak. 1866, *Beccari* (lectotype M; isolectotype M).
    = **Trypethelium cinereorosellum Krempelh.**
araucariae Vainio = **Pseudopyrenula diluta var. degenerans Vainio**
atroalba Vainio = **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**
aureomaculata Vaino, Étud. Class. Lich. Brésil 2: 207. 1890.
    Brazil. Minas Gerais, Caraça, 1885, *Vainio*, Lich. Bras. 1473 (isotypes BM, M)
    = **Astrothelium versicolor Vainio**
awajiensis Vainio, Bot. Mag. Tokyo 35: 76. 1921.
    Japan. Prov. Awaji, 5 May 1918, *Yasuda 242* (holotype TUR

Vainio 30380).
≡ **Pyrenula awajiensis (Vainio) Kashiw.**

balia (Kremp.) Müll. Arg., Flora 66: 249. 1883.
*Verrucaria balia* Kremp., Nuovo Giorn. Bot. Ital. 7: 48. 1875. Sarawak. 1866, *Beccari 34* (lectotype M).
≡ **Pyrenula balia (Kremp.) R. C. Harris, comb. nov.**

basilica (Kremp.) Müll. Arg., Flora 72: 68. 1889.
*Verrucaria* (*Pyrenula*) *basilica* Kremp., Bol. Acad. Nac. Ci. Republ. Argentina 3: 126. 1879. Argentina. *Lorentz & Hieronymus* (lectotype M; isolectotype BM).
≡ **Trypethelium basilicum (Kremp.) R. C. Harris, comb. nov.**

bengoana Vainio *in* Hiern, Cat. Afr. Pl. 2(2): 457. 1901.
Angola. Prope Quifandango ad flum. Bengo, Dec 1853, *Welwitsch 437* (isotype BM).
= **Polymeridium subcinereum (Nyl.) R. C. Harris**

bicincta Zahlbr., Repert. Spec. Nov. Regni Veg. 31: 200. 1933.
Formosa [Taiwan]. Rengechi, 30 Dec 1925, *Asahina F304* (holotype W).
= **Trypethelium tropicum (Ach.) Müll. Arg.**

calospora Müll. Arg., Bot. Jahrb. Syst. 6: 409. 1885.
Cuba. *Wright*, Verr. Cub. 234 (isotypes, BM, FH-Tuck 4090, UPS, US, W).
≡ **Trypethelium calosporum (Müll. Arg.) R. C. Harris, comb. nov.**

calospora var. rhodocheila Vainio, Proc. Amer. Acad. Arts Sci. 58: 145. 1923.
Trinidad. La Seiva Valley, 1912–13, *Thaxter 63* (holotype TUR Vainio 30796; isotypes FH, S, W).
= **Trypethelium calosporum (Müll. Arg.) R. C. Harris**
The bright rose-red pigment surrounding the ostiole for which this variety was named is present in the type variety, rendering Vainio's variety superfluous.

catervaria (Fée) Müll. Arg., Flora 66: 248. 1883.
*Verrucaria catervaria* Fée, Essai Crypt. Écorc. 90. 1824.
America meridionalis ad corticem *Cinchonae lancifoliae* (lectotype G).
= **Astrothelium variolosum (Ach.) Müll. Arg.**

ceratina (Fée) Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 30: 29. 1888.
*Pyrenula ceratina* Fée, Suppl. Essai Crypt. Écorc. Officin. 77, pl. 41, f. 3. 1837. In Peruvia ad corticem cichonarum (lectotype G; isolectotype G).
≡ **Trypethelium ceratinum (Fée) R. C. Harris, comb. nov.**

chionea (Mont.) Zahlbr., Cat. Lich. Univ. 1: 355. 1922.
*Verrucaria* (*Pyrenula*) *chionea* Mont., Ann. Sci. Nat. Bot. sér. 2, 19: 58. 1843. French Guiana. *Leprieur 613* (lectotype, selected here, PC-Montagne).
≡ **Polymeridium chioneum (Mont.) R. C. Harris, comb. nov.**
This name is an older name for *Polymeridium pleiomeroides* (Müll. Arg.) R. C. Harris.

cinereoglaucescens Vainio, Bot. Mag. Tokyo 35: 76. 1912.
Japan. Prov. Kozuke, 10 Dec 1917, *Yasuda 197* (holotype TUR Vainio 30813).
≡ **Trypethelium cinereoglaucescens (Vainio) R. C. Harris, comb. nov.**
This species seems closely related to *T. virens* Tuck. in its immersed

ascomata without differentiated pseudostroma, weakly IKI+ violet multiseptate ascospores and temperate distribution. It differs in larger and less aggregated ascomata and in larger ascospores more attenuated at the ends.

composita Vainio, Bol. Soc. Boteriana sér. 2, 177. 1929–30.

Mozambique. Near Palma, 1916, *Pires de Lima 310* (not seen), fide Makhija & Patwardhan (1992).

= **Trypethelium tropicum (Ach.) Müll. Arg.**

concatervata Vainio, Bot. Mag. Tokyo 35: 76. 1921.

Japan. Yokohama, *Maingay* (isotypes BM, FH).

= **Trypethelium virens Tuck.**

confluens G. Merr. *ex* Hedr. = **Pseudopyrenula diluta var. degenerans Vainio**

conica (Müll. Arg.) Müll. Arg., Flora 66: 249. 1883.

*Pyrenula conica* Müll. Arg., Linnaea 63: 43. 1880.

Angola. Secus flumen Quillu, *Soyaux* (holotype G).

= **Saccardoella**. This is a non-lichenized fungus and will be dealt with elsewhere by Sabine Huhndorf.

degenerans Vainio, J. Bot. 34: 292. 1896.

Dominica. Laudat, 1700 ft, *Elliot 912* (TUR Vainio 30782).

≡ **Bathelium degenerans (Nyl.) R. C. Harris**

deightonii Dodge, Ann. Missouri Bot. Gard. 40: 279. 1953.

Sierra Leone. Njala (Kori), on *Peltophorum africanum* v. *speciosum*, *Deighton M4340* (isotype BM).

= **Trypethlium tropicum (Ach.) Müll. Arg.**

diffluens (Nyl.) Müll. Arg., Flora 66: 248. 1883.

*Verrucaria diffluens* Nyl., Ann. Sci. Nat. Bot. sér. 4, 20: 252.1863.

Colombia. Bogotá, 2600m, *Lindig 2770* (isotypes BM, FH-Tuck 3970, M).

= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid.)

diremta (Nyl.) Müll. Arg., Flora 66: 249. 1883.

= **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**

dubia Vainio = **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**

The ascospore size (33–37 × 10–12 μm) is outside the normal range for *P. diluta* and could possibly be given recognition at the varietal or specific level if additional material supports such action. The thallus lacks lichexanthone.

duplex (Fée) Vaino, Étud. Class. Lich. Brésil 2: 208. 1890.

*Trypethelium duplex* Fée, Ann. Sci. Nat. Bot. 23: 437. 1831. ≡ *Trypethelium cascarillae* Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 30(3): 14. 1888.

Ad corticem *Crotoni cascarillae* (lectotype, selected here, G).

= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid.)

duplex var. simplicior Vainio, Bol. Soc. Broteriana sér. 2, 6: 177. 1929–30.

Mozambique. Palma, *Pires de Lima 265* (holotype TUR Vainio 34609).

= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid.)

elliptica Müll. Arg. = **Pseudopyrenula diluta var. degenerans Vainio**

The type is completely sterile as far as I can tell. On the basis of Müller's ascospore measurements it is assigned to P. *diluta* v. *degenerans*.

elmeri Vainio, Ann. Acad. Sci. Fenn. ser. A, 6: 354. 1921.

Philippines. Luzon, Sorsogon, Irosin, 1915, *Elmer 14655* (holotype TUR Vainio 30812; isotype US).

**≡ Trypethelium elmeri (Vainio) R. C. Harris, comb. nov.**

This species is distinctive in the combination of large multiseptate ascospores (13–15-septate, c. 90 × 14 μm), immersed ascomata without any pseudostromatal development and lacking or with poorly developed thalline cortex. I have also seen a collection from Sri Lanka (*Hale 47200*, US).

eluteriae (Sprengel) Vainio, Ann. Acad. Sci. Fenn. ser. A, 6(7): 353. 1921.

*Trypethelium eluteriae* Sprengel, Einl. Stud. Krypt. Gewächse 351. 1804. Type not seen.

**≡ Trypethelium eluteriae Sprengel**

eluteriae var. anacardii (Fée) Vainio, Bol. Soc. Broteriana sér. 2, 6: 177. 1929–30.

*Trypethelium anacardii* Fée, Ann. Nat. Sci. Bot. 23: 430. 1831.

*Trypethelium eluteriae* var. *expallidum* Müll. Arg., Mém. Soc. Phys. Hist. Nat. Genève 30(3): 16. 1888.

In cortice *Anacardii occidentalis* Guadelupensis, *Bertero* (lectotype, selected here, G).

**= Trypethelium eluteriae Sprengel**

eluteriae var. sprengelii (Ach.) Vainio, Bol. Soc. Broteriana sér. 2, 6: 177. 1929–30.

*Trypethelium sprengelii* Ach., Lichenogr. Univ. 306. 1810, nom. superfl.

**≡ Trypethelium eluteriae Sprengel**

eluteriae subsp. subsulphurea Vainio, Étud. Class. Lich. Brésil 2: 205. 1890.

Brazil. Rio de Janeiro, Septiba, 1885, *Vainio*, Lich. Bras. 413 (isotypes B, M).

**= Trypethelium eluteriae Sprengel**

endochrysea Vainio, Étud. Class. Lich. Brésil 2: 206. 1890.

Brazil. Minas Gerais, Caraça, 1885, *Vainio*, Lich. Bras. 1157 (isotypes B, M).

**≡ Bathelium endochryseum (Vainio) R. C. Harris**

endoxanthoides Vainio = **Pseudopyrenula diluta var. degenerans Vainio**

erumpens Müll. Arg. = **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**

Specimen received from G: Costa Rica. Boruca, 1893, *Tonduz*; does not agree with protologue: Boruca, *Pittier 6300*. However, measurements on G specimen agree with protologue. Tonduz collection distributed under Pittier & Durand, Pl. Costa Rica exsicc. number 6300? Such a collection is present at US.

flavicans Müll. Arg. = **Pseudopyrenula diluta var. degenerans Vainio**

follmannii Dodge, Nova Hedwigia 12: 308. 1966.

Chile. Aconcagua Prov., Los Molles, *Follmann 14852-D* (holotype FH-Dodge).

**= Polymeridium subcinereum (Nyl.) R. C. Harris**

galactina Shirley, Pap. & Proc. Roy. Soc. Tasmania 1893: 219. 1894.
Tasmania. St. Crispin's, *Weymouth 113* (not seen), fide Kantvilas (1988).
≡ **Pyrenula galactina (Shirley) Kantvilas**

heterochroa (Mont.) Müll. Arg., Flora 66: 248. 1883.
French Guiana. *Leprieur 20, 64, 66, 444, 450, 452, 470.*
(*452* isosyntype BM. I have seen only a single isosyntype and therefore propose no lectotype.).
= **Trypethelium aeneum (Eschw.) Nyl.**

illota (Nyl.) Vainio, Bot. Tidskr. 29: 149. 1909.
*Verrucaria diluta* Nyl., Bull. Soc. Linn. Normandie sér. 2, 3: 280. 1869 (*non* Fée), *Verrucaria illota* Nyl., Flora 59: 364. 1876.
Guadeloupe. *Husnot 464* (holotype H-NYL 418).
≡ **Lithothelium illotum (Nyl.) Aptroot**

infossa (Nyl.) Zahlbr., Cat. Lich. Univ. 1: 357. 1922.
*Verrucaria infossa* Nyl., Flora 69: 178. 1886.
São Thome. Bom Successo, 1290 m, *Moller* (holotype H-NYL 1034).
≡ **Trypethelium infossum (Nyl.) R. C. Harris, comb. nov.**
The thin-walled ascospores with a weak violet iodine reaction seem to relate *T. infossum* to the American *T. infuscatulum* Müll. Arg. It differs in smaller ascospores and in extremely well developed thalline cortex.

infuscatula (Müll. Arg.) Vainio, Ann. Acad. Sci. Fenn. ser. A, 6(7): 197. 1915.
*Trypethelium infuscatulum* Müll. Arg., Bot. Jahrb. Syst. 6: 389. 1885.
Cuba. *Wright*, Verr. Cub. 175 (isotypes, BM, FH, FH-Tuck 3966, US).
≡ **Trypethelium infuscatulum Müll. Arg.**

infuscatula var. tecomae Vainio, Ann. Acad. Sci. Fenn. ser. A, 6(7): 197. 1915.
Guadeloupe. Près du Camp-Jacob, sur un *Tecoma pentaphylla*, *Duss 1501* (holotype TUR Vainio 30780).
= **Trypethelium scorioides Leighton**

jordanii Dodge, Beih. Nova Hedwigia 12: 11. 1964.
Sierra Leone. Colony, Sugar Loaf Mountain, 610–730 m, *Deighton M4440* (holotype FH-Dodge).
= **Polymeridium quinquesepatatum (Nyl.) R. C. Harris**

limitata Szatala, Ann. Mus. Nat. Hung. n.s. 7: 17. 1956.
"Nova Guinea. Berlinhafen: in insula Seleo, ad ramulum arb. (L. Biró, no. V. 1, 4. VII. 1896.)" (not seen).
Based on the description, assuming Szatala had the genus correct
? = **Pseudopyrenula diluta var. degenerans Vainio**

majuscula H. Magn., Ark. Bot. n.s., 3(10): 233. 1956.
Hawaiian Islands. Oahu, Koolau, Pupukea forest reserve, on *Acacia koa*, 1948, *Fagerlind & Skottsberg 6883a* (holotype S).
= **Pyrenula massariospora (Starb.) R. C. Harris**

myriomma (Nyl.) Müll. Arg., Flora 66: 248. 1883.
*Verrucaria myriomma* Nyl., Ann. Sci. Nat. Bot sér. 5, 7: 346. 1867.
Colombia. Pie de Cuesta, 1200 m, *Lindig 98* (holotype H-NYL 1117; isotypes BM, FH, M, W).
= **Trypethelium annulare (Fée) Mont.**

neglecta Müll. Arg., Flora 68: 332. 1885.

French Guiana. *Leprieur 479* , comm. de Franques, 1879 (holotype G).
= **Trypethelium variolosum Ach.** (Thallus UV−; ascomata trypethelioid)

nitidiuscula (Nyl.) Müll. Arg., Flora 66: 248. 1883.
*Verrucaria nitidiuscula* Nyl., Acta Soc. Sci. Fenn. 7: 491. 1863.
Colombia. Villeta, 1200–2000 m, *Lindig 2829* (lectotype H-NYL 1123; isolectotypes FH-Tuck 3970, H-NYL 1124, M).
= **Trypethelium variolosum Ach.** (Thallus UV−; ascomata trypethelioid. Syn. *Trypethelium nitidiusculum* (Nyl.) R. C. Harris. See Harris, 1995.)

oahuensis H. Magn. = **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**

obvoluta (Nyl.) Zahlbr., Cat. Lich. Univ. 1: 357. 1922.
*Verrucaria obvoluta* Nyl., Acta Soc. Sci. Fenn. 7: 491. 1863.
Colombia. Choachi, *Lindig 809* (lectotype (Aptroot, 1991) H-NYL 1228 (not seen); isolectotypes H-NYL p.m. 7332, M, W).
≡ **Pyrenula obvoluta (Nyl.) R. C. Harris & Aptroot**

ochroleuca (Eschw.) Vainio, Étud. Class. Lich. Brésil 2: 209. 1890.
*Verrucaria ochroleuca* Eschw. *in* Martius, Icon. Pl. Cryptog. 16, pl. 8, f. 3–4. 1828. Brazil. Bahia, Caetité, *Martius* (lectotype M).
= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid. Syn.: *Trypethelium ochroleucum* (Eschw.) Nyl. See Harris, 1995.)

ochroleuca var. effusa (Müll. Arg.) Vainio, Étud. Class. Lich. Brésil 2: 209. 1890.
*Trypethelium ochroleucum* var. *effusa* Müll. Arg., Syst. Bot. Jahrb. 6: 392. 1885. Cuba. *Wright*, Lich. Cub. ser. 2, 566, 568 (isosyntypes H).
= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid.)

ochroleuca var. pallescens (Fée) Vainio, Étud. Class. Lich. Brésil 2: 209. 1890.
*Trypethelium pallescens* Fée, Ann. Sci. Nat. Bot. 23: 440. 1831.
"Surinam ad corticem arboris ignota" (lectotype G; isolectotype G).
= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid.)

ochroleuca var. subdissocians Nyl. *ex* Vainio, Bot. Tiddskr. 29: 147. 1909.
Thailand. Gulf of Siam, Koh Chang, *Schmidt XI* (holotype TUR Vainio 30761).
= **Trypethelium variolosum Ach.** (Thallus UV−.)
This is one of the annoying forms in the *ochroleucum-variolosum/ nitidiusculum-confusum* complex with subastrothelioid ascomata, i.e., with invaginations of the ascomatal wall.

octomera H. Magn., Ark. Bot. ser. 2, 3(10): 234. 1956.
Hawaiian Islands. Lanai, NW part of island, in dry forest on *Notocestrum* twig, 1948, *Fagerlind & Skottsberg 7038, 7112* (syntypes S).
= **Saccardoella**. The disposition of this non-lichenized species will be dealt with elsewhere by Sabine Huhndorf.

papulosa (Nyl.) Müll. Arg., Flora 66: 248. 1883.
*Verrucaria papulosa* Nyl., Ann. Sci. Nat. Bot. sér. 5, 7: 345. 1867.
Colombia. Pie de Cuesta, 1200 m, *Lindig 96* (holotype H-NYL 1127, isotypes BM, FH, M, W).
≡ **Trypethelium papulosum (Nyl.) Makhija & Patwardhan**

pentameria Vainio, Ann. Acad. Sci. Fenn. ser. A, 6: 355. 1921.

Philippines. Luzon, Bataan, Limay, 31 Dec 1909, *Robinson*, Bur. Sci. 9623 (holotype TUR Vainio 30818).
= **Polymeridium albocinereum (Krempelh.) R. C. Harris**
*Polymeridium albocinereum* is mainly American but also known from Africa. This collection extends the range to Asia.

polyphragmia Vainio, Bol. Soc. Broteriana sér. 2, 6: 178. 1930.
Mozambique. Palma, *Pires de Lima 303* (lectotype TUR Vainio 34713).
= **Polymeridium quinqueseptatum (Nyl.) R. C. Harris**

porinoides Müll. Arg., Flora 69: 331. 1885.
*Verrucaria porinoides* sensu Mont., Ann. Sci. Nat. Bot. sér. 2, 19: 59. 1843 (non *Pyrenula porinoides* Ach.). *Verrucaria pupula* sensu Fée, Essai Crypt. Écorc. 73. 1825 (*non* Ach.).
Ad cortices officin. (ex hb. Féeano) (isosyntype? M); French Guiana. *Leprieur 731* (isosyntype NY).
= **Trypethelium pupula (Ach.) R. C. Harris**
I have not yet examined all the syntypes so that the disposition is tentative. The usage of the epithets "porinoides" and "pupula" is badly confused. Müller clearly considered Fée's and Montagne's usages as misidentifications for which he published the replacement name *Pseudopyrenula porinoides*. This view is supported by the fact that Müller treated *Verrucaria pupula* Ach. and *Pyrenula porinoides* Ach. as separate species elsewhere.

portoricensis Hedrick, Mycologia 22: 248. 1930.
Puerto Rico. Near Mayagüez, 16 Dec 1915, *Fink 1025* (holotype MICH).
= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid.)

pudibunda (Mont. & v.d. Bosch.) Zahlbr., Cat. Lich. Univ. 358. 1922.
*Verrucaria pudibunda* Mont. & v.d. Bosch *in* Jungh., Pl. Jungh. 487. 1855. (Type not seen.)
? = **Trypethelium** (a guess based on original description)

pulcherrima (Fée) Vainio, Étud. Class. Lich. Brésil 2: 208. 1890.
*Trypethelium pulcherrimum* Fée, Ann. Sci. Nat. Bot. 23: 450. 1831.
In America ad corticem *Crotoni cascarillae* (lectotype, selected here, G, isolectotype M).
= **Trypethelium variolosum Ach.** (Thallus UV+ yellow; ascomata trypethelioid.)

pupula (Ach.) Müll. Arg., Flora 68: 331, 338. 1885.
*Pyrenula pupula* Ach., Synops. Meth. Lich. 123. 1814.
India Occid. Ad corticem *Cinchonarum* specierum (holotype H-ACH 832).
≡ **Trypethelium pupula (Ach.) R. C. Harris, comb. nov.**

pupuloides Choisy, Mém. Soc. Bot. France 1953–54: 58. 1954.
nom. nov. pro *P. porinoides* "(Nyl.)" Müll. Arg.
= **Trypethelium pupula (Ach.) R. C. Harris**

pustulata Vainio *in* Hiern, Cat. Afr. Pl. 2(2): 456. 1901.
Angola. Ambriz, prope Ambriz ad Calesia antiscorbutica, *Welwitsch 190* (isotype BM).
≡ **Trypethelium pustulatum (Vainio) Zahlbr.**

pyrenuloides Zahlbr. *in* Rechinger, Denkschr. Kaiserl. Akad. Wiss., Math.-

Naturwiss. Kl. 88: 12. 1911. [Solomon Islands.] Buka, in ramis et ramulis Hydrophyti, Sep 1905, *Rechinger 4756* (holotype W).

**= Trypethelium tropicum (Ach.) Müll. Arg.**

quintaria Zahlbr. *in* Handel-Mazetti, Symb. Sinicae 3: 20. 1930.

China. Kweitschou, bei Hwanggoso nächst Dschenning, 1060 m, lebende Stämme von *Antidesmia microphyllum*, 23 Jun 1917, *Handel-Mazetti 10427* (holotype, WU; isotype US).

**= a non-lichenized fungus whose affinities are unknown to me.**

ramosii Vainio, Ann. Acad. Fenn. ser. A, 6: 354. 1921.

Philippines. Luzon, Rizal, Aug 1911, *Ramos*, Bur. Sci 13635 (holotype TUR Vainio 30810).

**= Myriotrema s. lat.**

scoria (Fée) Vainio, Bol. Soc. Broteriana sér. 2, 6: 178. 1930.

*Trypethelium scoria* Fée, Essai Crypt. Écorc. 69. 1824.

America. Ad corticem *Crotonis cascarillae* (lectotype G; isolectotype G).

**= Trypethelium variolosum Ach.** (Thallus UV−; ascomata trypethelioid.)

sitiana Vainio = **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**

sphaerocephala Vainio *in* Hiern, Cat. Afr. Pl. 2(2): 456. 1901.

Angola. Loanda, ad corticum *Sterculiae*, *Welwitsch 191* (isotype BM).

**≡ Trypethelium sphaerocephalum (Vainio) Zahlbr.**

subgregaria Müll. Arg. = **Pseudopyrenula diluta var. degenerans Vainio**

subnudata Müll. Arg. = **Pseudopyrenula diluta var. degenerans Vainio**

subvelata (Nyl.) Müll. Arg., Flora 66: 249. 1883.

*Verrucaria subvelata* Nyl., Expos. Syn. Pyrenoc. 56. 1858.

India. Pondichery, *Perrotet* (lectotype, selected here, H-NYL 743; isolectotypes H-NYL 744, M).

**≡ Arthopyrenia subvelata (Nyl.) R. C. Harris, comb. nov.**

sulphurescens (Müll. Arg.) Müll. Arg., Flora 66: 249. 1883.

*Arthopyrenia sulphurescens* Müll. Arg., Flora 65: 518. 1882.

Australia. Queensland, Toowomba, *Hartmann*, [comm.] F. v. Mueller, 1882 (holotype G).

**≡ Polymeridium sulphurescens (Müll. Arg.) R. C. Harris, comb. nov.**

This is an older name for *Polymeridium oculatum* (Müll. Arg.) R. C. Harris See Harris (1993) for description, discussion and additional synonymy.

superans Müll. Arg. = **Pseudopyrenula diluta (Fée) Müll. Arg. var. diluta**

If one wishes to recognize a taxon with ascospores in the range of 30–35 × 9–11 $\mu$m and lichexanthone in the thallus, this name is available. However, this is the only collection seen with this combination of characters and does not seem worthy of specific recognition. The admixture noted by Müller as *P. diluta* is *P. diluta* var. *degenerans*.

tessella (Pers.) Graff, Mycologia 9: 16. 1917.

*Verrucaria tessella* Pers. *in* Gaudichaud, Voy. Uranie 183. 1827.

"*Gaudichaud*, in herb. Mus. Paris" (not seen).

This tentative disposition is based on Graff's usage as an older name for *Trypethelium ochroleucum* (Eschw.) Nyl.

**? = Trypethelium variolosum Ach.**

thelotremoides (Nyl.) Müll. Arg., Flora 66: 248. 1883.
*Verrucaria thelotremoides* Nyl., Ann. Sci. Nat. Bot. sér. 5, 7: 346. 1867.
Colombia. Río Negro, 1200 m, 1863, *Lindig 51* (holotype H-NYL 1113; isotypes BM, M, W).
≡ **Trypethelium thelotremoides (Nyl.) R. C. Harris**

tropica (Ach.) Müll. Arg., Flora 66: 248. 1883.
*Verrucaria tropica* Ach., Lichenogr. Univ. 278. 1810.
Insulis tropicis India occidentalis, *Swartz* (holotype H-ACH 707A).
≡ **Trypethelium tropicum (Ach.) Müll. Arg.**

trypethelizans (Nyl.) Zahlbr., Cat. Lich. Univ. 1: 359. 1922.
*Verrucaria trypethelizans* Nyl. *in* Crombie, J. Linn. Soc. London Bot. 20: 60. 1883.
Malacca. Tanjong, Apr 1866, *Maingay 149* (lectotype, selected here, BM; isolectotype H-NYL 1226), 253 (syntype BM; isosyntype H-NYL 1226).
≡ **Trypethelium trypethelizans (Nyl.) R. C. Harris, comb. nov.**

uberina (Fée) Vainio, Ann. Acad. Sci. Fenn. ser. A, 15(6): 353. 1921.
*Porina uberina* Fée, Essai Crypt. Écorc. 83. 1824.
Peruvia. Ad cortices *Cinchonarum* variarum specierum (holotype G; isotypes G, fide Aptroot, 1991).
≡ **Architrypethelium uberinum (Fée) Aptroot**

ubianensis Vainio, Ann. Acad. Sci. Fenn. ser. A, 15(6): 353. 1921.
Philippines. Ubian Island, 12 Oct 1906, *Merrill 5403 pr. p.* (holotype TUR Vainio 30798).
≡ **Trypethelium ubianense (Vainio) R. C. Harris, comb. nov.**
This species is part of a complex of Asian taxa with rather small multiseptate ascospores of which I have not seen enough material to explicate properly .

verrucosa Vainio, Ann. Acad. Sci. Fenn. ser. A, 6(7): 198. 1915.
Guadeloupe. Prope Camp Jacob, ad corticem *Syagri coccodis*, *Duss 1394* (TUR Vainio 30797).
= **Trypethelium tropicum (Ach.) Müll. Arg.**

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# THE LICHENS AND LICHENICOLOUS FUNGI OF THE QUEEN CHARLOTTE ISLANDS, BRITISH COLUMBIA, CANADA.
## 4. THE GENUS *FUSCIDEA* (FUSCIDEACEAE)

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### Abstract.

The genus *Fuscidea* is represented by three species on the Queen Charlotte Islands, one of which is new to science (*F. thomsonii* Brodo & V. Wirth). The other two species are *F. intercincta* and *F. mollis*. The Queen Charlotte species are described and discussed. Because only one other species, *F. lightfootii*, has been reported elsewhere in British Columbia, all four species are included in the identification key to make the coverage of the province complete.

### Introduction

The Queen Charlotte Islands comprise an archipelago about 45 km off the British Columbia coast in the hypermoist, temperate rain forest zone. Mountains rise to about 1000m, some of them occurring along the Pacific shore and forming long fiords. (See Brodo [1995] for a detailed description of the islands and their climate.) On these humid mountains and foggy coastal headlands, one can find a host of crustose lichens, many of which are poorly documented and understood. They include some that are unknown to science. *Fuscidea* is a good example of a genus that is insufficiently known in North America but is abundantly represented on the Queen Charlotte Islands.

The Fuscideaceae comprise a group of crustose lichen genera linked principally by their ascus morphology. The ascus tip of these genera generally present a layered or zoned appearance when stained with IKI. All have a relatively weakly or non-amyloid ascus wall, and a tholus with a strongly amyloid, highly refractive inner layer, covered by a weakly amyloid, often expanded layer that can appear gelatinous. An additional non-amyloid region is sometimes seen below the refractive inner layer. Hafellner (1984) mentions the presence of a superficial amyloid layer outside the non-amyloid "outer" wall, at least in *F. austera* (Nyl.) James, but in our species, this layer is absent or very hard to detect. The ascus tip contains no apical chamber or axial body. Oberhollenzer & Wirth (1984) also describe and discuss the ascus morphology in detail.

Genera of the Fuscideaceae tend to have dark thalli and apothecia. The family, including the Ropalosporaceae and Orphniosporaceae as recommended by Eriksson & Hawksworth (1993) and supported by Ekman (1993), has four representative genera in North America: *Fuscidea, Maronea, Orphniospora* and *Ropalospora*. Of these, only *Fuscidea* is found on the Queen Charlotte Islands, and so we will deal only with that genus in this paper.

Among the lecideaceous crustose lichens, the genus *Fuscidea* is relatively easily delimited by virtue of its unique asci, paraphyses and chemistry. The thallus in most species has a brownish tint (giving the genus its name), and the apothecia are very dark brown to black. The excipular structure found in species of *Fuscidea* is very variable. Some species have a dark or pale lecideine margin, but others have embedded, aspicilioid (cryptolecanorine) apothecia with no margin, or a margin that is vaguely thalline in structure. Oberhollenzer & Wirth (1984) have described this variation in detail and suggested that the genus could be divided into four informal groups based on excipular structure: the *cyathoides*-group, *kochiana*-group, *intercincta*-group and *curvula*-group.

Two of the three species of *Fuscidea* on the Charlottes fall into the *intercincta*-group, characterized by having immersed apothecia and small truncated spores. The most common of these has an IKI+ blue thallus medulla, a feature unknown for other members of the *intercincta*-group. In fact, most species of *Fuscidea* have a non-amyloid thallus medulla. (See, for example, Hertel [1977:195]). This common species appears to be undescribed and is named here as *Fuscidea thomsonii* Brodo & V. Wirth.. It forms part of the maritime coastal rock community together with other interesting crustose lichens that are common on the Queen Charlotte Islands but are rare elsewhere (e.g., *Caloplaca litoricola* Brodo and *Coccotrema maritimum* Brodo). This community is threatened by pollution from tanker traffic along the B.C. coast and boats involved with the extremely high levels of sport fishing in the area (Rolf Bettner, pers. comm.) and deserves special attention.

Among the "*intercinta*'s," *F. thomsonii* is distinguished by its generally pale, continuous thallus with an IKI+ dark blue medulla and barely expanded paraphyses tips that are heavily pigmented for 1/3 to 1/2 of their length. Typical *F. intercincta* s. str., with an IKI- medulla, is rare on the Charlottes.

## MATERIALS AND METHODS

The specimens included in this study were almost all collected by the first author on various expeditions covering all parts of the archipelago. These collecting efforts were described in Brodo (1995). Other specimens of *Fuscidea* were studied in UPS, H, M, and STU for comparison. All specimens examined and cited in this paper without herbarium designation are from the National Herbarium of Canada (CANL). Spore measurements were made in water mounts unless otherwise indicated. Measurements of spore volume were made following the methods of Hertel (1977), where Volume $\cong \pi/6 \times$ length x width$^2$ for L/W<1.9. Measurements are expressed as (E-)N-A-N(-E) where E= extreme values, N= normal values, A= mean value.

Iodine reactions in the asci and hymenia were observed with 1.5% or 0.15% solutions of IKI (Lugol's solution) either alone (indicated as an "IKI" reaction), or with pretreatment with 10% KOH, (sometimes neutralized with 2% acetic acid, then rinsed with water, and indicated as a "K/I" reaction).

Almost all specimens were analyzed with thin layer chromatography on Merck silica gel 60 $F_{254}$ glass plates, 10 x 20 cm, in three solvent systems following the methods of Culberson (1972) with later modifications (e.g., Mietzsch et al. 1992).

Color designations in the species descriptions (referred to by number) follow the ISCC-NBS Color-Name Charts developed by the U.S. Bureau of Standards, (Kelly 1965). References to exciple and apothecial margin types are based on Oberhollenzer & Wirth (1984).

The distribution maps were computer generated from latitude and longitude data using *QUIKMap 2.50* software (ESL Environmental Sciences Ltd., Sidney, B.C.) for MS-DOS computers.

## TAXONOMIC PART

***Fuscidea* V. Wirth & Vězda**, Beitr. Naturk. Forsch. Südwest-Deutschl. (Karlsruhe), **31**: 91 (1972). Type species: *Lecanora austera* Nyl., ≡ *Fuscidea austera* (Nyl.) P.James; = *Fuscidea aggregata* (Flotow) V. Wirth & Vězda.

Thallus dark brown to pale creamy- or greyish brown, thin or thick, rimose-areolate to areolate, often developing in 1-3 cm diameter patches, forming a mosaic, each patch delimited by a black prothallus. Prothallus almost always present, black or brown, conspicuous at the edge of the thallus and between the vegetative areoles. Cephalodia absent. Photobiont Trebouxioid.

Apothecia lecideine to aspicilioid, with margins well developed to absent. Apothecial disks black to dark brown due to a heavily pigmented epihymenium. Hymenium hyaline, although often streaked with brown pigments; IKI- (non-amyloid). Paraphyses simple, or slightly branched, especially at tips; tips expanded or not, with apical cell sometimes constricted at base, rarely submoniliform (with constricted cells for half the length of the paraphyses), free in KOH. Asci with strongly amyloid inner wall and a more-or-less well developed, weakly amyloid, apical, gelatinous envelope. Exciple weakly- or well-developed, radiate, pigmented brown or hyaline within, barely discernable in embedded apothecia. Hypothecium (sometimes called a subhymenium) consisting of anastomosing, ascogenous hyphae, hyaline, usually thin. Apothecial medulla (sometimes referred to as a hypothecium) composed of intertwined hyphae between the hypothecium and exciple, hyaline. Spores hyaline, frequently becoming brownish when old; non-septate or rarely one-septate, thin-walled, ellipsoid to slightly curved, often truncate, usually less than 11 µm long, sometimes more-or-less constricted at the center, without a "halo" or gelatinous epispore. Pycnidia embedded in younger parts of thallus, wall brown or pale, opening by a broad ostiole; conidia bacilliform, 3-5 x 0.7-1.6 µm in QCI material (2.5-5 x 1.2-2 µm fide Hertel [1977]).

CHEMISTRY. In North American species, medulla often containing divaricatic acid (PD-, K-, KC-, C-, UV++ blue-white), less frequently fumarprotocetraric acid (PD+ red, K-, KC-, C-); medulla IKI+ blue or IKI-.

HABITAT. Saxicolous on siliceous rock, or on acidic tree bark, especially conifers.

DISTRIBUTION. Most species of *Fuscidea* are found in cool, moist regions, either coastal and oceanic, or mountainous. The restriction of the Charlotte *Fuscideae* to the wettest part of the archipelago along the hypermoist west coast (with 2000-3000 mm precipitation) fits this pattern well (e.g., Fig. 6). Some corticolous species of *Fuscidea* have a more widespread, boreal distribution. Although no corticolous species have been recorded from the Charlottes, it would not be at all surprising to find *F. lightfootii* (Sm.) Coppins & P. James there in view of its occurrence near Vancouver (Aptroot 1996).

### KEY TO SPECIES OF *FUSCIDEA* IN BRITISH COLUMBIA

1(0). Growing directly on rock; thallus esorediate; spores not, or rarely, constricted . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2
Growing on tree bark; thallus almost always sorediate; spores distinctly constricted medially, sometimes one-septate . . . . . . . *Fuscidea lightfootii*

2(1). Thallus medulla IKI- . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
Thallus medulla IKI+ blue . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

3(2). Apothecia immersed in thallus, becoming slightly emergent when fully mature; disk frequently with sterile buttons (umbos) . . . . . . . *Fuscidea intercincta*
Apothecia sessile to constricted at base, disk smooth, without umbos . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Fuscidea mollis*

4(2). Apothecia entirely immersed in thallus; apothecial margin virtually absent, or less commonly prominent; thallus usually smooth to rimose areolate, less frequently dispersed areolate . . . . . . . . . . . . . . . . *Fuscidea thomsonii*
Apothecia sessile to slightly immersed in thallus but with prominent apothecial margins . . . . . . . . . . . . . . . . . . . . . . . . . . *Fuscidea* cfr. *thomsonii*

***Fuscidea intercincta* (Nyl.) Poelt in Poelt & Buschardt**, Norw. J. Bot. **25**: 127. 1978. ≡ *Lecanora intercincta* Nyl. , Flora **64**: 531. 1881. Type: Portugal, Beira Alta, Serra de Estrella, J. Henriques (Holotype: H-NYL 25173).

(Description based, in part, on Oberhollenzer & Wirth [1984].)

Thallus moderately thick, 0.2-0.4 mm, rimose-areolate to dispersed areolate or only rimose; dark greyish brown to brown. Soredia absent. Prothallus black, very conspicuous surrounding and between patches of areoles (Fig. 1).

Apothecia lecideine, immersed when young, becoming slightly emergent, 0.4-0.6(-0.8) mm in diameter; disks black when dry or wet, epruinose, flat to slightly convex, frequently having sterile buttons (i.e., umbonate) (Fig. 1). Paraphyses simple to slightly branched, not or barely expanded at the tips, slightly pigmented brown in the walls at the summits of some paraphyses. Apothecial margin black, paler in young apothecia, even, thick and prominent in mature apothecia or thin to almost excluded.

Hymenium 45-80 µm. Asci with IKI+ light blue or yellow walls, and an expanded cap. Exciple very reduced in sunken apothecia, and consists of only a few parallel and anticlinal rows of hyphae bordering the hymenium. Hypothecium 50-80(-100) μm, hyaline. Spores broadly ellipsoid, 8.5-11.5(-12.5) x (4-) 5.0-6.5(-7.5) μm (few seen in QCI specimens), length to width ratio 1.4-1.8, walls thin, without a halo. Pycnidia rather strongly raised, black; conidia bacilliform, 3-3.5 x 1-1.5 μm.

CHEMISTRY. Thallus cortex and medulla PD-, KOH-, C-, KC-; medulla IKI-. Contains divaricatic acid.

HABITAT: On non-calcareous rocks along lake shore.

DISTRIBUTION. QCI: Very rare; one population in Moresby Range. N. Am. Recently reported by Brodo (1995) as new to continent based on QCI specimen. World: SW Norway and SW Sweden, Portugal, British Isles and Queen Charlotte Islands.

SPECIMENS SEEN. Moresby Island: Takakia Lake, lakeshore rocks, *10909, 10920.*

COMMENTS. The Queen Charlotte specimens of *F. intercincta* are not well-developed, and the spores are somewhat larger in volume and broader, on average, than typical European examples, as can be seen from Figure 3. The specimens, however, seem to us to be conspecific with European populations.

Santesson (1993) includes *F. atlantica* (H. Magn.) P.James and Poelt within the circumscription of *F. intercincta*. It is true that some rounded, more-or-less constricted paraphyses tips could be found in one of our specimens (10909), but most paraphyses were not strongly expanded, and none were constricted below the second cell from the summit as can be seen in typical *F. atlantica* (see discussion under *F. thomsonii* below). We therefore retain both *F. intercincta* and *F. atlantica* at the species level.

*Fuscidea intercincta* is now known from four widely disjunct populations in the northern hemisphere, all with highly oceanic floras.

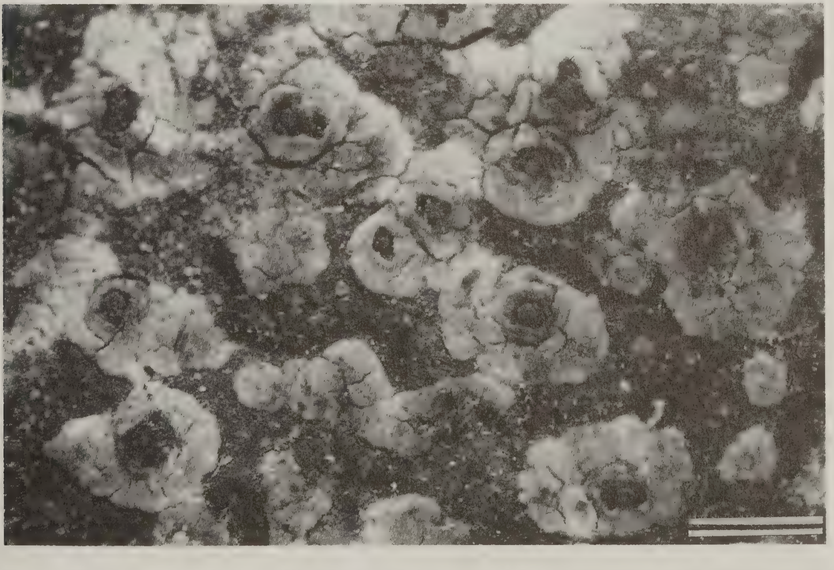

Fig. 1. *Fuscidea intercincta*, Queen Charlotte material, showing umbonate apothecia and dispersed thallus (*Brodo 10920*). Scale = 1 mm.

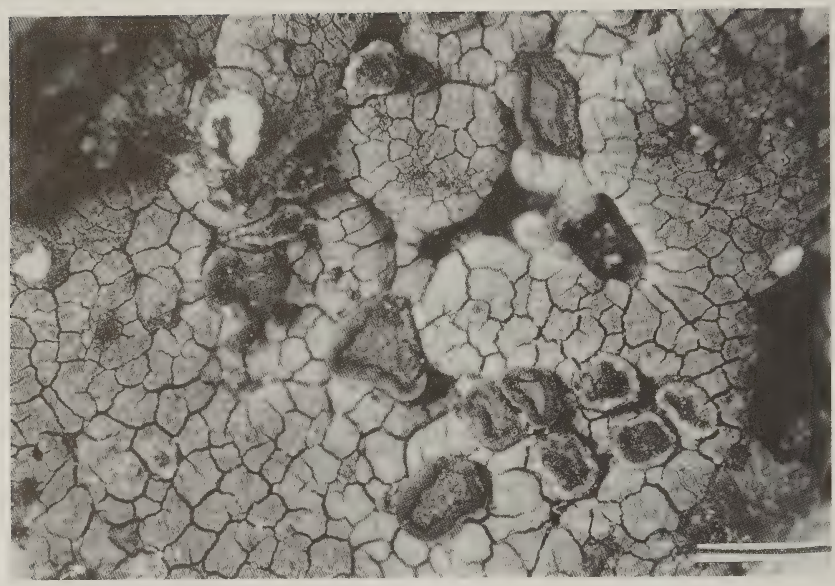

Fig. 2. *Fuscidea mollis*, Queen Charlotte material, with sessile apothecia on a rimose thallus (*Brodo 14227*). Scale = 1 mm.

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***Fuscidea mollis* (Wahlenb.) V. Wirth & Vězda,** Beitr. Naturk. Forsch. Südwest-Deutschl. (Karlsruhe), **31**: 92 (1972). ≡ *Lecidea rivulosa* β *mollis* Wahlenb., Flora Lapp. 472. 1812. Type: Norway. Finnmarken, Rypklubb, G. Wahlenberg (Lectotype: UPS).

Thallus clearly visible, thin, or thick in places, mostly continuous (Fig. 2); rimose to areolate, grouped into patches in a mosaic pattern, pale, pinkish brown (33) or pale grey to pinkish grey (264-10); soredia absent; edge indefinite. Prothallus black, conspicuous between patches of pale thallus.

Apothecia 0.5-0.8 mm in diameter, occurring singly, sessile to constricted at base, or almost raised on a stalk or stipe, flat when mature, smooth, without umbos (Fig. 2). Apothecial disks black or almost black, epruinose or sometimes lightly pruinose. Apothecial margin prominent, smooth, thick, even, the same color as the disk close to disk, or paler than the disk proximally.

Hymenium 65-87 µm high, hyaline. Epihymenium brown, with inspersed or superficial granules, unchanged with KOH (except granules dissolve). Hypothecium colorless or almost so, distinct from exciple; tissue between exciple and hypothecium often very lax, almost creating a cavity. Paraphyses coherent in water, free in KOH; tips elongate, slightly expanded, or more-or-less capitate with a rounded apical cell, constricted below the apical cell or not, 3.8-5.2 µm in diameter. Exciple *cyathoides*-type, variable: dark or carbonaceous only at edge, pale to hyaline within, but filled with opaque brown granules, unchanged or paler with KOH, unchanged with $HNO_3$. Asci club-shaped, *Fuscidea*-type, but with a poorly developed gelatinous envelope. Spores 8.0-9.5-11 x 5.0-6.0-6.8(-9) µm, length to width ratio 1.4-1.7; 8 per ascus. Pycnidia common, brown, immersed. Conidia bacilliform to ellipsoid, 3.0-4.9 x 1.4-1.6 µm.

CHEMISTRY. Thallus medulla and cortex PD-; K-; C-; KC-, medulla almost always IKI- (one specimen apparently IKI+ blue; see below). Contains divaricatic acid. HABITAT. Growing on non-calcareous dry rocks on ridges and bluffs, sea level to 150 m elevation.

DISTRIBUTION. QCI: mountains of southern Moresby Island. N.Am.: Queen Charlottes, Seward Peninsula of Alaska, western Hudson Bay, Baffin Island and New England mountains (Thomson 1997). World: Central Europe (especially the Alps), Pyrenees, Scandinavia and northern Scotland (Purvis et al. 1992), Northern Urals of Russia (Hertel 1991), Antarctica (Andreev 1988 [see Hertel 1991]), Japan and Bering region (Inoue 1981a).

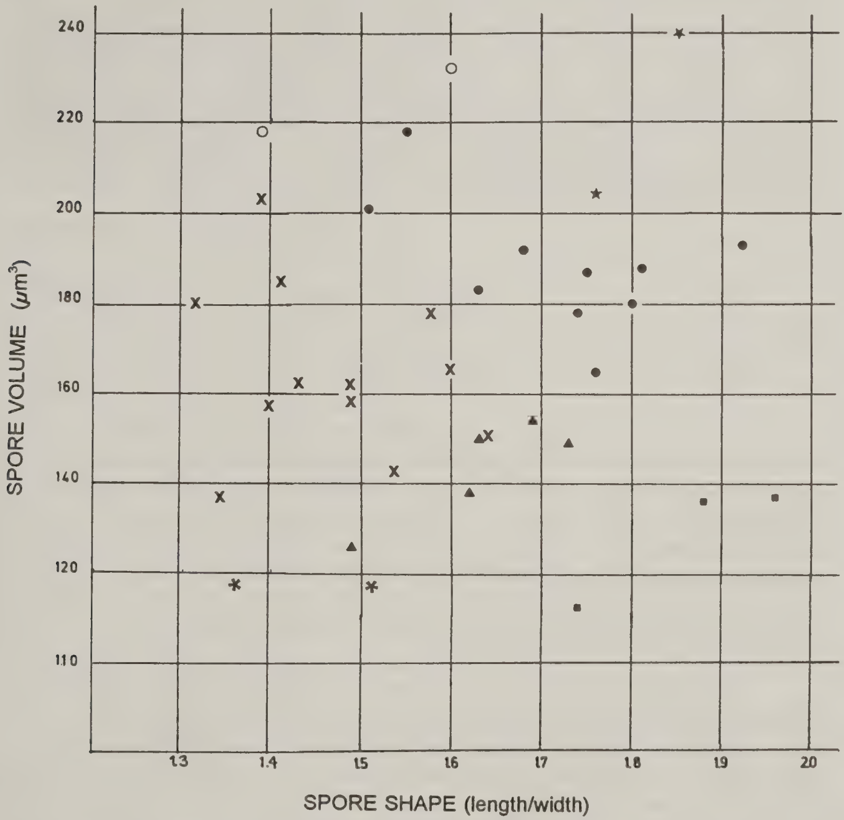

Fig. 3. Spore dimensions of members of the *Fuscidea intercincta* group (based on Oberhollenzer & Wirth [1984: Fig. 25]). ● = *F. intercincta* (European specimens); ○ = *F. intercincta* (QCI specimens); × = *F. thomsonii* (normal spores); * = *F. thomsonii* (small spores); ★ = *F. decincta*; ▲ = *F. atlantica*; ■ = *F. oculata* Oberholl. & V. Wirth.

SPECIMENS EXAMINED. Graham Island: Port Chanal, Athlow Bay, on boulder at 100 m elev., *10444* (p.p.; with *F. thomsonii*), *10434* (Lich. Can. Exs. 115). Moresby Island: Pocket Inlet, in open fens, *14227*; "Blue Heron Bay," north of Sunday Inlet, on quartz vein on summit rock, 150 m elev., *14094*. [*F.* cfr *mollis* (see discussion below): Chaatl Island, cove on west coast, facing ocean, on headland rocks, lower aerohaline, *26977*]

COMMENTS. The Queen Charlotte population was discussed briefly in Brodo (1977).

One specimen (*Brodo 26977*) somewhat resembles *F. mollis* but has an IKI+ blue medulla, and the apothecia, although sessile, are not markedly constricted at the base. (See discussion under *F. thomsonii*.) It was compared with authentic material of *F. submollis* Inoue (*Inoue 10700*, and *7814* [HIRO]), but that species has smaller, flatter apothecia with thin, black margins. The apothecia are sessile on convex areolae, quite unlike our material. For the present, no. *26977* can be considered as a chemically aberrant specimen of *F. mollis.* Variation in the medullary IKI reaction is also known in *F. maculosa* (H. Magn.) Poelt (Oberhollenzer & Wirth 1985).

### ***Fuscidea thomsonii*** **Brodo & Wirth, sp. nov.** (Figs. 4, 5)

*Fuscideae atlanticae* similis sed thallo pallido griseofusco vel flavidofusco, medulla IKI+ cyanoatra, et paraphysibus parum expansis, non-constrictis.

Typus: Canada. British Columbia, Queen Charlotte Islands, Moresby Island: east end of Mike Inlet on shore and along stream to exposed bluffs (Elevation 120 ft. [36 m]), 52°32'N, 131°45'W, *I. Brodo 14173*, 1 Aug. 1968 (Holotypus: CANL).

Etymology: In honour of the American lichenologist, John W. Thomson.

Thallus clearly visible, mostly continuous to dispersed areolate, more or less smooth or rimose to areolate (Fig. 4), light to dark greyish brown (60-61) to yellowish brown (76-79); soredia absent; edge definite, not lobate (but almost so). Prothallus usually present, black, conspicuous at thallus edge or between patches of pale thallus.

Apothecia 0.25-0.73 mm in diameter, occurring singly, either entirely immersed in thallus with disk level with thallus, or somewhat emergent; smooth, without umbos or rarely umbonate in part; disks black or almost black, epruinose (Fig. 4). Apothecial margin absent or even with disk to somewhat prominent, smooth, dark gray to dark brown, paler than the disk.

Hymenium (45-)55-67-77(-90) µm high, hyaline, or brownish above. Epihymenium brown, not at all granular. Hypothecium colorless or almost so, distinct from exciple (Fig. 5a). Exciple *intercincta-* to *atlantica*-type, dark or carbonaceous only at edge, pale to poorly defined within; unchanged with KOH or $HNO_3$. Paraphyses 1.7-2.0 µm thick, simple, or slightly branched at tips, slightly expanded but not constricted at septa, tips 3.1-4.0-4.7 µm in diameter, pigmented for a third to half its length, coherent in water, free in KOH (Fig. 5b). Asci club-shaped, clearly double-walled, with a darkly IKI-staining, thick, inner layer and a weakly amyloid, gelatinous, outer wall. Spores (6.2-)7.2-8.8-9.2(11.2) x (4.6-)5.2-6.0-6.8(-7.2) µm, length to width ratio 1.31-1.47-1.64; 8 per ascus (Fig. 5c). Pycnidia brown-black, embedded in thallus, sometimes abundant and conspicuous, but can be rare or sometimes absent. Conidia

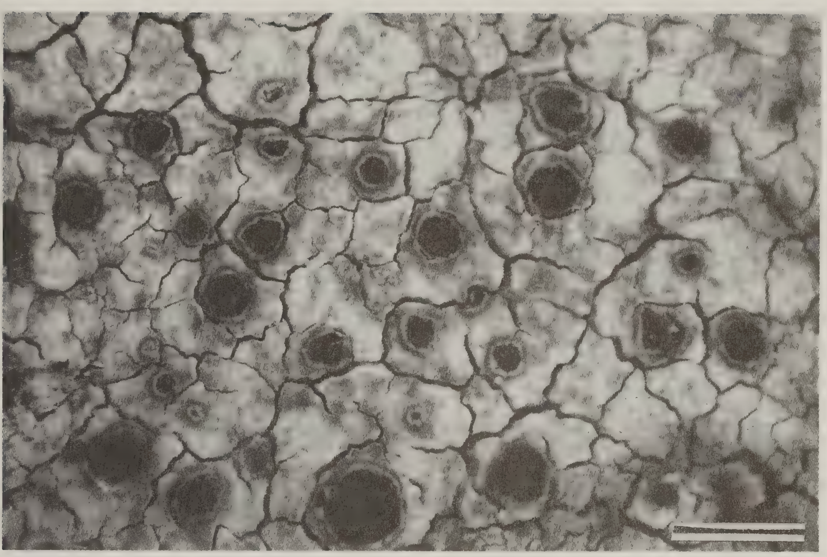

Fig. 4. *Fuscidea thomsonii*, holotype (*Brodo 14173*), habit. Scale = 1 mm.

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bacilliform-ellipsoid, 3-3.5 µm long.

CHEMISTRY. Thallus medulla and cortex PD-; K-; C-; KC-, UV++ blue-white; medulla IKI+ blue. Contains divaricatic acid.

HABITAT. Growing on silicious, shoreline rocks in aerohaline zone, at stream edges or on ridges in subalpine habitats.

DISTRIBUTION. Endemic to Queen Charlotte Islands; along the hypermoist outer coast and on adjacent bluffs and peaks (Fig. 6).

SPECIMENS SEEN. Graham Island: Rennell Sound, Seal Inlet, on vertical faces of exposed rock on bluff, *10266**. Hibben Island: on rock in salt spray zone, *14058*. Moresby Island: Kootenay Inlet, exposed bluff, *12155**; Upper Victoria Lake, 58 m elev., *12277*; Buck Point, rocks at edge of beach, *13989*; Bigsby Inlet, edge of stream, *17833*; Tasu, "Mine Mountain," 800 m elev., *23654*; Fairfax Inlet, shoreline rocks, aerohaline, *23668*. [*F.* cfr. *thomsonii* (see discussion below): Graham Island: Port Chanal off Athlow Bay, on boulder at summit, 100 m elev., *10444*.] * = small-spored (see Comments below).

COMMENTS. *Fuscidea thomsonii* clearly belongs to the *intercincta*-group in the sense of Oberhollenzer & Wirth (1984), but does not seem to fit within previously described species of that group. Our specimens were compared with species from Europe and Asia (Oberhollenzer & Wirth 1984; Inoue 1981a, 1981b), but none matched exactly. *Fuscidea atlantica* (H. Magn) P. James & Poelt comes closest to *F. thomsonii* but has constricted to submoniliform paraphyses tips involving at least 2-3 cells. The apical cells of the paraphyses in *F. thomsonii* are barely expanded. If they are constricted, the constriction is only below the first cell. The upper cells of the paraphyses are only lightly browned in *F. atlantica*, with little or no pigmentation remaining on the wall surface (Oberhollenzer & Wirth 1984), whereas in *F. thomsonii*,

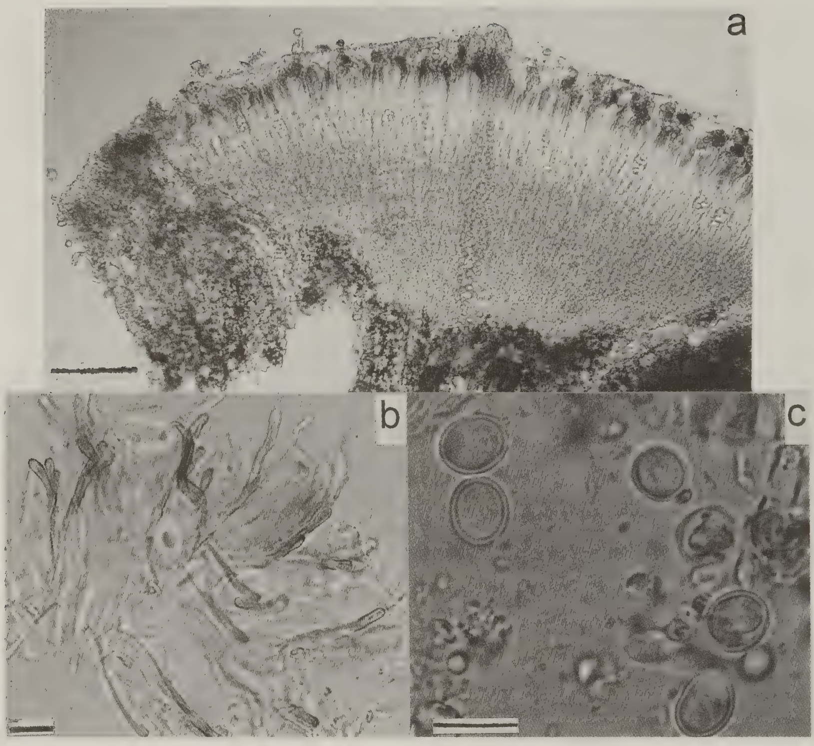

Fig. 5. *Fuscidea thomsonii*, holotype (*Brodo 14173*). a) Apothecial section. Scale = 100 µm; b) paraphyses. Scale = 20 µm; c) ascospores. Scale = 10 µm.

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the paraphyses tips have a conspicuous brown pigmentation coating the upper two or three cells (Fig. 5b). In addition, *Fuscidea atlantica* has an IKI- thallus medulla and the spores are, on the average, smaller and more ellipsoid (see below).

Other species we considered include *F. decincta* (Nyl.) Oberholl. & Wirth, which has larger spores ([8.5-]10.5-11.1-13.0[-14] x [4.5-]5.0-6.1-7.5[-8.5] µm, based on H-NYL 25172 [H!]), and *F. intercincta*, which has more emergent apothecia, tends to have more narrowly ellipsoid spores (although one of the Queen Charlotte representatives is at the broad end of the range; see Fig. 3), and has much lighter pigmentation on the tips of the paraphyses. Both these species are IKI- in the medulla.

Spore shape and volume of all members of the *intercincta*-group are compared in Fig. 3 where the data for *F. thomsonii* are added to those already published by Oberhollenzer & Wirth (1984: Fig. 25). The *F. thomsonii* data show the spores to be very broad, often subspherical in shape, with a wide range in volume (118 $\mu m^3$ to 201 $\mu m^3$).

*Fuscidea thomsonii* is, in fact, variable in a number of respects if one includes under that name all the specimens that have an IKI+ blue medullary reaction, partially or entirely immersed apothecia and broadly ellipsoid spores. The thallus, which is usually continuous rimose-areolate with a narrow brown-black prothallus, can consist of discontinuous patches surrounded by black prothalline tissue. The apothecia of such specimens, however, are sunken in the typical way and the spores dimensions are within the range of the species. Thallus type does not have any obvious correlation with habitat, but label data alone are not sufficiently detailed to permit a firm statement to that effect. Both shoreline and ridge-top specimens can show that morphotype. It may well be that discontinuous thalli reveal a particular stage of thallus development. This would have to be checked in the field.

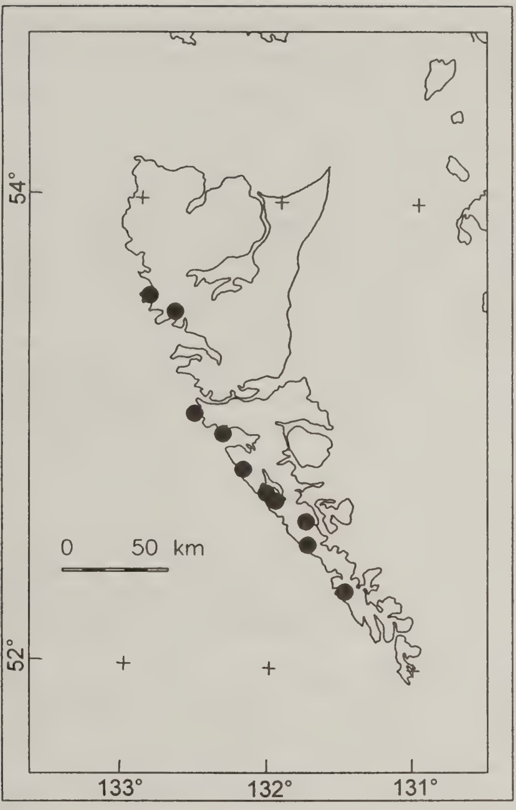

Fig. 6. Distribution of *Fuscidea thomsonii* on the Queen Charlotte Islands.

As indicated above and demonstrated in Figure 3, spore size is quite variable in *F. thomsonii*. Two specimens (with asterisks in the list) have particularly small spores (6.2-7.7-8.4 x 4.6-5.4-6.2 μm) but are otherwise typical.

Most perplexing, however, are three specimens that have particularly emergent apothecia, sometimes even developing a black apothecial margin. The apothecia are never constricted at the base as in *F. mollis* or *F. submollis* Inoue. The latter species, described from Japan by Inoue (1981a) has an IKI+ blue thallus medulla, but the thallus is made up of very thick, convex areolae, and the apothecia, with thin, pure black margins, are clearly sessile, not at all immersed. The spore, thalline and chemical characters of these Queen Charlotte specimens with emergent apothecia all fall within the range of variation seen in *F. thomsonii*, but in at least two cases, distinct taxa seem to be involved. No. *10455* from shoreline rocks at Port Chanal, Graham Island, has entirely black apothecial margins, and the apothecia are never innate to any degree. The thallus is minutely rimose and dark. We are leaving it without a name for the present. In no. *26977*, from coastal rocks on Chaatl Island, the apothecia have thick, thallus-colored margins and resemble those of *F. mollis* although they are not constricted at the base. It is possible that the specimen is an immature *F. mollis*, even though the thallus has an IKI+ blue medullary reaction. The third specimen, no. *10444* comes close enough to *F. thomsonii* to be tentatively included there. More collecting and field observations are obviously needed to clarify the situation, which is true for the genus as a whole because the populations of many species of *Fuscidea* seem to be genetically variable.

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This paper is dedicated to our friend and colleague, Dr. John W. Thomson, one of North America's most steadfast and productive lichenologists for over 50 years.

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# NOTES ON THE *ASPICILIA REPTANS* COMPLEX, WITH DESCRIPTIONS OF TWO NEW SPECIES

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**Abstract:** Two new fruticose species of *Aspicilia* are described from North America. ***Aspicilia californica*** Rosentreter, sp. nov. from San Benito County, California, and ***Aspicilia filiformis*** Rosentreter, sp. nov. from Jefferson County, Oregon. Both grow on soil and are similar to *Aspicilia reptans* (Looman) Wetmore, but have a more fruticose growth form. *Aspicilia californica* has smaller spores, more spores per ascus than *A. filiformis* and *A. reptans*, and has a KOH+ red cortex. *Aspicilia filiformis* has thin, black forked lobe tips, and well defined thallus margins compared to those of *A. reptans*. *Aspicilia reptans* is the most geographically and ecologically widespread North American endemic fruticose *Aspicilia* species discussed in this article. *Aspicilia filiformis* is known mostly from the Northern Rockies (Washington, Oregon, Idaho, Montana), while *A. californica* is known from only four counties in California.

**Key words**: *Aspicilia*, shrub steppe, arid lands, microbiotic crusts

## INTRODUCTION

This article is one in a series on *Aspicilia* species and other terricolous lichens that occur in the arid lands of western North America. John W. Thomson and his student Jan Looman first explored and published information about this unique lichen guild and its associated vascular plant and microbiotic crust communities (Thomson 1960, Looman 1962, 1964a, 1964b).

*Aspicilia reptans* (Looman) Wetmore is a North American endemic described by Looman (1962) from Saskatchewan, Canada as *Lecanora reptans* Looman. Jan Looman was the first North American lichenologist to specialize in grassland habitats. Historically, grasslands and arid shrub-steppe covered most of central and western North America. However, the majority of these areas have either been converted to agriculture or have been heavily impacted by livestock grazing (Rosentreter 1993). The lichen floras of these arid regions are poorly known. Exploration of remnant and pristine areas is often necessary to determine the original compliment of terricolous lichen species (McCune and Rosentreter 1992). Due to limited pristine areas to study following human and livestock impacts, as well as vast distances between pristine, lichen-rich plant communities and the difficulty in preserving soil lichens, undescribed taxa still occur in these arid habitats. Two such species are described in this paper.

Many lichen species found in North American arid lands are also present in similar arid land habitats of Asia and Europe. A review of the literature (Oksner 1971) and herbarium specimens from Asia has been conducted.

Weber (1967) proposed that some vagrant forms of *Aspicilia* were merely environmental modifications with the same genetic composition as crustose species on rock substrates. However, Weber (1977) later suggested that some vagrant taxa may be distinct species and recommended further field investigations to interpret these taxa. Hafellner (1991) considered pseudocyphellae, vegetative diaspores, ascocarp structure, and secondary chemistry as significant characteristics in the evolutionary lines of the Hymeneliaceae (formerly the Aspiciliaceae). Hafellner (1991) also noted that as the number of spores per ascus decreases there is often an increase in the size of individual spores. Field investigations on attached, loosely attached and vagrant *Aspicilia* have been conducted (Rosentreter 1993) and further observations are discussed in this paper. Terricolous species of *Aspicilia* and many other genera show a high degree of variation, but there are some good distinctions between taxa (Oksner 1971, Rosentreter 1993, McCune and Goward 1995).

## METHODS

Searches for *Aspicilia* taxa on soil were conducted throughout western North America, with emphasis on arid land sites. Thallus chemistry of representative specimens were analyzed using standard spot tests and thin layer chromatography. The type specimen of *Aspicilia reptans* was borrowed from the herbarium at the Experimental Farm, Swift Current, Saskatchewan, Looman 59-6114. North American material was compared to similar material from Russian steppe communities. Specimens of North American *Aspicilia* from ASU, BRY, COLO, DAV, F, H, ID, KPABG, KV, MICH, MONTU, OSC, RICK, TU, US, WIS and the private herbaria of Ann DeBolt, Trevor Goward, Bruce McCune, Bruce Ryan, and Sam Shushan were examined. Specimens examined included those of *A. reptans* and other terricolous species of *Aspicilia* sensu lato not cited later in the text. Additional Estonian and Russian specimens were borrowed from O.L. Blum. Specimens cited are in the author's herbarium unless otherwise noted.

## RESULTS AND DISCUSSION

In western North America, crustose and fruticose *Aspicilia* are frequently encountered at sites in good ecological condition. However, because of their small size and drab color, they are easily overlooked and thus infrequently collected and studied. Terricolous lichens are often misrepresented in herbarium packets as to the degree of attachment to the substrate. Some are labeled as vagrant when they are not truly vagrant, while others are listed as attached firmly to the soil when they were only intermittently attached to the soil or litter. For example, *A. hispida* Mereschk. is often reported as vagrant or growing loosely over soil. However, after examining hundreds of specimens, I have found that it always grows basally attached to the soil, though its point of attachment is easily broken.

Some specific background on *Aspicilia reptans* is helpful for comparison with the new species described below. *Aspicilia reptans* was described by Looman (1962) from the grasslands of Saskatchewan, Canada as "thallus thick, continuous, with long, radiating lobes. Lobes strongly convex or almost terete. Cortex ca. 20 μm thick; unchanged by reagents. Lower cortex white with sparse, short rhizinae. Apothecia rare, at first urceolate, later adnate; the disc black, the margin entire and colored like the thallus. Asci clavate, with two subglobose, thick-walled spores ca. 10 μm in diameter".

## Enumeration of New Species

***Aspicilia californica* Rosentreter sp. nov.** (Figure 1)
*Habitu Aspiciliae reptanti similis, sed thallo fruticosiori, et cortice* KOH+ *rubescenti.*

**Type:** California, San Benito County, Pinnacles National Monument, east end of High Peaks Trail, chaparral habitat, on soil and organic matter, 365 m, 29 June 1991, Rosentreter 7241 (**holotype**, WIS; **isotypes**, BRY, SRP).

Thallus fruticose, creeping and attaching at several points along the lobes, less than 30% of the thallus attached; lobes discrete, elongate, and stringy, up to 30 mm long, 0.5-1.2 mm wide, terete, tips typically single, unbranched; surface when dry is dull and irregularly white mottled, the color is whitish to gray-green and remains whitish in parts even when moist, pseudocyphellae lacking. Apothecia rare, 0.2-1 mm in diameter, immersed, disk black, occasionally pruinose on the disk, the margin is entire and colored like the thallus (whitish to gray-green), hymenium 60 μm thick, hyaline to brown; epithecium green with HCl and $HNO_3$; hypothecium hyaline 20-30 μm thick; paraphyses are moniliform; spores 8 per ascus, subglobose, 5.5 x 4 μm, or occasionally 6 per ascus and then 10 x 7μm diameter; cortex KOH+red, P+orange, C-, KC- (norstictic acid). On organic matter, rock, moss and litter, in chaparral habitats.

This species is similar to *A. reptans* but differs in that the thallus is more fruticose, the cortex is KOH+ red, and the spores are typically 8 per ascus. *Aspicilia californica* has subglobose spores

Figure 1. Habit of Aspicilia californica Rosentreter (Rosentreter # 7241).

that are smaller (5.5 x 4 μm) than those of *A. reptans* (10 μm). When dry, the thallus surface of *A. californica* is generally more whitish than in *A. reptans* or *A. filiformis*, and the color is little changed when moist, unlike the latter two, which turn bright to dull green when moist.

Additional representative specimens: U.S.A. CALIFORNIA: Amador Co.: Hilltop south of Ione, on red soil, W. A. Weber & R. Santesson L-44560, Lichenes Exsiccati-Boulder Colorado- No. 178 (COLO); Madera Co.: Bass Lake, 762 m NE of Fresno, California, R.W. Meyer *s.n.* January 1982 (COLO); Santa Barbara Co.: Aliso Canyon, Sierra Madre Mts., Cuyama area, chamise woodland, 1010 m, C. Bratt 3301 (herb. Rosentreter); San Benito Co.: Chalone Creek, Pinnacles National Monument, San Benito Range, on organic matter and soil, Rosentreter 7267 (SRP).

**Aspicilia filiformis Rosentreter sp. nov.** (Figures 2 & 3)
*Habitu Aspiciliae reptanti similis, sed thallo fruticosiori, et ramulis ultimis plus minusve divaricatis et nigrescentribus.*

**Type:** Oregon, Jefferson County, "The Island" Area of Critical Environmental Concern (ACEC), T12S, R12E, Sec. 3 & 10, ca. 20 km northwest of Redmond, Oregon, 730 m, pristine *Artemisia tridentata* ssp. *wyomingensis* habitat mixed with *Agropyron spicatum* and *Festuca idahoensis*, on soil, 28 March 1990, Roger Rosentreter 6521 (**holotype,** WIS; **isotypes,** ASU, BRY, CANL, COLO, OSU, SRP).

Thallus appressed fruticose, creeping and attaching at several points along the lobes, mat-forming, less than 50% of the thallus attached; lobes discrete, elongate, and stringy, typically short (5-10 mm) contorted and irregular in length, up to 15 mm long, 0.4-1 mm wide, terete, tips distinctly different from the main thallus branchs, often black with forked tips, like a snake's tongue, forming a prothallus, surface when dry olive, brown, or greenish, turning bright to dull green when moist, pseudocyphellae lacking. Apothecia rare, 0.5-1.5 mm in diameter, slightly immersed to sessile, disk reddish brown to black, the margin is entire and colored like the thallus (gray-green), rarely pruinose, hymenium 70-80 μm thick, epithecium 15-20 μm, green with HCl and $HNO_3$; paraphyses are moniliform; spores 2 per ascus, subglobose, variable in size, 18-26 x 16-24 μm in diameter, or occasionally 4 spores per ascus and then 12-16 x 11-16 μm. Cortex KOH- or weakly and slowly turning yellow, P-, C-, KC- (unknown substance). On organic matter, moss and dead grass clumps, in shrub-steppe and Columbia River grasslands habitats.

This species is similar to *Aspicilia reptans* but overall the thallus is more fruticose, with narrower, more elongate and stringy lobes, well defined margins, and lobe tips distinctly differentiated and often black and forked, like a snake's tongue. Many specimens of *A. filiformis* contain an unknown chemical that reacts weakly and slowly to KOH (turning yellow), in contrast to *A. reptans* which lacks any reaction to KOH. Spores of *Aspicilia filiformis* are larger (18-26 μm) than those reported for *A. reptans (*10 μm*)*. Several specimens, that are morphologically comparable to the type specimen of *A. reptans* have either two or four spores per ascus (Rosentreter 7400), however some spores are the typical size (10 x 11 μm) while others are larger (25 x 22 μm) than Looman reported (10 μm). Therefore, the best distinction between *A. reptans* and *A. filiformis* is the difference in lobe tip morphology and the more fruticose habit of *A. filiformis*. Apothecia are so rare in *A. reptans* that the spore sizes reported (Looman 1962) might not fully represented the inherent variation for this taxon (Hafellner 1991). The type specimen of *A. reptans* was not further dissected because to do so would have destroyed the remainder of the apothecium. (The Swift Current Experimental Farm,

Figure 2. Habit of *Aspicilia filiformis* Rosentreter (Rosentreter # 6521).

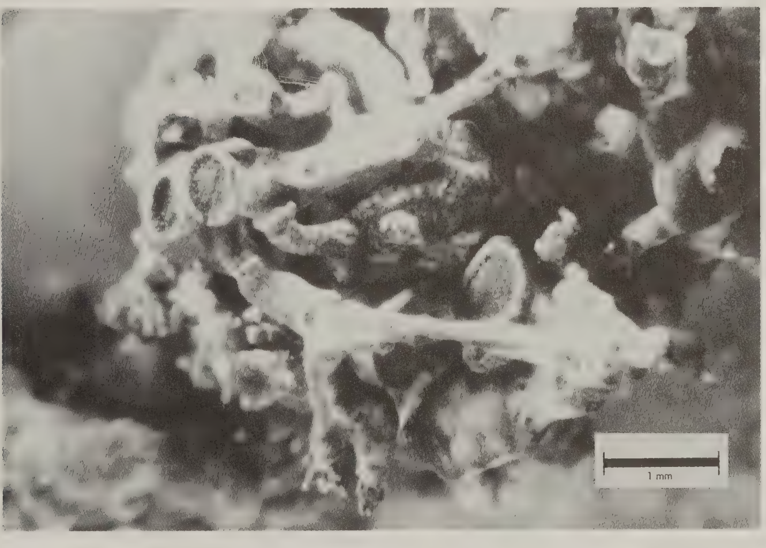

Figure 3. Close up of *Aspicilia filiformis* Rosentreter (Rosentreter # 6521).

original location for the type specimen, no longer wishes to maintain a herbarium so the type specimen will be redeposited in WIS).

*Aspicilia filiformis* and *A. californica* are more similar in habit to each other than to *A. reptans,* which is more adnate, glebose, or subsquamulose, becoming fruticose at only a few sites along the lobes. However, these two new taxa differ from each other in color, size, lobe tip morphology and chemistry.

Additional representative specimens: U.S.A. OREGON: Deschutes Co.: 43°20'N, 121°01'W, T14S, R12E, Sec. 33, 10 km west-north-west of Redmond, Oregon, 914 m, Rosentreter 9272 (SRP); Grant Co.: Ferris Creek Cap Rock, 1 mile north of Dayville, Oregon, approx. 48 km west of John Day, Oregon, T25S, R26E, Sec. 25, 975 m, Rosentreter 6462 (SRP); Wasco Co.: 50 km north of Madras between Shaniko and Antelope along Ward Creek, 44°58'N, 120°48'W, Lawrence Grassland Nature Conservancy Preserve, 1150 m, A. Rossman LL-836 (OSU, SRP, US). IDAHO: Ada Co.: South of Boise, Idaho, Pleasant Valley Road, T2N, R2E, Sec. 16, 823 m, Rosentreter 1983 (WIS, SRP); Castle Rock, NE of Boise, Idaho, T3N, R2E, Sec. 13, 792 m, Rosentreter 7579 (SRP); North end of Boise between Crestline and Ridgeline Drives, 43°33'N, 115°56'W, 762 m, Rosentreter 9140; Kuna Butte Study site, 43°31'N, 116°29'W, T1N, R1W, Sec. 3, 680 m, Rosentreter 9364 (SRP); Land parcel adjacent to Columbia Village subdivision, southeast end of Boise, Idaho, 43°31'N, 115°55'W, 853 m, Rosentreter 9486 (SRP); Custer Co.: Railroad Ridge, White Cloud Mts. 30 km east of Stanley, Idaho, 44°13'N, 114°03'W, 3040 m, Rosentreter 9381; Elmore Co.: Jct. Simco Road and Interstate 84, 38 km southeast of Boise, Idaho 43°20'N, 115°59'W, T2S, R4E, Sec. 36 S1/2, 1006 m, Rosentreter 6224; 7 km northwest of Mountain Home, Idaho, T3S, R6E, Sec. 17, 985 m, Rosentreter 6906; Gem Co.: Old Freeze Out Hill, Just south of Emmett, Idaho, T6N, R1W, 945 m, Rosentreter 6838 (SRP); Owyhee Co.: Badlands of Succor Creek on zeolitic earth, near McBride Creek, 43°19'N, 116°59'W, 1280 m, Rosentreter 7343. UTAH: Summit Co.: Wasatch-Cache National Forest, 1 km south of Bald Mountain, alpine, 3513 m, St. Clair BRY-C21863. WASHINGTON: Yakima Co.: South side of Ahtahnum Ridge, just west of the Union Gap, 46°32'N, 120°30'W, 395-460 m, B. Ryan 17096-b (ASU, SRP); Ft. Murray Wildlife Refuge 20 km south of Ellensburg, Washington 46°50'N, 120°33'W, 610m, B. Ryan 8785 (ASU, SRP). MONTANA: Beaverhead Co.: Just above trees west slope of Comet Mountain, Pioneer Mts., 45°28'N, 113°02'W, ca 2870, B. McCune 20950 (SRP, herb. McCune).

**Ecology and Distribution of Members of the *Aspicilia reptans* Complex**: The three *Aspicilia* species discussed have different ecological site preferences. *Aspicilia californica* is known only from relatively warm California chaparral sites. *Aspicilia filiformis* is best developed in arid Columbia River grassland and arid shrub-steppe sites, especially *Artemisia tridentata* ssp. *wyomingensis* habitats and *Agropyron spicatum* and *Festuca idahoensis* grasslands. *Aspicilia reptans* is best developed in cold shrub-steppe and Great Plains grassland microsites with greater snow cover. *Aspiciliareptans* is ecologically and geographically more widespread than *A. filiformis*. It is found in cold, arid habitats throughout most of central and western North America. *Aspicilia filiformis* is limited to the Columbia River grasslands and arid shrub-steppe habitats of the Northern Rockies (Washington, Oregon, Idaho, Montana). The exceptions are sites represented by single collections from windswept alpine microhabitats in Montana and Utah. At some sites within the Northern Rockies *A. filiformis* and *A. reptans* co-occur but they grow in slightly different microsites. These two *Aspicilia* species are fairly common but are inconspicuous, appearing as dead organic matter.

**Other Similar Taxa:** *Aspicilia hispida* and *A. fruticulosa* occur sympatrically with some of these taxa but have pseudocyphellae and a more erect growth habit (Rosentreter 1993). Odd specimens of *A. hispida* (W. A. Weber L-33,164) can be found that are prostrate in their growth form, but they retain pseudocyphellae and have wider lobes than any of the *A. reptans* complex. The two newly described *Aspicilia* species, in addition to *A. reptans,* demonstrate that there is a gradual transition in growth form from crustose through fruticose thalli. Confusion among the taxa within the *A. reptans* complex is due in part to their delicate and brittle lobe tips. Lobe tips are often broken during processing and while in storage. This vegetative fragmentation appears to be the primary form of reproduction and dispersal for these fruticose *Aspicilia,* which only rarely produce apothecia. *Aspicilia californica* and *A. filiformis* appear to be different from any of the fruticose species described from Eurasia. *Aspicilia reptans* is less adnate than the more crustose Eurasian species *A. terrestris* Tomin and *A. aspera* (Mer.) Tomin. Some of the North American specimens that are predominately adnate to the soil surface are comparable to *A. terrestris* and *A. aspera.*

*Megaspora verrucosa* has a thallus color similar to *A. reptans,* but it is consistently found in more mesic microsites on wood or decomposing organic matter rather than on soil, and typically is fertile with deeply sunken apothecia containing very large spores (>30 $\mu$m) and a much thicker thallus. *Aspicilia mastrucata* (Ach.) Th. Fr. often grows on moss over thin soil or rock, but only rarely on soil itself. It has very distinctive papillae on the areoles, some of which are branched. Papillae are often broken off in herbarium specimens. It is also brighter blue-green when wet or dry than the *Aspicilia* species discussed above, and in western North America it is generally found growing on clumps of the moss *Grimmia.* It is KOH+ red.

## Key to the Common Terricolous *Aspicilia* and Similar Species in Western North America

1. Spores large ($\geq 30\mu$); apothecia typically present, deeply sunken within the thallus; on organic material in mesic microsites ...... **Megaspora verrucosa** (Ach.) Hafellner & V. Wirth

1. Spores smaller ($<30\mu$); apothecia typically lacking, slightly sunken or sessile; on soil, rock, or organic material; typically in arid habitats ............................................ 2

    2. Thallus not attached to the substrate; habit globose; pseudocyphellae present only at the paired lobe tips .................... **Aspicilia fruticulosa** (Eversm.) Flagey.

    2. Thallus at least in part adnate to the substrate; habit not globose; pseudocyphellae laminal or lacking .......... 3

3. Thallus erect, basally attached; pseudocyphellae laminal .... .................................. **Aspicilia hispida** Mereschk.

3. Thallus creeping, attached at several points along the lobes; pseudocyphellae lacking ................................... 4

    4. Cortex K+ red; lobes generally thicker; lobe tips often single; chaparral ...... **Aspicilia californica** Rosentreter

4. Cortex K- or weakly yellow; lobes thin (≤0.3mm); lobe tips single or forked; grassland or shrub-steppe .......... 5

5. Thallus predominantly narrow, elongate and stringy (appressed fruticose); thallus margins well defined; lobe tips acute and distinctly different from main thallus, often black with forked tips (like snakes tongue's); medulla K- or weakly yellow .. .............................. **Aspicilia filiformis** Rosentreter

5. Thallus more areolate and attached to soil with only occasional stringy sections (like beads on a string); thallus margins poorly defined; lobe tips similar in color and texture to main thallus; medulla K- .................. **Aspicilia reptans** (Looman) Wetmore

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This article is dedicated to John W. Thomson, who has helped me and many other students of lichenology on the long road to understanding the diverse flora of North America. I thank herbarium curators for the use of facilities and specimen loans and Bruce McCune, Trevor Goward, and Bruce Ryan for allowing me to examine their personal herbaria. I also wish to thank Ann DeBolt, Jeanne Ponzetti, Bruce Ryan and Larry St. Clair for reviewing a draft of this manuscript.

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# PRELIMINARY REPORT ON THE SHORT, APOTHECIATE TAXA OF USNEA IN THE SOUTHWESTERN UNITED STATES

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## ABSTRACT

The apotheciate taxa of *Usnea* in Arizona, New Mexico, and western Texas, *U. arizonica* Mot. and a distinctive morphotype of *U. cirrosa* Motyka, differ chiefly in branching pattern, relative uniformity of fibril length, and papillation, the same features that separate this morphotype of *U. cirrosa* from the Mexican morphotype. A key compares the apotheciate taxa of the United States with *U. florida* (L.) Wigg. emend. Clerc of Europe and *U. cirrosa* of Mexico.

Most short apotheciate specimens of *Usnea* in the United States can be referred to two species aggregates—the *Usnea strigosa* (Ach.) A. Eaton group (see Tavares, 1987) and the *U. arizonica* Motyka—*U. subfusca* Stirt. aggregate. However, specimens of another, unrelated taxon occur in the mountains of Arizona, New Mexico and western Texas at 1500–3000 m. For the present, we are regarding these specimens as a distinctive morphotype of *Usnea cirrosa* Motyka, even though they are quite different from Mexican material in appearance.

In the mountain ranges extending from central Arizona to western Texas there are also specimens which are anatomically similar to *Usnea arizonica* (described from Santa Clara County, central California), but which have different chemistry. The broadly ranging northern California specimens of *U. arizonica* typically contain salazinic and usnic acids, whereas those of Arizona and New Mexico may lack salazinic acid. Asahina (1968) reported usnic acid with localized thamnolic acid. Only usnic acid is found in most *U. cirrosa* specimens from the southwestern United States, although salazinic acid has also been detected. Specimens of *U. cirrosa* in UC from Mexico contain usnic, salazinic, and norstictic acids.

There is no apparent overlap in the ranges of *U. arizonica* and *U. cirrosa* with the *U. strigosa* group; the latter taxa evidently do not extend as far west as Big Bend National Park in Texas (see distribution map, Hale, 1979). *Usnea arizonica* differs only in minor anatomical characteristics from *U. subfusca* of the eastern United States, and might be regarded as a synonym; however, there is a wide range of morphological variation in both taxa which should be carefully studied.

In his enumeration of the lichens of Big Bend National Park, Wetmore (1976) listed only two short apotheciate taxa: *Usnea arizonica* (key characters included: medulla K+ red; with few large branches from main axis and fibrils unequal in length) and *U. cirrosa* (key characters included: medulla K-; equal-sized branches mainly from base, with fibrils about equal in length). Short, apotheciate *Usnea* species in the catalog of Arizona lichens (Nash and Johnsen, 1975) are *U. arizonica*, *U. erinacea* Vain. (original record from Darrow, 1950, with identifications by C. W. Dodge), *U. florida* (L.) Wigg., and *U. florida* forma *strigosa* Ach. (syn. of *U. strigosa* [Ach.] A. Eaton). Additional species included in the catalog for New Mexico (Egan, 1972) are *U. ciliifera* Motyka, *U. intermedia* (Mass.) Jatta and *U. retifera* Motyka (original records from Bouly de Lesdain [1932], presumably based on identifications by Motyka), and *U. tristis* Motyka.

With respect to the Arizona reports, it seems probable that the specimens identified as *U. strigosa* are conspecific with the Texas specimens referred by Wetmore to *U. cirrosa*, and that the specimens identified as *U. florida* correspond to *U. arizonica* with a K- medulla. *Usnea erinacea*, a Mexican species, has red-orange cortical cell lumina like those of *U. rubicunda* Stirt. (Tavares, unpublished). No specimens with this characteristic have been seen in southwestern collections by the present authors, although one specimen from Mt. Lemmon, Arizona (*W. A. Weber, s.n., COLO S1758*; UC), was discolored with a few small red spots.

Fig. 1. *Usnea cirrosa*, southwestern morphotype; Mt. Lemmon, Santa Catalina Mts., Arizona, *C. F. & W. L. Culberson 10546* (UC); branching pattern with crowded fibrils of equal length. Bar = 1 cm. Fig. 2. Enlargement of thallus in fig. 1; interrupted line shows thickness of cortex, white outer medullary layer, and axis. Bar = 1 mm.


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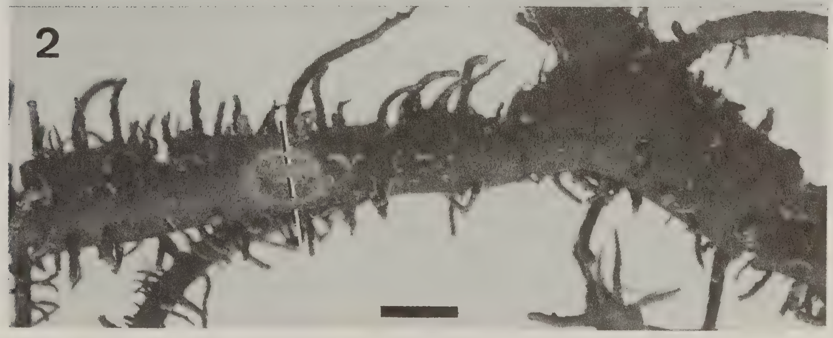
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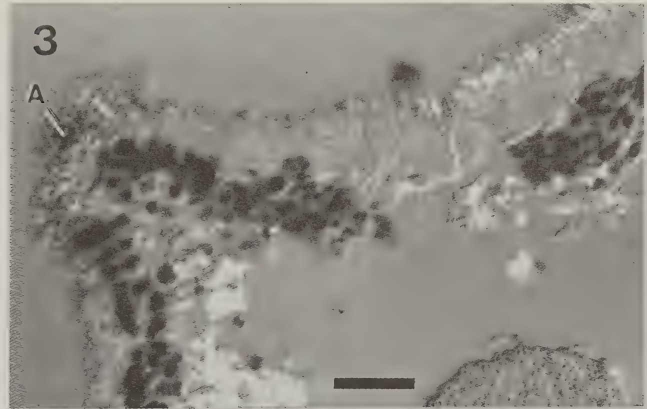
With respect to the New Mexico reports, Motyka apparently used the manuscript name *U. ciliifera* for the taxon he later described as *U. cirrosa*, judging from the label on specimens from La Cima Salazar in H (a collection of *U. cirrosa* was cited by Motyka [1936–38] from this locality). *Usnea intermedia*, a European species, was not reported for North America by Motyka (1936–38). *Usnea retifera* is closely allied to *U. arizonica*, and may be regarded as conspecific or as one of several taxa, mostly undescribed, comprising the *U. arizonica-U. subfusca* aggregate; material from the type collection (UPS) contains usnic and salazinic acids.

*Usnea tristis*, in the *Usnea strigosa* group in eastern United States, contains usnic acid and norstictic or psoromic acid. It has irregular papillation that produces inflated fibrils (see Tavares, 1987). Specimens resembling *Usnea arizonica* were issued under the name *Usnea tristis* Motyka as *Lich. Exs. COLO no. 116.* Because he detected thamnolic acid in specimens from *Lich. Exs. COLO no. 116*, Asahina (1968) referred the material to *U. florida*, which he also reported from Taiwan. However, Fiscus (1972) detected only usnic acid in one of several specimens that she tested (*UC 1317786, Lich. Exs. COLO no. 116*); furthermore, the spores are smaller (ca. 6.5 × 5μm) than those of *U. florida* (see Clerc, 1984).

Figs. 3–4. Cortical sections of *U. cirrosa*, southwestern morphotype, Socorro Co., New Mexico, *L. J. Giles 1134* (UC), lactophenol-cotton blue. Fig. 3. Portion of cortex showing marked variations in thickness locally (compare thickness at arrows). "A" indicates cluster of algal cells having reached most superficial portion of cortex, where they appear to be dividing in conjunction with surrounding fungal cells; probably represents early stage of fibril/branch development. Bar = 50 μm. Fig. 4. Young fibril (arrow) developing from algal and fungal cells in zone of thin cortex. Presence of algal cells near tip of structure and longitudinal orientation of surrounding fungal hyphae distinguish the young fibril from papillae. Bar = 30μm. Figs. 5–6. Sections of *U. cirrosa* thalli; Carindapaz, east of Ciudad Hidalgo, camino Maravatio-Senguio, Michoacán, Mexico, elev. 2200 m., 5.ii.1977, *L. Varela 157* (UC). Fig. 5. Localized proliferation of cortical tissue protruding upward to form papilla. Some hyphae arising from internal face of cortex appear to extend upward centrally into base of papilla. Lactophenol-cotton blue. Bar = 30μm. Fig. 6. Emergent apothecium, with deposition of red pigment on surface (indicated by arrow). Pigment may persist at edge of expanded disk. Bar = 100μm.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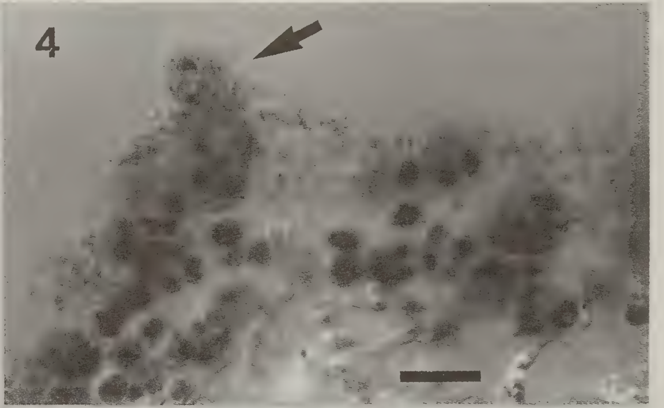
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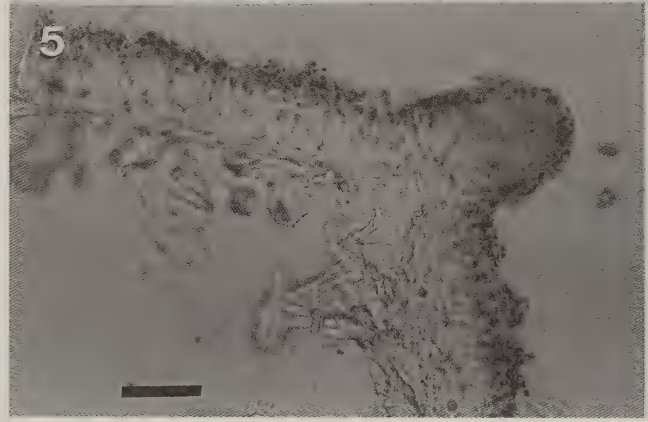
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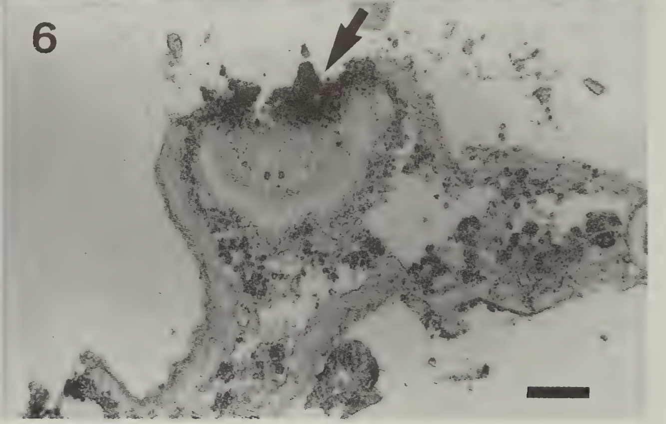
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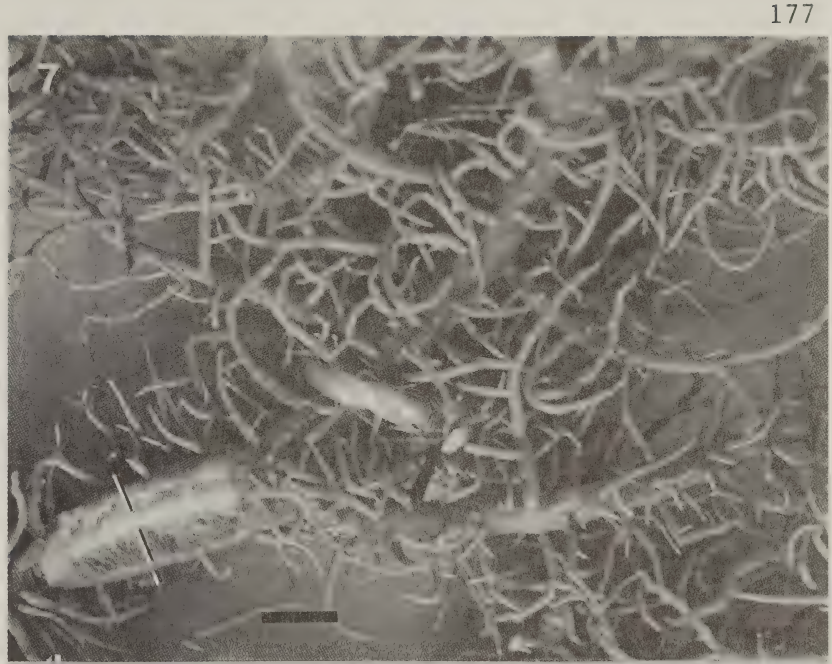
In contrast, *UC 1465808, Lichenes Americani Exsiccati* prepared by *M. E. Hale no. 225*, labelled *Usnea arizonica* Motyka, includes no specimens of *U. arizonica*, but only specimens similar in appearance to those from Big Bend National Park labelled *U. cirrosa* (*Anderson & Shushan s.n., COLO S18,676*). Most of these specimens have a narrow cortex, wide medulla with sparse hyphae, a moderately narrow axis, and apothecia with short, inflated marginal fibrils as in *U. cirrosa* of Mexico. However, unlike the Mexican specimens, which have fibrils and lateral branches of different lengths, the crowded, short, irregularly inflated fibrils of *UC 1465808* are even in length, their branches lack papillae, the outside of the cortex is densely granular, and only usnic acid has been detected, except for one specimen with usnic acid and a trace of salazinic acid. Included in the collection are specimens similar in appearance, but with wider axes and cortices; however, the outside of the cortex is covered with granules as in the more typical specimens.

Following is a key to the groups of short apotheciate taxa of *Usnea* in North America north of Mexico, contrasted to the Mexican morphotype of *U. cirrosa* and to *U. florida* (L.) Wigg. emend. Clerc (1984), which may be confined to Europe and western Asia. Because of the variation between individuals of *Usnea* species, several characters are usually given in most entries in the key; if, for example, the medulla is wider or denser than usual and the production of papillae minimal in a particular collection, one or two other characters should make an accurate identification possible. It may be necessary to cut away a small portion of the cortex of a specimen being keyed to expose the medulla and axis in the central part of the thallus, some distance from a branch base or the end of a segment. The term papilla is used here to include all frequently produced, rounded or cylindrical outgrowths of cortical tissue. In most of these taxa, fibrils often emerge from papillae, and papillae represent a stage in their development.

Fig. 7. Enlargement of thallus of *U. cirrosa*; *L. Varela 157* (UC); portion of cortex cut away, showing sparse medullary hyphae, thin cortex, and narrow axis (indicated by interrupted line); papillae sparse and indistinct. Bar = 1 mm. Fig. 8. Enlargement of thallus of *U. cirrosa*; Río Frío, Estado de México, Mexico, elev. 2750 m., *Frère Amable s.n.* (UC); shows abundant papillae (bracket), narrow axis and cortex (indicated by interrupted line), radiating medullary hyphae, and dense white outer medullary layer. Bar = 1 mm.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1. Base of thallus not black; papillae various or lacking. .................... 2
1'. Base of thallus black; papillae, if present, evenly cylindrical or tapered. ........................................................................................ 4

2. Papillation ranging from small to large papillae of irregular shape, from which fibrils may eventually extend; marginal fibrils of apothecia not crowded, some long and radiating; medulla of moderate density, sometimes with red pigment; eastern United States and Canada to Nova Scotia, west to Iowa, Minnesota, Arkansas, Oklahoma, eastern Texas.
.............*Usnea strigosa* (Ach.) A. Eaton aggregate (See Tavares, 1987)

2'. Papillae evenly cylindrical or tapered or else absent; marginal fibrils of apothecium short, crowded; medullary hyphae usually sparse; various geographical distributions.................................................................... 3

3. Papillae lacking; lateral branches and fibrils almost uniform in size; fibrils crowded, inflated or gradually tapering, uneven in outline; cortex often with dense outer granular layer; pycnidia not red-pigmented.
.............*Usnea cirrosa* Motyka (southwestern morphotype) (Figs. 1–4)

3'. Papillae present; lateral branches and fibrils of various lengths; cortex slightly shiny, without granular outer layer; pycnidia often red-pigmented.
..............................*Usnea cirrosa* (Mexican morphotype) (Figs. 5–9)

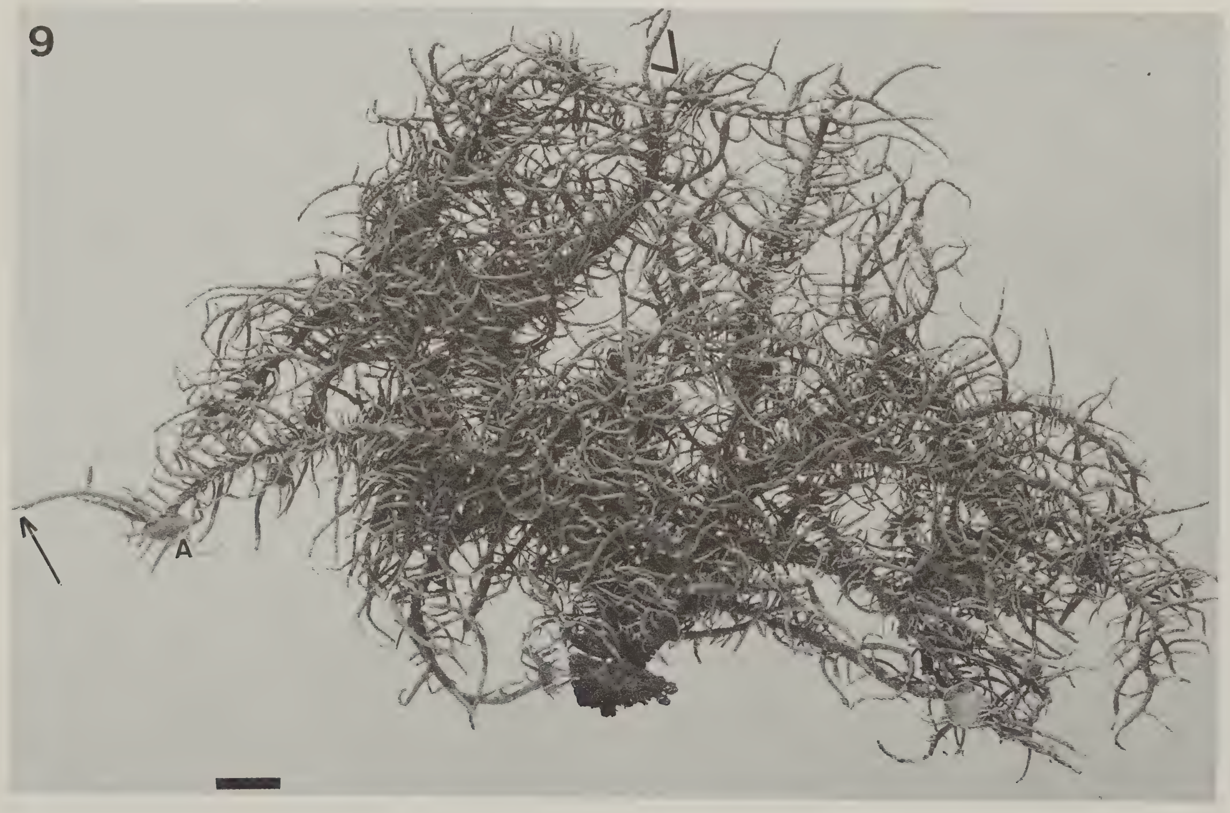
4. Base of thallus completely blackened; lateral branches widely differing in length, some fibril-like and others branching and rebranching; branches not inflated or constricted at base or at circumferential cracks; fibrils of different lengths, narrowing gradually from base; papillae present, sparse when fibrils numerous; marginal fibrils of apothecia uncrowded, often long................. 5

4'. Thallus with narrow black basal zone or irregular black marking; lateral branches and fibrils differing in length or almost uniform in size; branches sometimes constricted and inflated; fibrils often inflated; papillae present or absent; marginal fibrils of apothecia short, crowded............................... 7

5. Spores ca. 9–10.5(–12) × 6–7µm; cortex thick and medulla typically narrow, with densely interwoven hyphae; papillae often small, low, sparse; possibly restricted to Europe and western Asia.
.................*Usnea florida* (L.) Wigg. emend. Clerc (See Tavares, 1987)

5'. Spores ca. 6.5–9(–9.5) × 5.5–6.5(–7)µm; cortex and medulla usually moderate in width, the medullary hyphae loosely to densely interwoven; papillae usually abundant and regularly arranged, cylindrical, short to tall; North America. ............................................................................ 6

Fig. 9. *U. cirrosa*; Carrindapaz (older spelling), Michoacán, Mexico (19°41'07"N, 100°54'46"W; pers. comm., M. A. Herrera Campos), *G. Arsène 8052*, elev 2100 m., ii.1909 (Thomson Herbarium, ex Bouly de Lesdain Herbarium); densely fibrillose with red pycnidia (v-line above); arrow at left points to tip of branch bearing apothecium (A). Bar = 2 mm.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6. Papillae mostly regularly arranged, narrow in northern morphotypes, broader in Appalachian morphotype; fibrils gradually tapered, tips often subcapillaceous; branches and fibrils often conspicuously annulate (circumferentially cracked); Southern Appalachians, New Hampshire to Great Lakes (rarely found in the north).
.................................... *Usnea subfusca* Stirt. (Tavares, unpublished)
6'. Papillae narrow, often short, regularly arranged except when fibrils abundant; fibrils gradually narrowing to tip, not noticeably annulate; foveae sometimes present; abundant in Coast Ranges in Northern California, especially in oak woodlands; in scattered mountain ranges in Arizona, New Mexico, western Texas. .................... *Usnea arizonica* Motyka (Figs. 10–13)
7. Similar-sized large branches bearing short lateral branches of equal size and crowded short fibrils equal in length; outer cortex with dense granules; fibrils inflated or gradually tapering, uneven in outline; pycnidia not red-pigmented. ...... *Usnea cirrosa* Motyka (southwestern morphotype) (Figs. 1–4)
7'. Branches and fibrils of varying lengths; fibrils slightly inflated above base, evenly tapering; cortex slightly shiny on smaller branches and fibrils; pycnidia often red-pigmented; granules of red pigment persisting at edge of apothecial disks...... *Usnea cirrosa* Motyka (Mexican morphotype) (Figs. 5–9)

The following indicate some of the localities where these taxa have been collected in the southwestern United States. Lichen acid data are based partly on studies by Fiscus (1972) and partly on our chromatographic results (see Culberson et al., 1981):

***Usnea arizonica*:**
**Arizona**: Cochise Co., with *U. cirrosa*, Barfoot Park, 27.ix.1906, on *Pinus*, Flora of the Chiricahua Mountains, Arizona, U. S. A., no. *1430*, *J. C. Blumer*, elev. 2438–2510 m. (DS; det. as *U. cirrosa* by A. W. C. T. Herre; usnic, salazinic acids); Pima Co., Santa Catalina Mts., Mt. Lemmon, s. slope, on *Pinus*, *W. A. Weber s.n.*, 1.xi.1952 (*COLO S1758*; UC; det. as *U. arizonica* by Herre), usnic acid, one also with salazinic acid).

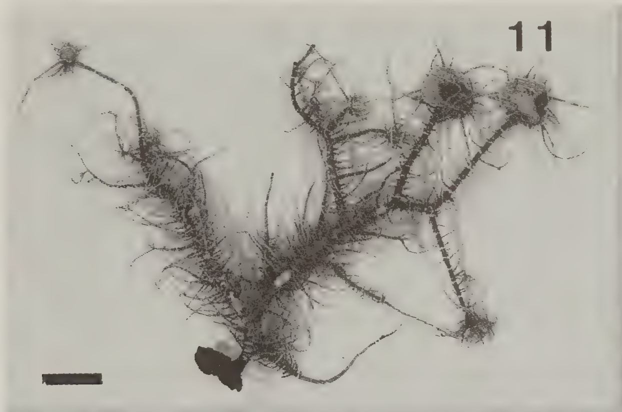
Fig. 10. Enlargement of thallus of *U. arizonica*; mixed conifer-hardwood forest, 1 mi east of Robert L. Stevenson State Park, Mt. St. Helena, elev. ca. 3000 ft., Sonoma-Napa Co. line, California, 8.iv.1971, *I. Tavares 2434 & E. Brubaker* (UC); shows axis and medulla of moderate width, with dense outer medullary layer; papillae in scattered groups (arrow). Bar = 1 mm.


10

**New Mexico**: Grant Co.-Sierra Co. line, Emory Pass, on conifer bark, *I. Tavares 4395 & E. Brubaker*, 14.iv.1996, 2499 m. (UC; usnic, salazinic acids, unknown in one specimen); Otero Co., 1 mi. s. of Cloudcroft, on *Abies concolor*, *W. A. Weber s.n.*, 23.iv.1964 (*Lich. Exs. COLO no. 116*, as *U. tristis*; UC; usnic acid); 1 mi. e. of Cloudcroft, under conifers, *I. Tavares 4375 & E. Brubaker*, 11.iv.1996, 2581 m. (UC; usnic acid).

***Usnea cirrosa* (southwestern morphotype):**
**Arizona**: Cochise Co., Chiricahua Mts.: Barfoot Park, on *Pinus*, Flora of the Chiricahua Mts., Arizona, U. S. A., no. *1430*, *J. C. Blumer*, 27.ix.1906 (DS; det. as *U. cirrosa* by Herre; usnic acid); Chiricahua Mts., Coronado Nat. Forest, Fly Peak Trail, *M. E. Hale s.n.*, 30.v.1977, 2700 m. *(Lichenes Americani Exsiccati no. 225* (as *U. arizonica*; usnic acid or usnic with salazinic acid); Graham Co., Graham Mts., top of Heliograph Hill near Stafford, on *Picea engelmannii*, *C. G. Humphrey s.n.*, 22.x.1935, 2804 m. (DS; det. as *U. arizonica* by Herre; usnic acid); Pima Co., Santa Catalina Mts., Mt. Lemmon, on *Pinus*, *C. F. & W. L. Culberson 10546*, 13.vi.1961, 1829–2438 m. (UC; det. as *U. cirrosa* by Motyka; usnic acid); Pima-Cochise Co. line, Rincon Mts., Manning Camp, on *Pinus reflexa*, *J. C. Blumer s.n.*, 10-12-1909, 2408 m. (DS; det. as *U. florida* by Herre; usnic acid, unknown).
**New Mexico**: Bernalillo Co., Sandia Cave, Sandia Mts., 2499 m., *C. B. Jones 178*, 17.ii.1968 (UC; usnic acid); Lincoln Co., Capitan Mts., Grays Peak on conifer, 1981 m., *B. Fink s.n.* (UC; det. as *U. florida*; usnic acid); Quay Co., e. of Tucumcari near Texas border, on *Juniperus*, *F. A. Wiley s.n.*, viii.1940 (DS; det. as *U. cirrosa* by Herre; usnic acid); San Miguel Co., Pecos, on *Pinus*, *D. Richards & F. Drouet s.n.*, 21.x.1939, 2100 m. (UC; det. as *U. florida*; usnic acid); Socorro Co., 12.5 miles w. of Magdalena, on *Pinus edulis*, *L. J. Giles 1134*, 5.vi.1972, 2195 m. (UC; usnic acid).

Fig. 11. Thallus of *U. arizonica*, Cloudcroft, New Mexico, *I. Tavares 4375 & E. Brubaker*, showing branching pattern. Bar = 1 cm. Fig. 12. Papillation in *U. arizonica*; on branches of *Quercus*, roadside at 21000 Fort Ross Rd., near Cazadero, Sonoma Co., California, *W. B. Sanders 97623.1*, 23.vi.1997; tissue proliferation in upper portion of cortex often appears to cause some tissue splitting in lower portion of cortex at base of papilla (arrow). This creates a hollow through which photobiont cells may penetrate into upper regions of the cortex, eventually stimulating organization of a fibril/branch at the site of the papillation. Bar = 30µm. Fig. 13. Papillation and sparse fibrils, *U. arizonica*; on *Salix scouleriana*, Larrabee Valley, Humboldt Co., California, elev. 670 m., *J. P. Tracy 8721*, 25.v.1930. Bar = 1 mm.



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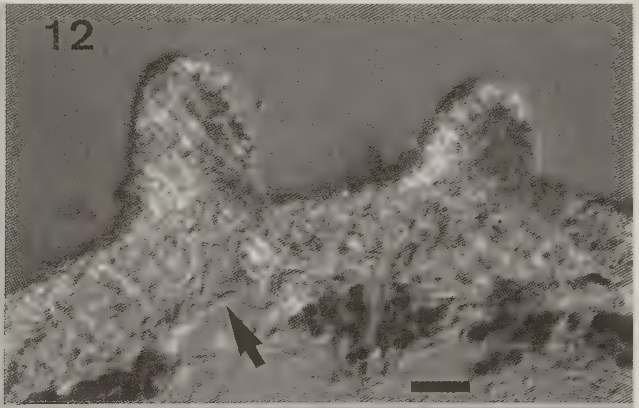

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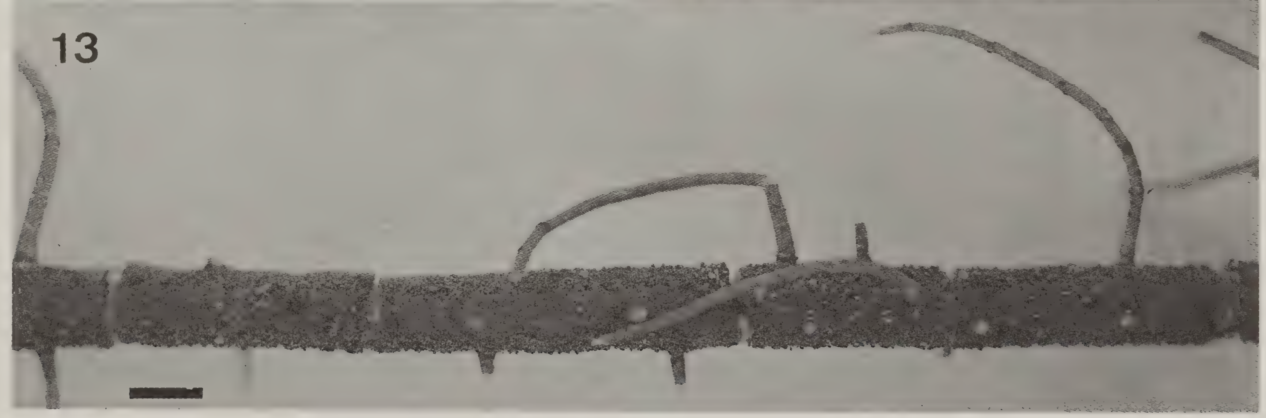

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**Texas**: Brewster Co., on *Pinus cembroides*, Big Bend Nat. Park, S. rim trail to Emory Pk., Chisos Mts., *R. A. Anderson & S. Shushan s.n.*, 8.vi.1959, 1524–2134 m. (*COLO S18,676*; UC; usnic acid); Jeff Davis Co., top of Locke Mt. at McDonald Observatory, on *Pinus edulis*, *D. Griffin III CL 40*, 23.vii.1968, 2069.5 m. (FSU; usnic acid).

In a collection of *Usnea arizonica* from a mixed forest of *Quercus*, *Juniperus*, *Pinus ponderosa*, and *Pseudotsuga* at Emory Pass, New Mexico (*I. Tavares 4395 & E. Brubaker*), papillae were often lacking; the medulla was broad and very loosely interwoven, resembling that of the regional morphotype of *U. cirrosa*; yet numerous, long, lateral branches, sparse, long, tapering apothecial fibrils, and a smooth, non-granular cortical surface suggested that this was an unusual population of *U. arizonica*, rather than *U. cirrosa.*

Branching pattern, chemistry, presence of papillation, and other characters separate the Mexican morphotype of *U. cirrosa* from the southwestern U.S. morphotype. However, there may be considerable differences in internal characters among specimens in the Southwest. For example, the medulla may become compact at breaks in the cortex and in the interior near exposed areas. In some specimens that otherwise are quite typical in appearance, the cortex can be quite thick and seems to form extra layers of cortical cells toward the exterior. Further study is needed in order to determine the range of characters involved. In the southwestern morphotype of *U. cirrosa*, the cortex may be covered with dense granules and consequently is dull in appearance. Along the branches, the dense, short fibrils, almost equal in length, are often irregularly undulant in outline. It may be advisable to describe the southwestern morphotype as a separate species.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
IN HONOR OF JOHN W. THOMSON.
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MYCOTAXON LTD., ITHACA, NY. 1998.

# *USNEA WIRTHII* IN WESTERN NORTH AMERICA

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## SUMMARY

*Usnea wirthii* Clerc in western North America is generally characterized by conspicuous dark red spots composed of clusters of cortical cells with red-pigmented walls; also characteristic are the variably inflated, minutely papillate branches bearing soralia. The most distinctive features are the narrow yellowish axial cord and wide medulla, which consists of a dense outer layer and a wide inner zone of sparse, distinct hyphae. A golden-yellow periaxial medullary layer is frequently present. Spot frequency, spot size and shape, intensity of red in spots, form of papillae, and frequency and form of soralia (sometimes isidiose, sometimes granular), arrangement of medullary hyphae, axial cord width, pigmentation of axial cord (sometimes lacking), and degree of inflation of branches all seem quite variable. Norstictic acid is commonly present in Californian specimens, whereas psoromic acid, though uncommon, may be randomly distributed geographically. However, these two acids appear to be accessories to two more or less constant unknowns and to usnic acid, which are the main secondary lichen products.

A short, soraliate *Usnea* bearing scarlet to crimson red spots is one of the most frequently encountered taxa along the Pacific coast in California. It was well known to A. W. C. T. Herre, who, on at least one occasion (annotation of UC 1206382), regarded the red spots as evidence of "disease." Elsewhere, Herre used the never-published name *Usnea glabrata* var. *rufomaculata* (referring to the red spots) to annotate a specimen (UC 1320520; Pilarcitos Canyon, San Mateo Co., *R. F. Cain s.n.*, 24.viii.1957; TRTC 26247). The taxon was formally described as *Usnea wirthii* by Clerc (1984), who based his description on specimens from continental Europe and North Africa. In a later publication (Clerc and Diederich, 1991), Great Britain and the west coast of North America were added to the range of the species. In the protologue, *U. wirthii* is described as a short, soraliate species characterized by yellow pigment in the axial cord and the adjacent medulla. Red spots are not mentioned in the original description, which was based on material that had become discolored during herbarium storage. Neither were the red spots mentioned in the first report of the species in North America (old collections from Washington—Clerc and Diederich, 1991). In her discussion of *U. glabrata* in British Columbia, Noble (1982) described red-spotted specimens, which were almost certainly *U. wirthii*, and concluded that she could not see evidence of infection associated with the red cortical spots. The red spots were mentioned as a characteristic of *Usnea wirthii* for the first time in Purvis et al. (1992), where they were described as purple. *Usnea wirthii* bears some resemblance to *U. glabrata* (Ach.) Vainio because of the soralia and inflated branches. In western North America, the red spots are sometimes confused with the orange-red cortical color in *U. rubicunda* Stirton. Consequently, one might expect to find *U. wirthii* misfiled in herbaria under these latter two names, or under *U. rubiginea* (Michaux) A. Massal., an epithet incorrectly applied to *U. rubicunda*. However, the cortical color in *U. rubicunda* is a less intense orange-red. The red spots in *U. wirthii* fade or become blackish and inconspicuous during herbarium storage, whereas the orange-red color remains visible in *U. rubicunda* and can be seen best in cortical sections.

Fig. 1. Specimen from *Rhamnus ilicifolia* Kellogg, 24.4 mi. s. of Gualala along coast, Sonoma Co., *I. Tavares 327* (with Joan Seear), 7.VI.1959); axial cord is exposed between some inflated segments; soralia mostly near branch apices. Each space on scale = 1 mm.

Fig. 2. Specimen from *Baccharis pilularis* DC., along Rabbit Run Trail, Tilden Nature Area, Tilden Regional Park, Berkeley Hills, Contra Costa Co., *R. Russo s.n.*, 8.I.1968. Note the curled soraliate tips of the branches; small soralia widespread on large branches; arrow to base of thallus. Bar = 5 mm.

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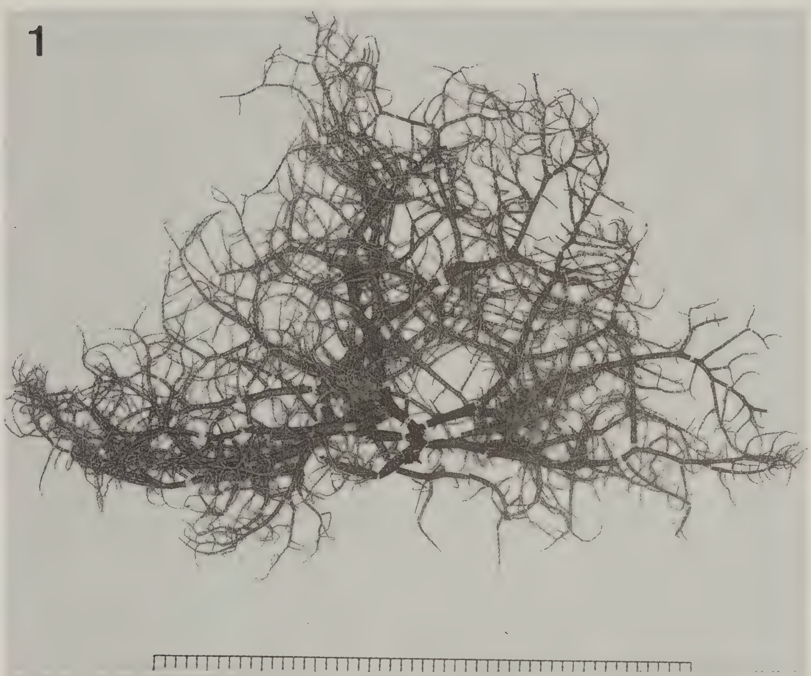

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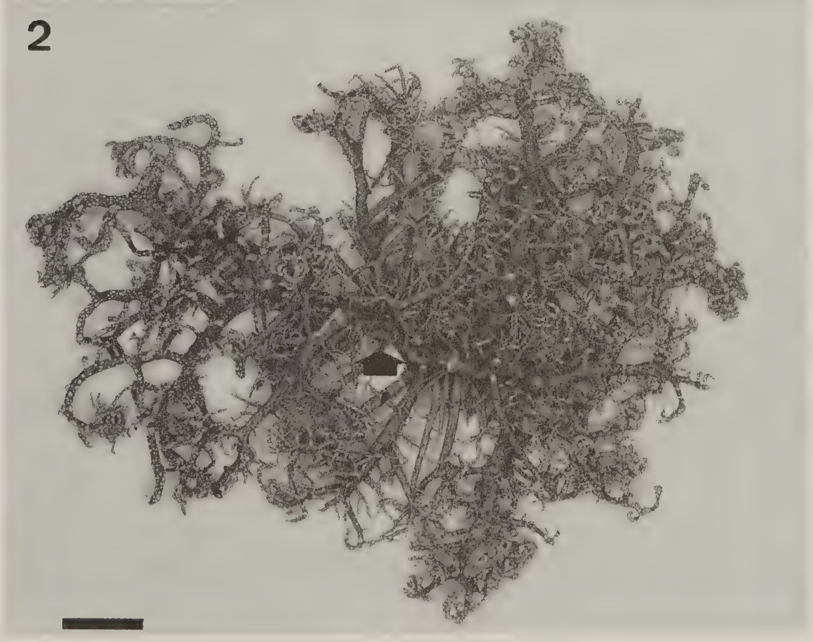


In North America, the most northerly known collections of *Usnea wirthii* are from Queen Charlotte Islands, Vancouver Island, and mainland British Columbia (Goward, Diederich, and Rosentreter, 1994; Goward and Schofield, 1983; and Noble, 1982, as a red-spotted form of *U. glabrata*). The most southerly known collections come from Punta Banda Peak on the Pacific coast of Baja California (*P. A. Bowler 509*, 25.xi.1971 [IRVC]) and an area further south near the center of the peninsula, west of Bahía de Los Angeles (*Walter Appleby 104*, 15.xi.1991 [UC]).

In California from the San Francisco Peninsula northward, it is common in coastal areas and in valleys and canyons extending eastward in the outer Coast Ranges. It often occurs as isolated thalli among other short *Usnea* species. It is found in all coastal counties from Del Norte County south through Santa Barbara County and in the Channel Islands. In the Eureka-Arcata area in Humboldt County, it has been observed at localities 6.5–19 km. from the coast. It is widespread in Sonoma and Mendocino Counties. In Marin County it is concentrated in a zone extending 16 km. inland. It has been found up to about 47.5 km. inland (St. Helena Rd.-Spring Mountain Rd., n. e. of Santa Rosa, Sonoma Co.; *I. Tavares, 1330c* [UC]). It is common in the Oakland-Berkeley Hills of Alameda and Contra Costa Counties. In Oregon and Washington it ranges inland to the western Cascades (McCune & Geiser, 1997). Thalli are generally on twigs and branches of various trees and shrubs, and rarely occur on rocks (for example, *S. C. Tucker 6494* in part, Bodega Bay, Sonoma Co. [UC]).

In California, the taxon takes various forms. Some specimens are long (to 7–10 cm.), strongly inflated, flaccid, and have an extremely narrow axial cord (figs. 1, 3; cortex ca. 50–60 μm, medulla ca. 200–225 μm, axial cord ca. 125–150 μm in width). Other thalli are short, slightly inflated, and more rigid. Strongly inflated segments, often with foveolae (shallow to deep depressions with rounded edges), are characteristic of many specimens, and there may be relatively long expanses of bare axial cord between segments (figs. 1, 3); in such thalli, the surface is generally shiny, with crowded, low, narrow-based papillae.

Papillae are localized protrusions of the cortex which initially are not accompanied by algae and medullary hyphae. Cortical protrusions that are low and broad-based, with strongly sloping sides, may be regarded as verruculae, and tend to open apically into soralia.

Fig. 3. Detail of branches of *Tavares 327*, showing narrow cortex and axial cord (between gaps in black line), wide medulla, red spots (indicated by v-line), exposed axial cord (arrow), and papillae (bracket). Bar = 1.4 mm.

3

Clerc (1987) mentioned low, subhemispherical lumps broader than tall, but he did not provide a term for them; Asahina (1956) described verruculae as minute pimples gradually raised from the surface and eventually perforated. The tubercles in fig. 26b on p. 623 in Purvis et al. (1992) protrude strongly, unlike the inconspicuous soralia-producing protuberances in *U. wirthii.*

Some specimens are compact, with crowded branches, and have slightly shiny, inflated branches abundantly covered with verruculae; narrow-based papillae may occur only in a few places (fig. 2; cortex ca. 50–60 μm, medulla ca. 250 μm, axial cord ca. 150 μm in width). Other, divergently branched thalli have slightly shiny cortex, variable papillation, and weakly constricted articulations marked by a white margin of medullary tissue (figs. 4, 5; cortex ca. 60 μm, medulla ca. 225 μm, axial cord ca. 275 μm in width).

The soralia are variable in size and occur chiefly near branch apices and on short branchlets or fibrils; they arise through small openings on inconspicuously elevated, broad-based protrusions, and then enlarge, but rarely envelop the branch tips. Often, soralia are more widely distributed and occur close together on thalli in which the papillation on larger branches is broad-based (figs. 2, 4). Small isidioid structures sometimes occur in the soralia.

Young, white fibrillar initials emerge individually through protrusions in the cortex. The cortex of the protrusion remains as a short pedestal-like elevation subtending the fibril, which darkens in color and elongates. Thalli with many fibrils have fewer large expanses of papillae than sparsely fibrillose specimens. When soralia are widespread on the thallus, there may be only a few places where groups of narrow papillae occur (for example, the thallus in fig. 2). Papillae vary somewhat in size and shape. They do not arise simultaneously but new ones are produced seemingly at random among existing papillae. Well-developed papillae are ca. 50 μm tall, ca. 45 μm wide at the base and ca. 35 μm wide at the apex, and they appear to be short-cylindrical with rounded apices (fig. 3). Shorter, younger papillae slope to a more pointed apex (figs. 6, 7).

Fig. 4. Specimen from chaparral, along Martin Rd. ca. 0.5 mi. from junction with Pine Flat Rd., 0.7 mi. from Bonny Doon, Santa Cruz Co., *S. C. Tucker 6412*, 25.IV.1966 (UC 1403604). There is little inflation of segments, which are separated by white medullary rings. Each space on scale = 1 mm.

Fig. 5. Detail of branches of *Tucker 6412*, showing papillation (see arrow), abundant small soralia on larger branches (bracket), excavate soralia near branch apices (indicated by v-line), flared ends of some segments with white medulla exposed (see lines). Bar = 0.8 mm.


4


5

At first, in the formation of red spots, a faint tinge of color may be seen; later, the area may turn a deeper red. Sometimes red spots appear to "bleed" into surrounding cortex or have red papillae arising from them. Red spots may be strongly concentrated on the side of the thallus exposed to the sun.

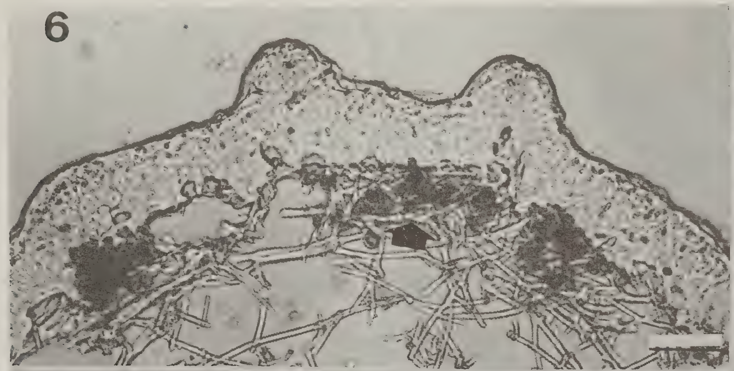
Cortical cell lumina are moderate in width (ca. 1.25–1.50 [–2]) µm; figs. 6, 7) and the red portions of the cortex consist of areas with deposition of red pigment in the cortical cell walls surrounding the cell lumina (figs. 8, 9). In well developed red spots, some lumina may be darker than the surrounding wall material, indicating that pigment has entered the cytoplasm.

The medulla of *U. wirthii* is composed of sparse medullary hyphae, either radiating toward a narrow, dense, outer medullary layer, or else very loosely interwoven. Few specimens have been seen that have relatively wide axial cords and little inflation (see figs. 4, 5; in this thallus, the outer dense medullary layer is thicker than usual).

Although the measurements given by Clerc (1984) indicated that the medulla is narrower than the axial cord, he mentioned inflation of branches associated with a very lax medulla, and bare stretches of axial cord between some segments as well as annular cracks with white rings of medullary tissue. He described the medulla as being dense or sublax, whereas in North American material it is generally extremely lax, with sparse medullary hyphae.

*Usnea wirthii* was described as having psoromic acid (two unidentified substances and an unknown fatty acid were also mentioned); additionally, the existence of a norstictic acid chemotype was reported near Barcelona, Spain (Clerc, 1984). The specimens from Washington and from Britain, reported by Clerc and Diederich (1991), contained psoromic acid. However, Clerc (1997) indicated that norstictic acid is typical of areas outside of Europe (more specifically, it is common in British Columbian specimens, as reported by P. Halonen [pers. comm.]).

Figs. 6–9. Strawberry Canyon, Berkeley Hills, Alameda Co., *W. Sanders s.n.*, V.1997. Figs. 6–7. Transverse sections of papillate cortex; lactophenol-cotton blue stain. Fig. 6. Two papillae on surface; dark algae (see arrow) and medullary hyphae visible under cortex. Bar = 40 µm. Fig. 7. Papilla, enlarged; cortical cell lumina visible (between lines), with dark algal cells and medullary hyphae in interior. Irregular hyphal growth below papilla (indicated by arrow) may be initial stage in fibril formation. Bar = 20 µm. Figs. 8–9. Transverse cortical sections at red spot. Bars = 10 µm. Fig. 8. Darker cortical color in the central spot (between arrows) extends down through the cortex. Fig. 9. Section at slightly different level, showing the dark color enveloping the cortical cell lumina (indicated by v-line). Note irregular junction of medulla and cortex (see arrow).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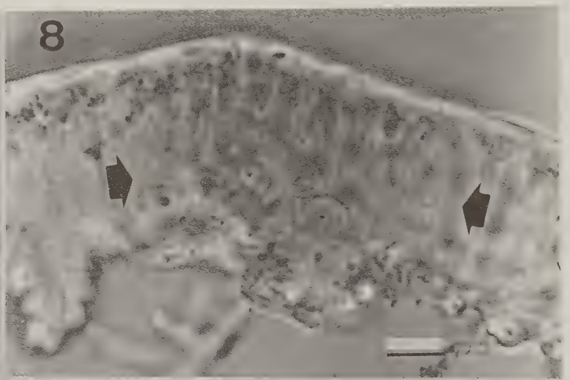
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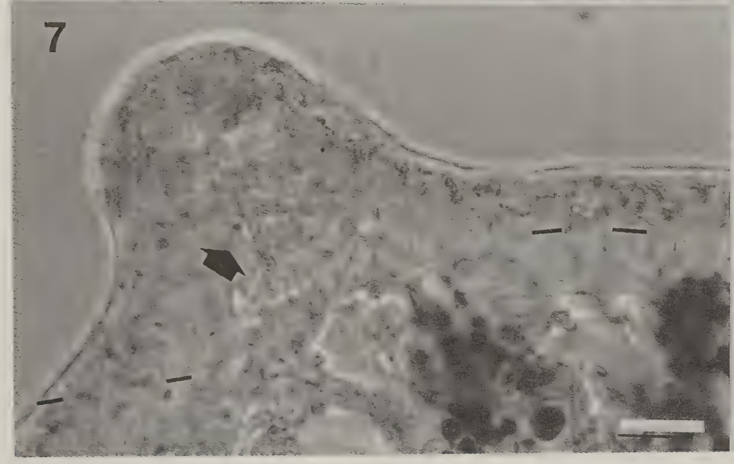
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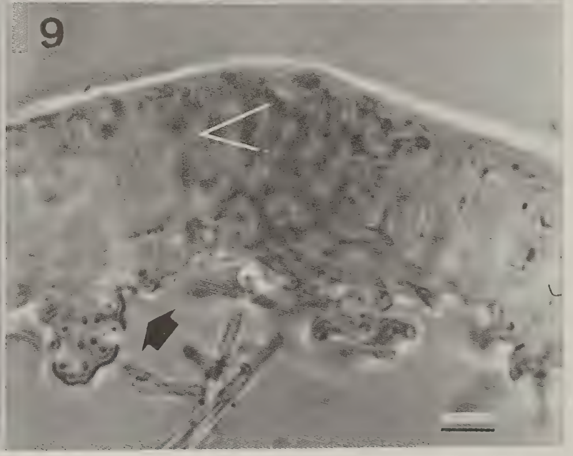
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A preliminary chromatographic survey of 41 collections of *Usnea wirthii* from nearly the full range of the species on the Pacific coast of North America was carried out. This survey showed that norstictic and psoromic acids behave like inconstant accessories to usnic acid and two more or less constant unknowns, which are the principal and characteristic secondary products in our area. These form spots between psoromic acid and salazinic acid in standard solvent G (Culberson et al., 1981). An effort is under way to definitively identify the unknown substances and to survey more material. There are other variably present accessory substances (D. Wright, unpublished). Much of the southern material has accessory norstictic acid, while psoromic acid is uncommon but not rare and may be randomly distributed geographically.

With respect to yellow pigmentation, Clerc (1984) did not mention the other examples that have been reported in the literature—for example, *Usnea flavocardia* Räsänen of Chile (Räsänen, 1936) and *Usnea grandisca* Motyka of Peru (Motyka, 1936–1938). *Usnea grandisca* was described as having a wide, sulphur-yellow medulla with a rusty rose subcortical layer.

A comparison of *U. wirthii* with the type collection of *U. flavocardia* (H) shows the following differences, in addition to the densely divided branch apices of the latter: in *U. flavocardia*, the medulla is more densely interwoven, almost cottony, and lacks a distinct, dense, outer medullary layer. There is noticeable looseness only in medulla of the wider branches, as compared to western North American *U. wirthii* and to Corsican material (Ponte Leccia, on *Erica arborea*, 160 m. elev., 29.vii.1968. K. Kalb [Kalb Herbarium]), which have very sparse medullary hyphae and a dense outer layer. Both species have narrow axial cords and thin cortices.

In *U. flavocardia*, very small fibrils and the tips of larger fibrils have pale red areas in which dark red pigment surrounds cortical cells and appears in the inner wall layers of those cells, as well as being diffusely distributed through the cortex. The surface of the cortex is covered with small, broad-based papillation; on fibrils and small branches, these papillae form crowded, small soralia that may fuse and become excavate.

The red pigmentation in *U. wirthii* is similar to that of *U. michauxii* I. I. Tav., an apotheciate taxon of southeastern United States (Tavares, 1987). In *U. michauxii* (medulla wide, cottony, the medullary hyphae interwoven, with a thick, dense, outer layer) there is also a concentration of dark red color in small spots in the cortex. The color seems to be diffused through the cell walls in the cortex and appears to be in some lumina; it is a deeper red than the color in cortical cell lumina of *U. rubicunda*. Red pigmentation also occurs in some specimens of *U. cirrosa* Motyka (I. Tavares and W. Sanders, unpublished).

There is considerable variation in *U. wirthii* in western North America, with some shiny, almost smooth, extremely inflated specimens having long bare expanses of axial cord between some segments, and other duller, more compact specimens having more conspicuous papillae and white medullary rings separating weakly inflated segments. Thin cortices, red spots and yellow axial cords, together with sparse medullary hyphae, are the primary characteristics for recognition of this taxon in western North America. Specimens without spots have perhaps been overlooked because other diagnostic characters have not been taken into account.

In Europe, North Africa, and the Canary Islands, a similar amount of variation might be expected. However, the variants in that area might be quite different in branching pattern, axial cord width, and cortical and medullary characters. Small thalli from Tenerife, Canary Islands, were heavily red-spotted with cortical cell lumina ca. 1.25–1.5 µm wide and the axial cord was golden yellow (on *Erica arborea*, *P. C. Silva s.n.*, 8.x.1991 [UC]). In specimens from Ponte Leccia, Corsica (on *Erica arborea*, 160 m. elev., 29.vii.1968, *K. Kalb s.n.* [Kalb Herbarium]), cortical cell lumina were ca. 1–2 µm wide, but red spots were not evident and the axial cord was yellowish; the thalli were abundantly papillate, with short, thin fibrils. Among specimens that might be included in *Usnea wirthii* in a broad sense were thalli from southeast of Chechaoen, Rif Range, Morocco (3.vi.1971, *W. L. Culberson & C. F. Culberson 15,648* [DUKE]; cortical cell lumina ca. 2–3 µm wide, mostly uncolored axial cords, abundantly long-fibrillose, without noticeable papillation and lacking red spots) and a thallus from La Gomera, Canary Islands (SE of Garalonay, on *E. arborea*, *P. Clerc 11631–11633* [in part], 23.ix.1986 [BERN]; cortical cell lumina ca. 1.5–3 µm wide, a mostly uncolored axial cord, abundant short fibrils, some papillate areas, red spots absent).

The possible pattern of morphological and anatomical variation among specimens of *Usnea wirthii* in Chile should be investigated (see report of its occurrence in Aconcagua Province; Clerc, 1997). A specimen collected farther north in Chile (Coquimbo Province, Department Ovalle, Las Cardas, on twigs of *Fuchsia lycioides* along with taxa having dense medullas, *C. Skottsberg s.n.*, 1.V.1955 [H]) has the following characteristics: 1. red spots, a wide medulla with sparse hyphae, and a yellow axial cord; 2. small, low, broad-based verruculae, very sparsely distributed and with no indication that narrow-based papillae also occur; 3. soralia widely separated and enlarging to envelop the branch apices, leaving the axial cord exposed; 4. cortical cell lumina ca. 2–3 µm wide; 5. Sparsely divided branch apices.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
IN HONOR OF JOHN W. THOMSON.
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# LICHENS AND ALLIED FUNGI OF SOUTHEAST ALASKA

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## ABSTRACT

A checklist of 508 lichen and allied fungal species with regional habitat, distribution and abundance information has been compiled for southeastern Alaska. The lichen flora of this region is a rich mixture of Pacific Northwest temperate rain forest and Arctic components, and is enhanced by topographic and habitat variations within the region. Great expanses of old-growth forests and excellent air quality provide habitat for many lichens elsewhere rare or imperiled. New to Alaska are: *Biatora cuprea*, *Biatoropsis usnearum*, *Calicium adaequatum*, *Candelaria concolor*, *Cetraria islandica* ssp. *orientalis*, *Chaenotheca brunneola*, *Chaenothecopsis pusilla*, *Cladonia dahliana*, *Cystocoleus ebeneus*, *Erioderma sorediatum*, *Gyalidea hyalinescens*, *Hydrotheria venosa*, *Hypocenomyce sorophora*, *Ionaspis lacustris*, *Lecanora cateilea*, *Lecidea albofuscescens*, *Leptogium brebissonii*, *Mycoblastus caesius*, *Nephroma occultum*, *N. sylvae-veteris*, *Trapeliopsis pseudogranulosa*, *Usnea chaetophora*, *U. cornuta*, and *U. fragilescens*. New to the US are: *Calicium lenticulare*, *Heterodermia sitchensis*, *Leptogium subtile*, and *Tremella hypogymniae*.

## INTRODUCTION

For this special volume of papers we present an updated checklist of lichens and their habitats in the southeastern region of Alaska, a state long favored by Dr. Thomson's investigations. Although still incomplete, this checklist represents over 100 years of exploration, from early coastal surveyors to modern lichenologists. Like Dr. Thomson, all have appreciated the beauty and diversity of life offered by the Fungal Kingdom in remote Alaska. We hope this checklist will be used as a conservation tool and as a starting point for further additions to the regional lichen flora.

## HISTORY OF LICHENOLOGY IN SOUTHEAST ALASKA

Lichenological exploration of the southeastern region of Alaska, known locally as Southeast Alaska, has a relatively short history. In a detailed summary of historic expeditions, outlined here, Krog (1968) credits the earliest botanical collections to A. Kellogg, surgeon to the US Coastal and Geodetic survey party in 1867. Lichens he collected were reported by Tuckerman (1882). Members of later US coastal surveys, W.H. Dall and T.H. Bean (Rothrock 1884) also collected lichens. Grace E. Cooley (1892) and James M. Macoun of the Canadian Geological Survey (1902) made important early collections of vascular plants and lichens (Brodo 1995a). R. Reuleaux (Stizenberger 1895), and R.S. Williams (Howe 1911) collected a few lichens at Sitka and Skagway, respectively. In 1904, Cummings reported on collections by W.M. Canby, W.H. Evans, and W. Trelease and other members of the Harriman Expedition. Some of these collections are still unique and are cited in the present report.

Twentieth century investigations include those of McKechnie in Ketchikan (Howe 1913), A.S. Foster, T.C. Frye and D. Waynick (Herre 1919, Magnusson 1932), E. Hultén (Degelius 1937) and W.J. Eyerdam (Thomson 1950). L.D. Stair collected in Yakutat (1947), C.J. Heusser in the Juneau icefield (1954), and H.A. McCullough in the Mendenhall Valley (1965). Of these, several collections identified by Herre, Heusser and McCullough are still unique to the regional flora.

The first modern flora to include Southeast Alaska, *Macrolichens of Alaska*, was prepared by H. Krog (1968). It included species from her forays to 14 different sites in Southeast Alaska during the 1950s, the earlier reports, and previously unreported herbarium specimens. J.W. Thomson's now standard reference, *American Arctic Lichens 1. The Macrolichens* (1984), mapped the distribution of arctic species in se AK, with many new species and locations since Krog's report. In 1967, J.W. Thomson and T. Ahti collected in Haines and at milepost 33 on the Haines Highway in a *Populus trichocarpa-Picea sitchensis* forest (Thomson & Ahti 1994), adding additional species to the regional flora. In 1997, R. O'Clair, S. Lindstrom and I. Brodo described marine lichens of Southeast Alaska's intertidal, salt spray and splash-influenced zones. T. Tønsberg's visits have also been productive (e.g. 1993 and other species in this list). The 1980's and 90's have seen immense progress toward the solution of regional taxonomic problems by many researchers, especially Irwin Brodo and Trevor Goward in neighboring Queen Charlotte Islands and British Columbia, respectively (see Brodo 1995a and the "Literature Cited" section of this paper). These taxonomic works have been critical and prerequisite to the present inventory of lichens in Southeast Alaska.

Explorations previous to the 1970s emphasized areas near towns in Southeast Alaska, especially Juneau, Sitka, Ketchikan, Haines and Skagway. This was a natural consequence of the roadless condition, rugged terrain, high transportation costs, and general inaccessibility of the region. Beginning in 1980, one of the authors (Stensvold) started collecting lichens in remote areas throughout the region as an ancillary activity to other US Forest Service field work. Between 1989 and 1993 the present authors began a systematic inventory of lichens in forested and alpine habitats throughout se Alaska as part of an air quality study for the Tongass National Forest (Geiser et al. 1994a). Assisted by float plane, helicopter, boat and other resources of the US Forest Service, we were able to investigate many previously unexplored areas and compile comprehensive habitat and distribution data for lichens, emphasizing macrolichens, from about 275 sites (Geiser et al. 1994b). That work increased the regional inventory to 453 species, a little less than half new to se Alaska. The present list adds 58 species collected by us and others since 1994, updates nomenclature, includes voucher numbers for rare and poorly known species, and improves the habitat information provided in the first inventory.

## STUDY AREA

Southeast Alaska is a narrow geographic area, about 190 km wide by 900 km long. It is oriented in a northwesterly-southeasterly direction, located between 54°40' and 60°30' N, and between 130° and 140° W (Fig. 1). It is bounded on the west by the Pacific ocean, to the north by the Fairweather Mountain Ranges and to the east by the Coastal Mountain Range. A myriad of mountainous, fjord-cut islands, known as the Alexander Archipelago, dominates Southeast Alaska. Some mainland peaks exceed 3000 m in height, while those on the islands are generally less than 1200 m tall. The surficial landscape reflects a combination of glacial sculpting, tectonic uplift, and isostatic rebound. Common topographic features include steep slopes, deep valleys, fjords, glacial horns, arêtes, U-shaped valleys, moraines, and outwash plains. Most active glaciers are located on the mainland and are retreating. Some reach salt water, creating sea-level arctic-alpine habitats near their termini. The ten major rivers of the region originate in Canada. The Stikine River has the largest drainage area, followed by the Alsek, Taku and Chilkat. In the extreme north, the Yakutat area consists of a foreland of glacial and marine deposits forming a low coastal plain backed by the rugged, glacier-clad St. Elias Mountains. The 6.8 million ha Tongass National Forest encompasses most of the region. The area is sparsely populated with a total population < 55,000; the largest town, Juneau, the state capitol, had a population < 27,000 in 1992 (US Census Bureau).

## INFLUENCES OF CLIMATE AND TOPOGRAPHY ON THE LICHEN FLORA

Due to the inland waterways and proximity to the Pacific Ocean, most of Southeast Alaska experiences a hyper-maritime climate: high humidity, high precipitation, considerable cloudiness and small temperature fluctuations. Average annual precipitation ranges from 152 to 508 cm; increasing with elevation (Harris et al. 1974). Average monthly temperatures at sea-level range from -3 to 3° C in January and 10 to 18° C in July (Leslie 1989). While much of Southeast Alaska is covered by rock and ice, below 900 m one finds a lush extension of the temperate rain forest belt of the Pacific Northwest. *Tsuga heterophylla-Picea sitchensis* forests and open peatlands of *Pinus contorta/Sphagnum* dominate the steep and more gentle slopes, respectively. Stands of large *Picea sitchensis* are found in well-drained glacial valley bottoms, riparian areas, and along marine beach fringes, while *Thuja plicata*, *Chamaecyparis nootkatensis*, and *Tsuga mertensiana* occur in more poorly drained sites. *Populus trichocarpa*, *Alnus rubra*, and *Salix* spp. are common in river floodplains. Forest vegetation types are classified in DeMeo (1988), Martin et al. (1995), Pawuk & Kissinger (1989) and Shephard (1995). Typical lichen species of the common vegetation types are described in Geiser et al. (1994a). About 1014 vascular plants (Stensvold nee Muller 1982) and 533 bryophyte species (Worley 1972) are known from the region.

The northeast mainland lies in a transition zone between marine and continental climates. Transitional species not found elsewhere occur just 50 km nw of Haines (Thomson and Ahti 1994 site GG) and in the Skagway vicinity, e.g. *Cladina mitis*, *Collema curtisporum*, *Collema subflaccidum*, *Hypogymnia occidentalis*, *Melanelia exasperatula*, *M. olivacea*, *M. septentrionalis*, *M. stygia*, *Nephroma expallidum*, *N. occultum*, *N. sylvae-veteris* and *Pilophorus cereolus*. A gradient of continental influence, and dispersal of inland species westward by winter wind patterns also affects the flora in mainland river valleys. Normally the Coastal and Fairweather Mountain Ranges form a barrier to most weather from between Southeast Alaska and BC. But in winter, under certain conditions of temperature and pressure gradients, cold air cascades out of Canada through passes and channels such as Glacier Bay, Lynn Canal, Taku Inlet, the Stikine R. valley and the Unuk R. valley at wind speeds of 160 km/h or more. In addition, if the cold air mass over Canada is deep enough, cold air will descend over the Juneau Ice Field, Tracy and Endicott Arms and the Whiting R. valley, all of which have glaciers or ice fields as sources. Species found exclusively in forests of these mainland valleys include: *Cetrelia alaskana*, *Heterodermia speciosa*, *Leptogium cyanescens*, *L. furfuraceum*, *L. saturninum*, *Leptogium subtile*, *Leptogium teretiusculum*, *Lobaria retigera*, *Lopadium disciforme*, *Melanelia multispora*, *Nephroma isidiosum*, and *Sticta wrightii*.

The epiphytic macrolichen flora of tiny forested marine islands, or isolated peninsulas, can be spectacularly different or diverse compared to the surrounding forested shorelines. For example, at the Shrine of St. Therese I. near Juneau and Gut I. at the mouth of the Stikine R., a dramatic cover of *Usnea* spp and *Ramalina menziesii* replaces normally abundant *Alectoria sarmentosa*. While we have never found *Pseudocyphellaria rainierensis* to be common, most collections are from small marine islands. Lichens of shore rocks form another interesting element, these are discussed and illustrated in O'Clair et al. 1996.

## ENDEMISM, DIVERSITY, RARE SPECIES AND CONSERVATION ISSUES

Refugia from glacial episodes during the late Wisconsin period are postulated to account for a regional flora relatively rich in species that are endemic or common in North America only in the Queen Charlotte Islands or in Southeast Alaska. Some show remarkable disjunctions with other regions of the world. Examples include species of *Amygdalaria*, *Bryoria*, *Coccotrema*, *Fuscopannaria*, *Fuscidea*, *Micarea*, *Ochrolechia* and *Rhizocarpon*, among other genera (Brodo 1992b, 1993, 1995). In contrast, much of the Yakutat forelands were glaciated as recently 300 years ago and few endemic species were found there.


60
Yakutat
59
140
139
138
Skagway
Haines
59
Juneau
58
Southeastern
Alaska
Chichagof Is
Admiralty Is
CANADA
Baranof Is
Kruzof Is
57
Sitka
Kupreanof Is
Kuiu Is
Petersburg
Stikine R
Mitkof Is
Wrangell
Wrangell Is
56
GULF OF ALASKA
Unuk River
Revillagigedo Is
Prince of Wales Is
Ketchikan
133
132
131
130
MAPSCALE 1:4308480
20
0
20
40
60
80
Miles
SCALE is 1 INCH = 68 MILES

In addition, Southeast Alaska appears to be the population center for rare Pacific Northwest endemics such as *Hypogymnia oceanica*, *Kaernefeltia californica* and *Hypogymnia duplicata*. Nearly pristine air quality throughout the region combined with the wet, oceanic climate enhances the diversity, biomass and distribution of highly pollution sensitive lichens such as *Usnea longissima* and members of the cyanobacteria-containing genera *Collema* (6 spp), *Leptogium* (12), *Lobaria* (8), *Nephroma (10)*, *Pannaria* and *Fuscopannaria* (8), *Peltigera* (22) and *Pseudocyphellaria* (4). These lichens represent an extension of the Pacific Northwest temperate rain forest into coastal Alaska. About 69 species, i.e. 14% of the flora, have not been reported further north in Alaska and apparently reach the northern extent of their range in se AK. These species entries are preceded by a "+" in the list below.

Extensive stretches of virgin forest harbor many old-growth dependent or associated lichens such as *Heterodermia sitchensis*, *Leptogium brebissonii*, *Lobaria oregana*, *Nephroma occultum*, *N. sylvae-veteris*, *Pannaria ahlneri*, *Parmotrema chinense*, *Pseudocyphellaria rainierensis*, and *Sticta wrightii*. The region is also home to 26 species of *Stereocaulon* and 64 species of *Cladina* and *Cladonia* ca, a strikingly rich diversity within these genera. In all, more than fifty species considered imperiled due to logging, other forest management practices, pollution or development in neighboring British Columbia (Goward 1996) and Oregon and Washington (FEMAT 1993, USDA & USDI 1994) occur in Southeast Alaska.

Most lichens in Southeast Alaska are rare or poorly known. Some rare species are also rare world-wide (see Geiser et al. 1994a, Fig. 6). Of the species with adequate data to determine regional distribution, we have categorized 45 as extremely common, "A", 106 as common, "C", 64 as infrequent, "I", and 69 species as rare, "R". (See KEY below for further explanation of these terms). The remainder, about 225 species (45%), were considered too poorly known to rate. From a conservation viewpoint, less than half the flora has yet been demonstrated to occur even infrequently within the region.

## KEY TO SPECIES LIST

A= abundant; large numbers of individuals can be found throughout Southeast Alaska in many habitats or in a few widespread habitats.
C= common; the lichen is widely distributed in Southeast Alaska or is regularly observed within specific, but not common, habitats.
I= infrequent; the lichen is only occasionally observed in the described habitat.
R= rare; the lichen is known from less than five sites due to scarcity of its required habitat or low population.
If no letter appears, the habitat was not sampled sufficiently to make an estimate, or we did not systematically sample the growth form (i.e. crustose lichens).

Regional substrates, habitats and distribution are described for all abundant, common and infrequent species. Distribution maps and extended habitat descriptions for these species can be found in Geiser et al. (1994a & 1994b). For rare and poorly known species we provide specific location data, voucher numbers, and, if available, literature citations. Substrate and habitat from those specific collections, rather than regional generalizations, are given. All species were collected by us and have vouchers in the Tongass National Forest Lichen Herbarium (TNFS) in Petersburg, Alaska, unless otherwise noted. Vouchers have also been distributed to the Canadian Museum of Nature (CANL), University of Alaska, Fairbanks (ALA), Oregon State University (herb. McCune), the Smithsonian Institution (US), and University of Wisconsin (WIS). Collections by others have been included and referenced but not checked. Lichen nomenclature follows Esslinger & Egan (1995).

Most soils in Southeast Alaska have an organic surface horizon. In the species list below, "organic soil" is used somewhat interchangeably with "humic soil" and even "humus" or "soil". Location (forest, peatland, subalpine, alpine) indicates additional soil properties. Soils of peatlands are poorly drained and excessively wet. They are histosols, i.e., strongly acidic (pH 3.5-5), almost entirely organic and continually saturated. Soils of forests drain more freely, usually occur on sloping terrain and tend to become spodosols. Spodosols have a deep, acidic (pH 4-5) surface horizon of organic duff, litter and humus. There is no permafrost in Southeast Alaska. Both soil types also dominate subalpine and alpine areas although soil depth and development decrease with increasing elevation. "Mineral soils", usually the upper horizon of a sandy or gravely entisol or inceptisol, have a low organic content, a higher pH, and are well-drained. Mineral soils and exposed gravels can be found along floodplains of streams and rivers and on recent glacial moraines. Exposed rocks occur on shorelines, subalpine and alpine areas and higher, avalanche chutes, along road cuts, and in rock pits. Elsewhere, unless part of a vertical cliff, most rocks and other mineral materials are buried under a thick layer of organic soil and moss.

Interpreting voucher specimen information: If the specimen was collected and identified by us, only the TNFS voucher number is given. For vouchers not determined by us, the determiner's name follows the voucher number(s). If the specimen was not collected by us, the collector's name precedes the voucher number. Collections by Rita O'Clair and Sylvia and Stephen Sharnoff were determined by Irwin M. Brodo. The latter are part of the Sharnoff private lichen collection now housed in Ottawa and likely to be deposited in CANL. All collections by Dr. Brodo are at CANL. In all other cases if the collection is not at TNFS, then the acronym for the herbarium where it is stored follows the collectors name and number.

Other abbreviations:

AK= Alaska, se AK = Southeast or southeastern Alaska, BC = British Columbia, CA= California, N Am = North America, OR= Oregon, PNW= the Pacific Northwest of N Am, generally northern CA through se AK; QCI= Queen Charlotte Islands; WA= Washington.
e = east, eastern; n = north, northern; s = south, southern; w = west, western
I. = Island, Is. = Islands, L. = Lake, Mtn.= Mountain, R. = River.

* = new to AK, ** = new to US, + = the only AK records are from se AK.

## SPECIES LIST

***Alectoria nigricans*** (Ach.) Nyl. C; on rock and soil; subalpine to alpine.

***Alectoria ochroleuca*** (Hoffm.) Mass. (2) C; on organic soils; subalpine to alpine.

***Alectoria sarmentosa*** (Ach.) Ach. **subsp. *sarmentosa***. A; on bark and lignum of coniferous trees and deciduous shrubs; all forested elevations.

**-subsp. *vexillifera*** (Nyl.) D. Hawksw. R; in subalpine and alpine. Auke L., Juneau (Brodo & Hawksworth 1977).

***Allantoparmelia almquistii*** (Vainio) Essl. 0n acid rock in exposed subalpine and alpine localities. *823 det. Ryan*, *3255*, *3215*.

***Allantoparmelia alpicola*** (Th. Fr.) Essl. On acid rock in exposed inland subalpine and alpine localities; Mt. Roberts, near Juneau (Krog 1968).

***Amandinea coniops*** (Wahlenb. *in* Ach.). In lee of rocks nw of Haines (Thomson & Ahti 1994).

***Amandinea punctata*** (Hoffm.) Coppins & Scheid. On bark of *Alnus*; beach at Big Bay, w Baranof I. *2094*.

***Amygdalaria consentiens*** (Nyl.) Hertel, Brodo & M. Inoue. C; on alpine rocks and soil. Sheridan Peak, Kupreanof I.; Cosmos Range, Elbow Mtn. and Thunder Mtn., mainland *646 & 3481 det. Ryan*, *18*, *519 det. Thomson*.

+***Amygdalaria continua*** Brodo & Hertel. On subalpine rocks near the waterfalls at Falls L., mainland. Endemic to QCI (Brodo & Hertel 1987) and se AK. *3169 det. Ryan*.

***Amygdalaria elegantior*** (H. Magn.) Hertel & Brodo. On rock; sea level to alpine. LeConte Bay, mainland and Crystal Mtn, Mitkof I. *350*, *2012*

+***Amygdalaria haidensis*** Brodo & Hertel. On rock; shore of Swan L., 421m., mainland *3194 det. Ryan*. Endemic to QCI (Brodo & Hertel 1987) and se AK.

***Amygdalaria panaeola*** (Ach.) Hertel & Brodo. On alpine rocks, to sea level near glacier terminus; Rowan Mtn, Kuiu I. and LeConte Bay, mainland. *351*, *843*. Also in Yakutat (Gowan 1989).

***Amygdalaria pelobotryon*** (Wahlenb.) Norman. On alpine rocks; Sheridan Pk., Kupreanof I. *3213 det. Ryan*.

***Amygdalaria subdissentiens*** (Nyl.) Mas. Inoue & Brodo. On shoreline rocks in or just above the salt-spray zone, and on exposed alpine ridges (Brodo & Hertel 1987). Bear Claw Mtn, s Kupreanof I. *3151 det. Ryan*.

***Arctomia delicatula*** Th. Fr. R; on *Pinus contorta* and on rock. Possibly overlooked because of its small size. Bold I. s of Ketchikan, *1049 det. Thomson*, and Waterfall Peak, mainland, *3232 det. Ryan*.

***Arctoparmelia incurva*** (Pers.) Hale. On rock in the mainland alpine; w of n fork Bradfield R. *Krieckhaus 3439 det. Ryan*.

***Arctoparmelia separata*** (Th. Fr.) Hale. On beach rocks at Woewodksi I. and at Spurt L., mainland, *404*.

+***Arthonia punctiformis*** Ach. On *Alnus* at Augustine Bay, Dall I. (Herre 1919).

***Arthonia phaeobaea*** (Norman) Norman. On beach rocks in the splash zone above the intertidal zone. Rowan Bay, Kuiu Is, *946 det. Ryan*, and Starrigavan Bay, Sitka

(O'Clair et al. 1996).

***Arthrorhaphis citrinella*** (Ach.) Poelt. On humic soils in the high alpine, 1510 m., Juneau Ice Field (Heusser 1954).

***Asahinea chrysantha*** (Tuck.) Culb & C. Culb. On boulders, plant debris and humus, occasionally on soil; Mendenhall Valley (McCullough 1965).

+***Aspicilia gibbosa*** (Ach.) Körber. On rocks; Glacier Bay (Cummings 1904).

***Bacidia beckhausii*** Körber. On trees nw of Haines (Thomson & Ahti 1994).

+***Bacidia nivalis*** Follmann. On alpine rocks; Thunder Mtn., *969 det. Thomson.*

***Baeomyces placophyllus*** Ach. On moss on an unnamed alpine peak w of Elbow Mtn. near the BC border, *3284.* Also expected on sandy, clayey and organic soils (Thomson 1967).

***Baeomyces rufus*** (Hudson) Rebent. I; on rocks and a stump above high tide line, on subalpine and alpine rocks; on wood, moss and soil.

***Bellemerea cinereorufescens*** (Ach.) Clauzade & Roux. On alpine rock, Kupreanof I., *3219 det. Ryan.*

****Biatora cuprea*** (Sommerf.) Fr. On Gastineau Peak, *Brodo 26356 det. C. Printzen.* Containing argopsin.

***Biatora vernalis*** (L.) Fr. On *Alnus* along beach fringe, *3441 det. Ryan.*

****Biatoropsis usnearum*:** Räsänen. Parasitic on *Usnea filipendula* ; along forested beach of Dog Cove, Dog I., s of Ketchikan, *1881 det. Ryan.* See also Diederich & Christiansen (1994).

***Brigantiaea fuscolutea*** (Dickson) R. Sant. On soil or rock in subalpine and alpine habitats, on mosses and small plants and on lower branches of *Picea*, on lacustrine rocks. Swan L., mainland, *3193 det. Ryan*; at Gastineau Peak, Juneau, *O'Clair s.n*; and nw of Haines (Thomson & Ahti 1994)

***Brodoa oroarctica*** (Krog) Goward. On siliceous alpine rock; Rowan Mtn., Kuiu I., *844 det. Thomson.*

***Bryocaulon divergens*** (Ach.) Kärnefelt. I; on soil among mosses and other lichens.

***Bryocaulon pseudosatoanum*** (Asah.) Kärnefelt. C; corticolous on *Picea sitchensis*, *Pinus contorta*, and *Tsuga heterophylla* in open forests; low to subalpine elevations.

***Bryoria bicolor*** (Ehrh.) Brodo & D. Hawksw. C; corticolous on *Pinus contorta*, *Picea sitchensis*, and *Tsuga heterophylla* in open forests; sea level to subalpine. Once on alpine rock.

***Bryoria capillaris*** (Ach.) Brodo & D. Hawksw. C; corticolous on conifers and deciduous shrubs, particularly in riparian and beach habitats; sea level to subalpine.

+***Bryoria carlottae*** Brodo & D. Hawksw. C; primarily on *Pinus contorta* and *Tsuga heterophylla* in low elevation peatlands and open mixed-conifer forests; occasionally subalpine. Endemic to the QCI (Brodo & Hawksworth 1977) and se AK.

+***Bryoria cervinula*** Mot. *ex* Brodo & D. Hawksw. I; primarily on open grown *Pinus contorta* and *Tsuga heterophylla* ; low elevations to subalpine. Endemic to

BC and se AK (Brodo & Hawksworth 1977).

**Bryoria chalybeiformis** (L.) Brodo & D. Hawksw. On a totem pole at Chief Shakes I., Wrangell, *1592 det. Brodo.*

**Bryoria friabilis** Brodo & D. Hawksw. I; corticolous on conifers and deciduous shrubs in all forest types.

**Bryoria fuscescens** (Gyelnik) Brodo & D. Hawksw. I; on *Pinus contorta* and *Picea sitchensis* in open forests, low elevations to subalpine.

**Bryoria glabra** (Mot.) Brodo & D. Hawksw. C; corticolous and lignicolous on conifers and deciduous shrubs in coniferous forests; low elevations to subalpine.

**Bryoria lanestris** (Ach.) Brodo & D. Hawskw. I; corticolous on *Pinus contorta* and *Picea sitchensis* in open mixed conifer forests.

**Bryoria nadvornikiana** (Gyelnik) Brodo & D. Hawksw. R; corticolous on conifers; on small marine islands (Dog I. in the far s, *1867* ; Gut I. in the Stikine R. flats, *533* ; and the Myriad Islands w of Chichagof I. *2053 det. Brodo.*

**Bryoria nitidula** (Th. Fr.) Brodo & D. Hawksw. On rock in the mainland alpine, nw of Skagway and Thunder Mtn vicinity, *33 det. Thomson.*

**Bryoria pseudofuscescens** (Gyelnik) Brodo & D. Hawksw. R; on rotting stump at high tide line at Mallard Slough, Stikine R., *3083.* Also on conifers near Mendenhall L., Juneau (Krog 1968) and near Skagway (Thomson 1984).

**Bryoria subcana** (Nyl. *ex* Stizenb.) Brodo & D. Hawksw. R; on *Pinus contorta* in a mid-elevation peatland nw of Sheridan Peak, *770.*

**Bryoria tenuis** (E. Dahl) Brodo & D. Hawksw. C and widespread; corticolous and lignicolous on conifers and *Alnus*; low elevation to subalpine forests; on alpine rocks.

**Bryoria trichodes** (Michaux) Brodo & D. Hawksw. subsp. *americana* (Mot.) Brodo & D. Hawksw. and subsp. *trichodes*. A; corticolous on conifers; low elevation to subalpine. About 85% of our collections were subsp. *americana*. The remainder were subsp. *trichodes* or intermediates between the two. Subsp. *americana* was recently elevated to species level, *B. americana* (Holien 1997).

**Buellia alboatra** (Hoffm.) Th. Fr. On lacustrine rock, low elevation sites; Spurt L., mainland, *391 det. Thomson*, Harvey L., Woewodski I., and s Kupreanof I. along Petersburg Ck.

**Buellia erubescens** Arnold. On young *Alnus rubra* at forest edge along tidal mud flats at Mallard Slough, n arm Stikine R., *3064 det. Ryan.*

**Buellia papillata** (Sommerf.) Tuck. On exposed shore rocks in LeConte Bay, *352 det. Thomson.*

+**Buellia spuria** (Schaerer) Anzi. On beach rocks at Rowan Bay, Kuiu I., *949 det. Thomson.*

**Bunodophoron melanocarpum** A. Massal. R; on *Tsuga heterophylla* at Dall I., *Kreikhaus 3368.*

***Calicium adaequatum** Nyl. On *Alnus rubra* ; beach at Mallard Slough, Stikine R., *3075 det. Ryan.* This species possibly restricted to *Alnus* worldwide (Tibell 1975).

****Calicium lenticulare** Ach. On snag in forest near Ess L., mainland, *3351 det. Ryan.* Otherwise known in the w hemisphere only as far n as Mexico (Tibell 1992).

+**Calicium viride** Pers. On trunks of conifers and dead limbs of trees; Zarembo I. (Herre 1919).

+**Caloplaca atrosanguinea** (G. K. Merr.) Lamb. On *Salix* (Thomson & Ahti 1994).

**Caloplaca citrina** (Hoffm.) Th. Fr. C; on vertical or overhanging rocks in the salt spray zone. Occasionally on wood. See also (Arup 1993, O'Clair et al. 1996).

**Caloplaca ferruginea** (Huds.) Th. Fr. On bark or wood of conifers and deciduous woody plants; Mendenhall Valley (McCullough 1965).

**Caloplaca flavogranulosa** Arup. Strictly maritime; on horizontal rocks in the salt spray zone beneath bird perches, also on vertical rocks and driftwood (Arup 1993, O'Clair et al. 1996).

**Caloplaca holocarpa** (Hoffm. *ex* Ach.) M. Wade. On driftwood; w Lynn Canal near Skagway, *Sharnoff 1488.05.*

**Caloplaca litoricola** Brodo. On beach rocks at or just above high tide line. Common at Sitka; endemic to BC and se AK (Arup 1995, O'Clair et al. 1996).

**Caloplaca pollinii** (Massal.) Jatta. On *Populus* along the Unuk R., 2 km from BC border, *1145 det. Thomson.*

**Caloplaca verruculifera** (Vainio) Zahlbr. In the salt spray zone beneath bird perches on Aaron I. in Lynn Canal; not strictly maritime (O'Clair et al. 1996).

***Candelaria concolor** (Dickson) Stein. R; on twigs of *Picea sitchensis* on beach at Kadin I., mouth of Stikine R., *3442 det. Ryan.*

**Candelariella aurella** (Hoffm.) Zahlbr. On sandstone on Heceta I. (Herre 1919).

**Candelariella canadensis** H. Magn. On humic soils in the Mendenhall Valley near Juneau (McCullough 1965).

**Cavernularia hultenii** Degel. A; on twigs of conifers and deciduous shrubs; low elevation to subalpine forests.

**Carbonea vorticosa** (Flörke) Hertel. On rock near Visitors Center, Mendenhall Glacier, Juneau, *Brodo 25982.*

**Cavernularia lophyrea** (Ach.) Degel. A; on twigs of conifers, rarely on deciduous shrubs; low to mid elevation forests. PNW endemic.

**Cetraria aculeata** (Schreber) Fr. C; on organic soils in open *Pinus contorta* peatlands and other open forests.

**Cetraria ericetorum** Opiz. I; on humic soils in subalpine and alpine habitats; Thunder Mtn, mainland, *499*, Crystal Mtn, Mitkof I., *2014 det. McCune*, ridge on sw Etolin I., *1192 det. McCune.*

**Cetraria islandica** (L.) Ach. subsp. *islandica.* C; on humic soils with other lichens and mosses, sometimes in rock crevices. In low elevation peatlands but more common in subalpine and alpine habitats.

-**subsp. *crispiformis*** (Räsänen) Kärnefelt. I.

*-**subsp. *orientalis*** (Asah) Kärnefelt. On mineral soils in deciduous shrub habitat on the Patterson R., mainland, *2469*, and the Mendenhall Glacier moraine trail, *2797 det. Brodo* ; in humic soil in a *Pinus contorta* peatland along Ward Ck,

near Ketchikan, *2788 det. Brodo.*

***Cetraria muricata*** (Ach.) Eckfeldt. I; on organic soil in open lowland peatland at Cape Fanshaw, mainland, *1147.*

***Cetraria nigricans***: Nyl. I; on rock in alpine habitats; Hall Peak, Kupreanof I., *3363 & 3383 det. Ryan*, and Thunder Mtn., mainland, *526.*

***Cetrariella delisei*** (Bory *ex* Schaerer) Kärnefelt & Thell. On ground at Mt. Roberts, Juneau (Krog 1968).

***Cetrelia alaskana*** (C. Culb. & Culb.) Culb. & C. Culb. R; on *Alnus* along the Stikine R. *1361 det. Thomson.*

***Cetrelia cetrarioides*** (Duby) Culb. & C. Culb. C; on deciduous trees and shrubs and *Picea sitchensis* along freshwater and marine beaches.

*****Chaenotheca brunneola*** (Ach.) Müll. Arg. On bark and wood of *Picea sitchensis.* One collection along Indian R. Trail, Sitka, in hollow created by ax, *3313.*

***Chaenotheca chrysocephala*** (Turner *ex* Ach.) Th. Fr. On bark of *Picea sitchensis* along uplifted beach at Cape Fanshaw, *2524* and on *Taxus brevifolia*, Dog I. s of Ketchikan.

+***Chaenotheca stemonea*** (Ach.) Müll. Arg. On conifer bark in a 125 yr. old *Picea sitchensis* stand on Mitkof I., *1342 det. Thomson.*

*****Chaenothecopsis pusilla*** (Ach.) A.F.W. Schmidt. In hollow of a *Picea sitchensis* snag, Indian R. Trail, Sitka, *3314 det. Ryan.*

***Chrysothrix candelaris*** (L.) J.R. Laundon. In vertical swaths on the trunks of *Picea sitchensis* along uplifted beach at Cape Fanshaw, *2525.*

***Cladina arbuscula*** (Wallr.) Hale & Culb. subsp. *beringiana.* A; on organic soils; peatlands of all elevations.

***Cladina ciliata*** (Stirton) Trass var. *tenuis* (Flörke) Ahti & M.J. Lai. I but widespread; on organic soils; peatlands of all elevations.

***Cladina mitis*** (Sandst.) Hustich. R; on sand and gravel in open areas with continentally influenced climates. In glacial outwash of the Mendenhall Glacier terminal moraine, *2798 det. Brodo*, and near Skagway, *Sharnoff 1487.01.*

***Cladina portentosa*** (Dufour) Follmann. C; on organic soils with other lichens and mosses; mainly in low elevation peatlands but not uncommon in subalpine and alpine elevations. Most collections not identified to subspecies.
- **subsp. *pacifica*** (Ahti) Ahti. Jamboree Bay, w Baranof I., *3104.*

***Cladina pseudoevansii*** (Asah.) Hale & Culb. R; on organic soil at Nichols Bay (Krog 1968).

***Cladina rangiferina*** (L.) Nyl. A; on organic soils in peatlands and open grown forest stands from low to subalpine and alpine elevations.

***Cladina stellaris*** (Opiz) Brodo. I; on organic soils in peatlands and open forest types; sea-level to alpine.
-var. *aberrans* (Abbayes) Ahti (1) I-R; Pike Lakes, Yakutat, *2448.*

***Cladina stygia*** (Fr.) Ahti. C; on organic soils in peatlands of all elevations. Often overlooked; distinguished from *C. rangiferina* by its black stereome and red pycnidial jelly (Ahti & Hyvönen 1985).

***Cladonia alaskana*** A. Evans. On moss-covered alpine rocks and humic soils; Crystal Mtn, Mitkof I., *890 det. Thomson*, Horn Cliffs and unnamed peak e of Thunder Mtn, mainland, *3346 & 965 det. Ryan.*

***Cladonia albonigra*** Brodo & Ahti. C; in peatlands and open forests on organic soils among mosses, logs, rocks, and trunks or low branches of conifers, especially *Pinus contorta.*; low elevation to alpine. Both grayanic positive and deficient strains. PNW endemic (Brodo & Ahti 1996).

***Cladonia amaurocraea*** (Flörke) Schaerer. C and widespread; on organic soils in peatlands and open forests; sea-level to alpine.

***Cladonia asahinae*** J.W. Thomson. R; on trunk of *Alnus* and moss-covered *Picea sitchensis* branches; Yakutat lowlands, *2815, 3299, 3301 det. Brodo.* Protolichesterinic acid chemotype found only as far n as QCI (Brodo & Athi 1996).

***Cladonia bacilliformis*** (Nyl.) Glück. R; on rotting wood; forested coast of Tebenkoff Bay, Kuiu I., *2290 det. Thomson.*

***Cladonia bellidiflora*** (Ach.) Schaerer. A; corticolous and lignicolous on bases and sometimes lower branches of conifers in most forest types. Common on soil, rarely on rock. Low elevation to alpine.

***Cladonia borealis*** S. Stenroos. A; corticolous on conifers in forested habitats, on rocks and humic soils in open better drained habitats. Low elevation to alpine.

***Cladonia cariosa*** (Ach.) Sprengel. I; on humic soils with other lichens and mosses.

***Cladonia carneola*** (Fr.) Fr. C and widespread; on lower conifer trunks and branches, and on rocks. Forested and alpine elevations.

***Cladonia cenotea*** (Ach.) Schaerer. One collection from a decomposing beach log, the other on ground in a *Picea sitchensis* forest near Skagway; *2690, 205 det. Thomson.*

***Cladonia cervicornis*** (Ach.) Flotow subsp. *verticillata* (Hoffm.) Ahti. On sandy soils, rock outcrops, on thin humic soils, and old rotten logs (Thomson 1984). On Mt. Roberts near Juneau and Deer Mtn. near Ketchikan (Krog 1968) and unnamed peak w of Elbow Mtn, mainland, *3283.*

***Cladonia chlorophaea*** (Flörke *ex* Sommerf.) Sprengel. C; mainly on bark and lignum of conifers and deciduous shrubs in forested habitats. On rocks and humic soils in open better drained habitats. Low elevation to subalpine forests; also in alpine habitats.

***Cladonia coniocraea*** (Flörke) Sprengel. A; primarily on bark of conifers, rarely on deciduous shrubs. Low elevation to subalpine forests.

***Cladonia cornuta*** (L.) Hoffm. A; on bark of conifers (except *Pinus contorta*) and deciduous shrubs in many forest types. Also in humus with other lichens and mosses, sometimes in rock crevices, in open areas.

***Cladonia crispata*** (Ach.) Flotow **var. *crispata.*** C; mainly on coniferous bark in *Pinus contorta* and mixed conifer open forests. Also found in humic soils with other lichens and mosses, and on rock. Low elevation to alpine.

***Cladonia cryptochlorophaea*** Asah. I; on bark and lignum of conifers and deciduous shrubs in forested habitats. On humic soils among mosses in better drained habitats. Gut I., mouth of Stikine R.; Thimbleberry L. trail, Sitka; trail to Harlequin L., Yakutat. *539*, *2251*, *1612*.

***Cladonia cyanipes*** (Sommerf.) Nyl. On thin humic layer with other lichens and mosses over glacial moraine; terminus of Herbert Glacier, n of Juneau, *2841 det. Brodo*.

***Cladonia* cf. *dahliana*** Kristinsson. On rocky alpine cliff e of Horn Mtn, mainland, *3366 det. Ryan*. With atranorin and psoromic acid, basal squamules small, lacking podetia. Known from Iceland, Greenland, Baffin I. (Kristinsson 1974) and the PNW (Hammer 1995).

***Cladonia deformis*** (L.) Hoffm. I; on bark of conifers, also on rocks and humic soils; low elevation to subalpine forests.

***Cladonia ecmocyna*** Leighton **subsp. *intermedia*** (Robbins) Ahti. C; usually in humic soils with other lichens and mosses. More frequent in subalpine and alpine habitats and over thin humus on glacial moraines, but also found in low elevation peatlands.

***Cladonia fimbriata*** (L.) Fr. A; on bark and lignum of conifers, usually on bases of trunks or lower branches. Also corticolous on deciduous shrubs and once found on rock. In most forest types, low elevations to subalpine.

***Cladonia furcata*** (Hudson) Schrader. A; mainly on humus in low elevation open *Pinus contorta*, mixed conifer, *Picea sitchensis* and *Tsuga heterophylla* forests. Also on bark of conifers (bases of trunks or lower branches) and mossy rocks.

***Cladonia gracilis*** (L.) Wild. subsp. *turbinata* (Ach.) Ahti and subsp. *vulnerata* Ahti and subsp. *elongata*. (Jacq.) Vainio. A; most common in open areas in better drained sites with other lichens and mosses; peatlands, open forests, subalpine and alpine.

***Cladonia granulans*** Vainio. R; on soil; 5 records in N Am noted by Thomson (1984), 3 from se AK on Douglas I., Harbor Mtn. near Sitka, and Saxon Village near Ketchikan (Krog 1968).

***Cladonia homosekikaica*** Nuno. On moss-covered rock, terminus of Herbert Glacier, n of Juneau, *3293 det. Brodo*.

***Cladonia humilis*** (With.) J.R. Laundon. R; on soil and rotting logs; in the Juneau vicinity and n Kuiu I. (Thomson 1984).

***Cladonia kanewskii*** Oksner. I; on humic soils among mosses; subalpine. Also collected in the Juneau vicinity, *Imshaug 28641*, *28876*, *28979*, *28935*, *H and MSC*.

***Cladonia macilenta*** Hoffm. R; along Loop Rd. in Juneau, Ward L. near Ketchikan and the Indian R. Trail near Sitka (Krog 1968).

***Cladonia macilenta*** var. ***bacillaris*** (Nyl.) Glück. R; On old logs, tree bases, earthen banks and humus in forested locations; along the Indian R. Trail near Sitka (Krog 1968) and n Kuiu I. (Thomson 1984).

***Cladonia macrophylla*** (Schaerer) Stenh. I; on soil, moss-covered rock and conifer trunks, sea level to alpine elevations; Goose Cove, n Baranof I. and Crystal Mtn., Mitkof I., *2663 & 912 det Thomson*; Shakes Slough, Stikine R., *1413 det. Brodo*.

***Cladonia macrophyllodes*** Nyl. I; on rock, moss-covered soil and rock crevices, Thunder and Elbow Mtns., mainland, *527, 656, 3276.*

***Cladonia maxima*** (Asah.) Ahti. A; in organic soil in raised hummocks in peatlands; from low elevation to alpine, where it can occur on rocks. *C. gracilis* ssp. *vulnerata* can also grow very long podetia in humid coastal conditions; our collections may be that species.

***Cladonia merochlorophaea*** Asah. I; on moss-covered alpine rock, Sheridan Pk, Kupreanof I., *224 det. Ryan*; on dwarf *Tsuga mertensiana*, subalpine sw Etolin I., *1197 det. Thomson*; Harlequin L. trail, Yakutat lowlands, 1612.

***Cladonia metacorallifera*** Asah. I but widespread; on bark or wood of conifers in open forests to subalpine; on beach logs; on rock, soil or moss in non-forested and alpine habitats.

***Cladonia nipponica*** Asah. R; on boulders and on soils near Mendenhall L. and Mt. Roberts near Juneau, Harbor Mtn. near Sitka (Krog 1968) and the Ketchikan vicinity (Thomson 1984).

***Cladonia norvegica*** Tønsberg & Holien. R-I; corticolous and lignicolous at the bases or moss-covered branches of conifers, occasionally on decaying logs. Tom's L., Prince of Wales I., *3297 det. T. Ahti*; Juneau vicinity, and the Indian R. Trail near Sitka (Tønsberg & Goward, 1992).

***Cladonia ochrochlora*** Flörke. A; on bark and lignum of coniferous trees and deciduous shrubs. Common to most forest types but not occurring in the subalpine or alpine.

***Cladonia phyllophora*** Hoffm. I; moss-covered or bare sand, gravel or rock. Mendenhall Glacier terminal moraine and Patterson R., mainland, *2805 & 2443 det. Brodo*; and on *Picea sitchensis* in Brotherhood Park, Juneau, *1571.*

***Cladonia pleurota*** (Flörke) Schaerer. C; on soil or rocks, occasionally on bark. Occurring at low elevations on the mainland, notably the Stikine R.; primarily a subalpine and alpine species on the islands.

***Cladonia pocillum*** (Ach.) Grognot. R-I; on a large outcrop of shore rocks, with other lichens and mosses; Windham Bay, mainland, *2685 det. Thomson.*

***Cladonia pyxidata*** (L.) Hoffm. I; primarily on soil or rocks, occasionally on lower branches or bases of conifer trunks. In forested and open habitats, sea level to subalpine.

***Cladonia ramulosa*** (With.) J.R. Laundon. On *Picea sitchensis* at Cannon Beach, Yakutat, *3445 det. Ryan.*

***Cladonia rei*** Schaerer. I; Mendenhall L. vicinity, Juneau (Krog 1968).

***Cladonia scabriuscula*** (Delise) Nyl. C; primarily on organic soils, also on moss-covered rock and bark of conifers (low branches, crotches and bases of trunks). Most common in mixed conifer forests and open *Tsuga heterophylla/Thuja* or *Tsuga mertensiana* forests. Not found in subalpine, alpine, *Pinus contorta* peatlands or deeply shaded *Picea sitchensis/Tsuga heterophylla* forests.

***Cladonia schofieldii*** Ahti & Brodo. R; on fully exposed soil or rock, mainly in high elevations. Thunder Mtn, mainland, *656 det. Brodo.* Endemic to BC and AK (Brodo & Ahti 1996).

***Cladonia squamosa*** Hoffm. A; on bark and lignum of conifers, where it grows on lower branches, crotches and trunk bases. Also occurring on soil and rocks. Common to all coniferous forest habitats; low elevation to subalpine.

-**var. *subsquamosa*** (Nyl. *ex* Leighton) Vainio. C; on mossy logs and rocks, on trunks, snags and stumps of conifers.

***Cladonia stricta*** (Nyl.) Nyl. On bark of *Picea sitchensis*, Limb I., Stikine R., *346 det. Brodo.* Also on Gastineau Peak near Juneau, *Brodo 26317.*

***Cladonia subfurcata*** (Nyl.) Arnold. C; in low elevation peatlands on organic soils with other lichens and mosses. Also occurring on rock in subalpine, alpine and low elevation glacial termini.

***Cladonia subulata*** (L.) F.H. Wigg. I-R; on rocks or soil in open areas and forests; Yankee Basin Tr., and lateral moraine of Herbert Glacier, both n of Juneau, *358 & 284 det. Brodo.*

***Cladonia sulphurina*** (Michaux) Fr. A; corticolous on conifers in mixed conifer and *Pinus contorta* forests, in other open forested associations, and on subalpine *Tsuga mertensiana.* On soil humus with other lichens in mosses in gravely, well drained low elevation sites.

***Cladonia symphycarpa*** (Flörke) Fr. I; on mineral soils, gravels and moss-covered rock or soils in glacial moraine, forested, subalpine and alpine habitats. Easily overlooked as only basal squamules are normally present.

***Cladonia transcendens*** (Vainio) Vainio. I; on bark and lignum of conifers. On low branches and bases of tree trunks in most low elevation coniferous forest types. Not found in subalpine or alpine.

***Cladonia turgida*** Hoffm. On mineral and humus rich soils; Mt. Roberts and Mendenhall L. vicinity, (Krog 1968).

***Cladonia umbricola*** Tønsberg & Ahti. A; on decaying wood or trunks of conifers and *Populus.* Corticolous on lower branches, crotches and trunks of conifers. In *Pinus contorta, Picea sitchensis/Tsuga heterophylla* forests and most forest types. Not found in alpine habitats.

***Cladonia uncialis*** (L.) F.H. Wigg. C and widespread; on ground in open peatlands from low elevation to alpine. Both squamatic acid containing and deficient chemotypes.

***Cladonia verruculosa*** (Vainio) Ahti. A; corticolous and lignicolous on bases and sometimes lower branches of conifers, common on soil and rock. Most forest types from low elevation to alpine, also on beach logs, and on soil, moss and gravel at glacial termini.

***Cladonia wainioi*** Savicz. R; on organic soils in subalpine and maritime peatlands. Similar to *C. thomsonii* and *Cladina rangiferina* but containing atranorin and merochlorophaeic acids; probably undercollected. Indian R. Trail, *3310 det. Ryan.*

+***Coccotrema maritimum*** Brodo. On beach rocks in extensive colonies at the upper edge of, or just above salt-spray zone, usually just above the *Verrucaria maura* and forming a distinct white zone of variable width depending on the amount of local wave and wind action. Sometimes on vertical surfaces of highly exposed rocks on slopes facing the open water but up to 700 m above the shore. Port Alexander, Yamani Inlets, Redfish Bay, all on Baranof I.; *3113& 3122 det. Ryan, 2654 det. Brodo.* Described from the QCI (Brodo 1973). Only US records.

***Coccotrema pocillarium*** (Cummings) Brodo. On bark, logs or trees in coastal forests usually at the beach edge. W Chichigof and Baranof Islands, *3312 det. Ryan.* The type collection is from Faragut Bay in se AK. W N Am endemic, AK to OR (Brodo 1973).

***Collema curtisporum*** Degel. On *Populus trichocarpa* nw of Haines (Thomson & Ahti 1994).

***Collema fecundum*** Degel. C; on acidic and moss-covered rocks in the salt spray zone (O'Clair et al. 1996).

***Collema furfuraceum*** (Arnold) Du Rietz. C; on bark of *Populus trichocarpa* in riparian areas at lower elevations.

***Collema nigrescens*** (Hudson) DC. C; on bark of *Populus trichocarpa* in riparian areas at lower elevations.

***Collema subflaccidum*** Degel. On rock at high tide line, Kadin I., Stikine R., *3447 det. Ryan.* On *Populus* near Haines (Thomson & Ahti 1994).

***Collema tenax*** (Sw.) Ach. On soil, usually calciferous (Thomson 1984). Reported by Herre (1919).

***Cornicularia normoerica*** (Gunn.) Du Rietz. Expected on well- lit, siliceous rocks, boulders and cliffs in wind-swept, alpine or glacially influenced areas (Thomson 1984). Known from Muir Glacier in Glacier Bay National Park (Krog 1968).

****Cystocoleus ebeneus*** (Dillwyn) Thwaites. On *Pinus contorta* twigs and wood; near Petersburg, *T. Tønsberg 16577 BG.*

***Dactylina arctica*** (Richardson) Nyl. In humic soils; subalpine and alpine of ne mainland only. Mendenhall Glacier Trail (Krog 1968) ; Goat L. ne of Skagway, *3503.*

***Dactylina beringica*** C.D. Bird & J.W. Thomson. On humus in the subalpine and alpine; Juneau area (Thomson 1984).

***Dactylina ramulosa*** (Hook.) Tuck. Subalpine and alpine; Mt. Roberts near Juneau (Krog 1968).

***Dendriscocaulon intricatulum*** (Nyl.) Henssen. I; on bark of *Picea sitchensis*, *Alnus*, and *Salix*. At low elevations on the mainland; one island site, in subalpine. Collected nw of Haines (Thomson & Ahti 1994).

***Dermatocarpon intestiniforme*** (Körber) Hasse. On calcareous rock below mean high tide line, Naukati Bay, Prince of Wales I., *2566.*

***Dermatocarpon luridum*** (With.) J.R. Laundon. On seasonally inundated rock in open waterways from low elevation to alpine in BC (Goward et al. 1994b). Howkan Bay, near Ketchikan (Krog 1968).

***Dermatocarpon miniatum*** (L.) W. Mann. On rock in the supralittoral zone.

***Dermatocarpon rivulorum*** (Arnold) Dalla Torre & Sarnth. R; on rocks in alpine stream bed, Elbow Mtn, mainland, *3266.*

***Diploschistes muscorum*** (Scop.) R. Sant. subsp. *muscorum*. On moss-covered alpine rocks; Hall Peak, Kupreanof I., *3332.*

***Ephebe lanata*** (L.) Vainio. On rock; ridge above Ward Ck., Ketchikan area, *2792*, and terminal moraine of Herbert Glacier *2852.*

**Epilichen scabrosus** (Ach.) Clem. *ex* Hafellner. On *Baeomyces rufus* in a Juneau icefield nunatak (McCullough 1965).

+**Erioderma mollissimum** (Samp.) Du Rietz. R; on conifer bark in open forest, Almalga Trail, n of Juneau, *2369 det. Brodo.*

***Erioderma sorediatum** D.J. Galloway & P.M. Jørg. R; on twigs in *Picea sitchensis/Tsuga heterophylla* forest along beach.

**Euopsis pulvinata** (Schaerer) Nyl. On Gastineau Peak near Juneau *Brodo 26317.*

**Farnoldia jurana** (Schaerer) Hertel. On rock; beach at Yakutat, and Cosmos Range and Thunder Mtn., mainland alpine; *659 det. Thomson, 3174 & 3181 det. Ryan.*

**Flavocetraria cucullata** (Bellardi) Kärnefelt & Thell. I; on ground in alpine sites.

**Flavocetraria nivalis** (L.) Kärnefelt & Thell. I; in humic soils with other lichens and mosses; subalpine and alpine. Thunder Mtn., and unnamed peak w of Elbow Mtn., mainland, *502 & 3286.*

+**Fuscopannaria ahlneri** (P.M. Jørg.) P.M. Jørg. R on *Picea sitchensis* in the Yakutat lowlands, *1618.*

**Fuscopannaria laceratula** (Hue) P.M. Jørg. I; hypermaritime on beach rock, conifers, and *Alnus* at; on Kadin I. near mouth of Stikine R., *3465 & 3466 det. Ryan*, Sokoi Is. near Petersburg, *39 det. Thomson*, Table Bay, s Kuiu I., *1890* and Yakutat lowlands, *1595 & 1656.*

**Fuscopannaria leucophaea** (Vahl) P.M. Jørg. On *Populus trichocarpa* or over other lichens. So far found only on the coastal mainland in Yakutat and the Unuk R. valley.

**Fuscopannaria leucostictoides** (Ohlsson) P.M. Jørg. I; on conifers and deciduous trees, especially bases of trees, or over other lichens in open forests, *1157 det. Ryan, 1017 & 2833.* Rare endemic, se AK to n CA with disjuncts in ID (McCune & Geiser, 1997).

**Fuscopannaria maritima** (Ohlsson) P.M. Jørg. On thin moss and rock above the upper tide line in the salt spray zone. Aaron I. in Lynn Canal *Brodo 26010, 26074, 26393* and Starrigavan Bay, Sitka, *O'Clair 3383.* Endemic, se AK to n WA (O'Clair et al. 1996).

**Fuscopannaria praetermissa** (Nyl) P.M. Jørg. With moss on thin soil overlying rock; on beaches within splash zone at sw Chichagof I. and Sokoi Is., and in mainland subalpine at Swan L., *2772 det Thomson, 2619 det. Ryan.*

**Fuscopannaria saubinetii** (Mont.) P.M. Jørg. I; on rock with mosses and/or humus; on conifers and deciduous trees in various forest types; low elevation to subalpine.

**Graphis scripta** (L.) Ach. C; on bark and trunks of *Alnus* and *Acer* in hardwood stands and beach edges.

***Gyalidea hyalinescens** (Nyl.) Vezda. On rocky outcrop in subalpine forest, on rocks in creeks at low and mid elevations; Kupreanof I., and Muddy R. drainage, mainland. *3333, 3348, 3338 det. Ryan.*

****Heterodermia sitchensis** Goward and Noble. R; on *Alnus* ; floodplains, lower Stikine R., *2563 det. T. Goward.* A rare coastal epiphyte known from BC (Goward 1984).

***Heterodermia speciosa*** (Wulfen) Trevisan. C; on deciduous trees and conifers, especially *Populus trichocarpa* and *Picea sitchensis*. All records are from mainland river valleys. *O'Clair 3464 det. Ryan, 3382, 1014, 1737.*

***Hymenelia epulotica*** (Ach.) Lutzoni. On rocks subject to inundation or flushing; in the mainland alpine. Elbow Mtn. *3274 det. Ryan.*

****Hydrotheria venosa*** J.L. Russell. On rock in streams shaded by forest, n of Portage Bay, Kupreanof I. *3358, 3360 det. Ryan.*

***Hyperphyscia adglutinata*** (Flörke) H. Mayrh. & Poelt. On hardwoods in Glacier Bay (Cummings 1904).

***Hypocenomyce leucococca*** R. Sant. On *Pinus contorta* near Petersburg, *T. Tønsberg 16579 BG.*

****Hypocenomyce sorophora*** (Vainio) P. James & Poelt. On *Pinus contorta.* wood. Near Petersburg, *T. Tønsberg 16581 BG.*

***Hypogymnia apinnata*** Goward & McCune. A; on trees, especially conifers in all forest types, sea-level to subalpine. PNW endemic (Goward & McCune 1993). Most easily differentiated from *H. enteromorpha* by its PD- reaction.

***Hypogymnia duplicata*** (Ach.) Rass. A; on trees, especially conifers, in *Pinus contorta* peatlands and mixed conifer forests; sea level to subalpine.

***Hypogymnia enteromorpha*** (Ach.) Nyl. A; on trees, especially conifers in all forest types; sea level to subalpine.

***Hypogymnia inactiva*** (Ach.) Nyl. C; on conifers, especially *Pinus contorta*, in open peatlands.

***Hypogymnia occidentalis*** L. Pike. R except in ne mainland in continental transition zone; on *Picea* and other trees. Burro Creek near Skagway, *K. Glew 810728-11 WTU*, and near Haines (Thomson & Ahti 1994).

***Hypogymnia oceanica*** Goward. C; on trunks and branches of open-grown *Pinus contorta*; also corticolous on *Picea sitchensis* and *Tsuga heterophylla* in other forest types, and on *Alnus* and *Malus* in the beach-forest ecotone. Low elevations. PNW endemic; rare in BC and southward (Goward 1988, McCune & Geiser 1997).

***Hypogymnia physodes*** (L.) Nyl. C; on conifers and deciduous shrubs. Most common on trees along marine beaches and riparian areas. Occurring sporadically in mixed conifer and *Pinus contorta* open forests and other open stands. Low elevations.

***Hypogymnia tubulosa*** (Schaerer) Hav. C; on conifers and deciduous shrubs in open forests throughout, particularly on beach or freshwater edges.

***Hypogymnia vittata*** (Ach.) Parrique. C; on conifers and deciduous shrubs in most forest types. Low elevation to subalpine.

***Hypotrachyna sinuosa*** (Sm.) Hale. C; on trees and shrubs in open *Picea sitchensis* and mixed *P. sitchensis/Alnus* forests at lower elevations.

***Icmadophila ericetorum*** (L.) Zahlbr. A; on bark and lignum of conifers, particularly on bases of trunks and on rotting snags.

***Imshaugia aleurites*** (Ach.) S.F. Meyer. R; on tree branches at Cape Fanshaw, mainland.

***Ionaspis lacustris*** (With.) Lutzoni. On rocks in creek bed in alpine and subalpine habitat on Waterfall Peak, mainland, *3236 det. Ryan.*

+***Kaernefeltia californica*** (Tuck.) Thell & Goward. I; on *Pinus contorta*, in open peatland forests at low elevation, hypermaritime localities. PNW endemic; se AK to CA.

***Lecanora cateilea*** Ach.) A. Massal. On *Salix*; nw of Haines, *Ahti 21423*, *21427 H.*

***Lecanora cinereofusca*** H. Magn. On *Alnus* along beaches. Kadin I. and Mallard Slough, Stikine R.; Rowan Bay, n Kuiu I; and Banana Pt., s Mitkof I. *3355*, *3442*, *3472*, *3070 det. Ryan.*

***Lecanora circumborealis*** Brodo & Vitik. On bark of deciduous trees and shrubs, low elevations; Unuk R., *451.*

***Lecanora contractula*** Nyl. On beach rocks. Our single collection pale, C-, lacking well developed lobes, *946 det. Ryan.* Also collected on the vertical sides of a shaded rock, sea cliff at top of Sunshine Cove, Auke Bay, *Brodo 26018.*

***Lecanora epibryon*** (Ach.) Ach. On rock in second growth forest, Port Camden, n Kuiu I., *876.*

***Lecanora expallens*** Ach. On beach log at high tide line, se Mitkof I., *3357 det. Ryan.*

***Lecanora fuscescens*** (Sommerf) Nyl. On beach edge *Alnus rubra* at Goose Cove, n Baranof I., *2659 det. Ryan.* In BC also in subalpine and alpine habitats (Goward et al. 1994a).

***Lecanora leptacina*** Sommerf. On mossy rock in alpine; Sheridan Peak, Kupreanof I. and Cosmos Range, mainland, *3249 & 3173 det. Ryan.*

***Lecanora muralis*** (Schreber) Rabenh. C; on beach rocks exposed to salt spray above the intertidal zone. Thalli of coastal AK and BC material are often unusually thick. On Aaron I. in the Lynn Canal it occurs on shoreline rocks below bird perches (O'Clair et al. 1996).

***Lecanora orae-frigidae*** R. Sant. C; strictly maritime, occurring only on driftwood, frequently alongside *L. xylophila* and *Xylographa opegraphella* (O'Clair et al. 1996).

***Lecanora poliophaea*** (Wahlenb.) Ach. C; on rock in the salt spray zone (O'Clair et al. 1996).

***Lecanora polytropa*** (Hoffm.) Rabenh. C; on rock in subalpine and alpine habitats.

***Lecanora pulicaris*** (Pers.) Ach. On bark of *Alnus* ; *2876 det. Ryan.* Also reported from a Juneau icefield nunatak (McCullough 1965).

***Lecanora salicicola*** Magnusson. On *Salix* nw of Haines (Thomson & Ahti 1994).

***Lecanora straminea*** Ach. Strictly maritime; on beach rocks in the salt spray zone and beneath bird perches (O'Clair et al. 1996); at Washington Bay, Kuiu I., *Eyerdam 1003 G*, *MIN*; *Eyerdam 1155 COLO*, *G; and Eyerdam 4026 G*, *UPS*; on Baranof I., June 13, 1880, *Bean s.n. (in packet of L. muralis) US* ( Ryan, 1997).

+***Lecanora strobilina*** (Sprengel) Kieffer. On *Alnus*; Unuk R., mainland, *458 det. Thomson.*

***Lecanora symmicta*** (Ach.) Ach. On rotting beach log, False I., se Chichagof I., *2660 det. Thomson*; on *Alnus rubra* along LeConte Bay, *927 det. Ryan*; and nw of Haines (Thomson & Ahti 1994).

***Lecanora xylophila*** Hue. C; on stabilized driftwood, bark and trees along marine beaches. See also O'Clair et al. (1996).

***Lecanora zosterae*** (Ach.) Nyl. On driftwood. Near Skagway, w side of Lynn Canal, *Sharnoff 1488.01.*

*****Lecidea albofuscescens*** Nyl On bark of *Picea sitchensis*, at beach fringe; Kadin I., Stikine R., *3451 det. Ryan.*

***Lecidea atromarginata*** H. Magn. On calcareous rock (Thomson 1979); Mendenhall Valley (McCullough 1965).

***Lecidea efflorescens*** (Hedl.) Erichsen. On *Alnus*, *Populus* and *Salix*. Bank of Herbert R., n of Juneau and Yakutat (Tønsberg 1993).

***Lecidea erythrophaea*** Flörke *ex* Sommerf. On *Picea* nw of Haines (Thomson & Ahti 1994).

***Lecidea lapicida*** (Ach.) Ach. On rocks near a stream outlet at Baranof L. where it was locally abundant and probably intermittently submerged, *2753 det. Thomson.* Also on rock at visitors center, Mendenhall Glacier, Juneau, *Brodo 25982.*

***Lecidea limosa*** Ach. On bare soil in meadow, Twin Creeks area, Mitkof I., *3365 det. Ryan.*

***Lecidea praenubila*** Nyl. On rock near Visitors Center, Mendenhall Glacier, Juneau, *Brodo 25982.*

***Lecidea roseotincta*** Coppins & Tønsberg. On *Alnus*, *Picea sitchensis* and *Salix* especially along river banks. Yakutat, Sitka, and Juneau vicinities (Tønsberg 1993).

***Lecidea silacea*** Ach. On rocks in a marine bay of Prince of Wales I. (Herre 1919). There is a rust colored morph of *L. lapicida* which can be misidentified as *L. silacea.* This lichen has undergone several taxonomic revisions since 1919 and its inclusion in this inventory is tentative.

***Lecidella asema*** (Nyl.) Knoph & Hertel **s. lato**.

***Lecidella effugiens*** (Nilson) Knoph & Hertel. On rocks near beach, sea cliff at top of Sunshine Cove, Auke Bay, *Brodo and others 26024B.*

***Lecidella euphorea*** (Flörke) Hertel. On dead *Alnus sinuata* branch overhanging beach; Glass Peninsula, Admiralty I., *2701 det. Thomson.*

***Lecidella stigmatea*** (Ach.) Hertel & Leuckert. On acidic or calcareous rocks in the salt spray zone; Sunshine Cove in the Lynn Canal (O'Clair et al. 1996); Mirror Harbor, Chichigof I., *1 det. Thomson.* Can grow on old bones. Also on alpine rocks, Bear Claw Mtn, s Kupreanof I., *3156 det. Ryan.*

+***Lecidella subincongrua*** (Nyl.) Hertel & Leuckert. Vertical rock surfaces in the salt spray zone near Sitka (O'Clair et al. 1996).

***Lecidoma demissum*** (Rutstr.) Gotth. Schneider & Hertel. C; on rock and soil in rock crevices in subalpine and alpine habitats; Thunder Mtn, *661.*

***Lepraria cacuminum*** (Massal.) Lohtander. On acid, mossy rocks, and acid bark, soil and other lichens; Bear Claw Mtn., s Kupreanof I., *3141 det. Ryan.*

+***Lepraria lobificans*** Nyl. On bark and detritus; Auke Bay, Juneau, *Atwood 18219, 18211a det. L. St. Clair.*

***Lepraria neglecta*** (Nyl.) Erichsen. On rock; Klondike Gold Rush Park, n of Skagway and Waterfall Ridge above Thomas Bay, mainland, *3235.*

***Leprocaulon subalbicans*** (Lamb) Lamb & Ward. On soil or on soil on rocks or in crevices of rocks (Thomson 1984); Mt. Roberts near Juneau (Krog 1968).

***Leproloma membranaceum* var. *chrysodectoides*** J.R. Laundon. Single collection from rocky cliff, high elevation mainland.

***Leproloma vouauxii*** (Hue) J.R. Laundon. On rock near low elevation road cut. Subalpine and alpine in BC (Goward et al. 1994a). Also known to occur on stone and bark (especially deciduous), bare surfaces, mosses, liverworts, soil and mountain rocks (Purvis et al. 1992).

****Leptogium brebissonii*** Mont. On tree branches at Petroglyph Beach, Wrangell, J. Jordan *3390 det. Ryan.* Known in N Am from BC (Goward et al. 1994a), OR and WA (McCune et al. 1997).

***Leptogium burnetiae*** Dodge. C; primarily on bark of deciduous trees and shrubs, more rarely on *Picea sitchensis*, in deciduous or *P. sitchensis*/deciduous forests at low elevations.

***Leptogium californicum* s. lato**. On sea cliff at top of Sunshine Cove, Auke Bay, *Brodo 26013.* This morph is close to *L. lichenoides* but has flattened, laminal "isidia".

***Leptogium corniculatum*** (Hoffm.) Minks. C and widespread; on thin soil on rock in open coastal sites at lower elevations, especially in crevices, on beach rock in the splash zone, once on *Alnus*. See also O'Clair et al. (1996).

***Leptogium cyanescens*** (Rabenh.) Körber. I-C; corticolous; mainly on deciduous shrubs (*Alnus* and *Salix*) but also on *Picea sitchensis.* Collected only in the Unuk and Stikine R. valleys, these rivers originating in the BC interior.

+***Leptogium furfuraceum*** (Harm.) Sierk. R; on bark of Alnus; Unuk and Stikine R. valleys, mainland, *468 det. Thomson.*

***Leptogium hirsutum*** Sierk. I-R; on bark of deciduous trees and decaying logs along Loop and Granite Basin Roads in Juneau (Krog 1968).

***Leptogium lichenoides*** (L.) Zahlbr. I-R; on *Populus* along river edge, 15 Mile I., Stikine R, *3206 det. Ryan* and on rock in splash zone, Naukati Bay, Prince of Wales I., *2569.* On s Kuiu I. (Thomson 1984).

***Leptogium saturninum*** (Dickson) Nyl. C; on bark of deciduous trees and shrubs (*Alnus*, *Populus* and *Salix*). Collected only on major, mainland river valleys (Unuk and Stikine) and from the Yakutat lowlands.

*****Leptogium subtile*** (Schrader) Torss. R; on *Populus* along river edge, 15 Mile I., Stikine R., *3206.* The only other N Am reports are from BC (Goward & Ahti 1992).

***Leptogium tenuissimum*** (Dickson) Körber. R; on *Populus trichocarpa* in the Unuk valley on the mainland and Kadin I. at s end of Kupreanof I., *469 det. Thomson.*

+***Leptogium teretiusculum*** (Wallr.) Arnold. R; on twig of *Picea sitchensis* along the Stikine R., *1370 det. Thomson.*

***Lobaria hallii*** (Tuck.) Zahlbr. C; on deciduous trees and shrubs (*Populus, Alnus and Salix*) and *Picea sitchensis* in low elevation stands; especially in river valleys.

***Lobaria kurokawae*** Yoshim. R; among mosses on soil and rocks (Thomson 1984). Mendenhall L., Mendenhall Glacier and Herbert Glacier, all near Juneau (Jordan 1973).

***Lobaria linita*** (Ach.) Rabenh. A; on the bases, trunks and branches of conifers and deciduous trees and shrubs; low to subalpine elevations; also common on mossy subalpine and alpine rocks. Not in low elevation peatlands or *Pinus contorta* forests. Our collections are mostly var. *tenuior*, i.e. large, reticulately ribbed, fertile and growing on trees. Var. *linita*, found in alpine habitats, tends to be smaller, reticulately wrinkled and sterile (Jordan 1973).

***Lobaria oregana*** (Tuck.) Müll. Arg. A; mainly on branches and trunks of conifers and on deciduous shrubs in forested stands at low elevations. Sometimes found on *Alnus* but usually yellow in color in such cases. Not found in open mixed-conifer forests or *Pinus contorta* peatlands.

***Lobaria pseudopulmonaria*** Gyelnik. R; on soil and among mosses, sometimes on rocks (Thomson 1984). Known from Mendenhall L. area (Jordan 1973).

***Lobaria pulmonaria*** (L.) Hoffm. C; most commonly associated with stands of deciduous shrubs or *Populus/Picea sitchensis* forest. On bark of coniferous and deciduous trees, and shrubs. Low to subalpine elevations. Not found in *Tsuga heterophylla* or *Pinus contorta* forests.

***Lobaria retigera*** (Bory) Trevisan. R; on branches of *Picea sitchensis* and *Alnus*; major river valleys (Stikine and Unuk) originating in interior BC and the Patterson R., mainland. *2433 det. Brodo, 481 det. McCune, 1292, 1113,764, 333.*

***Lobaria scrobiculata*** (Scop.) DC. C; on bark. Most frequent in low elevation riparian habitats of deciduous shrubs or *Populus trichocarpa / Picea sitchensis.* Not in *Tsuga heterophylla* or *Pinus contorta* forests.

***Lopadium disciforme*** (Flotow) Kullhem. Corticolous on *Picea sitchensis* trunk in old growth forest and alpine habitats. Kadin I., mouth of Stikine R., *3469 & 3468 det. Ryan.* On *Salix* in Haines (Thomson & Ahti 1994).

***Loxosporopsis corallifera*** Brodo, Henssen & Imshaug. C; on *Pinus contorta*, especially lower surfaces of branches in open *P. contorta* peatlands. Also on *Thuja plicata*, *Picea sitchensis*, *Tsuga heterophylla*. PNW endemic (Brodo & Henssen 1995).

***Massalongia carnosa*** (Dickson) Körber. I; on alpine, moss-covered rocks. Sheridan Peak, Kupreanof I. and Cosmos Range and Elbow Mtn., mainland, *3248, 3188 & 3280 det. Ryan*; Skagway, *Sharnoff 1486.19.*

***Melanelia commixta*** (Nyl.) Thell. C; on rock in coastal localities, subalpine and alpine.

***Melanelia exasperatula*** (Nyl.) Essl. R; on trees nw of Haines (Thomson & Ahti 1994).

***Melanelia fuliginosa*** (Fr. *ex* Duby) Essl. R; on twigs of *Picea sitchensis*, Kadin I., mouth of Stikine R., *3442 det. Ryan.* Shipley Bay, Kosciusko I. (Herre 1919).

**Melanelia hepatizon** (Ach.) Thell. C; on alpine rocks.

**Melanelia multispora** (A. Schneider) Essl. R; on *Alnus* and other deciduous trees and shrubs. Mallard Slough, Stikine R., *3080 det. Ryan*, Mendenhall L. area (Krog 1968) and nw of Haines (Thomson & Ahti 1994).

**Melanelia olivacea** (L.) Essl. R; on *Alnus* nw of Haines (Thomson & Ahti 1994).

**Melanelia septentrionalis** (Lynge) Essl. R; on hardwoods nw of Haines (Thomson & Ahti 1994).

**Melanelia sorediata** (Ach.) Goward & Ahti. On rock at LeConte Bay, mainland, *442*. Also occurs on bark (Thomson 1984).

**Melanelia stygia** (L.) Essl. On rock. On AB Mountain Trail near Skagway, *Sharnoff 1486.04*.

**Melanelia subaurifera** (Nyl.) Essl. I-R; on trees in open to somewhat sheltered low elevation forests in BC (Goward et al. 1994b). Indian R. Trail near Sitka and Saxman Village near Ketchikan (Krog 1968).

+**Menegazzia terebrata** (Hoffm.) A. Massal. C; on deciduous trees and shrubs, especially *Alnus*, in low elevation, riparian habitats.

**Micarea assimilata** (Nyl.) Coppins. On rocks or moss-covered rock in subalpine and alpine habitats; Crystal Mtn. Mitkof I., Swan L., mainland, and s Prince of Wales I., *892 det. Thomson*.

**Micarea incrassata** Hedl. On alpine soils and rock; Thunder Mtn, mainland, *9*, *22*, *23*, *& 662 det. Thomson*.

**Mycobilimbia berengeriana** (Massal.) Heffellner & V. Wirth. On exposed soil in an open mixed conifer forest.; Spurt L., mainland, *83*.

**Mycobilimbia tetramera** (De Not.) W. Brunnbauer. On soil, alpine summit, 1040m, Gastineau Peak near Juneau, *Brodo 26356*.

**Mycoblastus affinis** (Schaerer) Schauer. Corticolous in forests, also on beach logs; Myriad Is., w of Chichigof I., *6931*, *23391*, *1257*, *& 1375 det. Ryan;* and near Petersburg, *Tønsberg 16583 BG*.

***Mycoblastus caesius** (Coppins & P. James) Tønsberg. On *Pinus contorta*; near Petersburg, *Tønsberg 16580 BG*.

**Mycoblastus sanguinarius** (L.) Norman. C; widespread on all conifers and all major deciduous trees and shrubs in most forest types; low elevation to subalpine.

+**Neofuscelia subhosseana** (Essl.) Essl. R; single collection growing under a colony of *Stereocaulon* on rock covered by a thin layer of humus; LeConte Bay, mainland, *365 det. Thomson*.

**Nephroma arcticum** (L.) Torss. I; on moss and mossy rocks, and moss-covered conifer trunks, sea level to alpine.

**Nephroma bellum** (Sprengel) Tuck. A; on fine branches of most conifers and deciduous trees and shrubs in open to somewhat shaded forests at low elevations. Most frequent along beach fringes.

**Nephroma expallidum** (Nyl.) Nyl. R; on moss-covered soil on AB Mountain Trail near Skagway. *Sharnoff 1485.36*.

**Nephroma helveticum** Ach. A; on branches of *Picea sitchensis* and deciduous trees and shrubs in open forests at lower elevations, particularly beach fringes.

+-**subsp. *helveticum*** *3392 & 3394 det. Ryan, 312.*

-**subsp. *sipeanum*** (Gyelnik) Goward & Ahti.

***Nephroma isidiosum*** (Nyl.) Gyelnik. I; on branches of *Picea sitchensis* and deciduous trees and shrubs (*Alnus*, *Populus* and *Salix*); along mainland river valleys originating in the BC interior (Unuk and Stikine Rivers), the Patterson R., mainland and in the Yakutat lowlands.

***Nephroma laevigatum*** Ach. R; on branches of *Picea sitchensis* and on deciduous shrubs from the Stikine R. valley and Cape Fanshaw on the mainland, Harvey L. trail, Woewodski I., *620*, and the Myriad Islands on the outer w coast. Also at Faragut Bay (Kincaid 1899).

****Nephroma occultum*** Wetmore. On *Picea sitchensis*; Chilkoot L. State Recreation Area, *Sharnoff 1393.32*. A rare; old growth dependent lichen known from BC s to WA and OR. The ecological epicenter of this lichen is considered to be the transition zone between oceanic and humid continental climates (Goward 1995, Wetmore 1980).

***Nephroma parile*** (Ach.) Ach. C; mainly on deciduous trees and shrubs (*Alnus*, *Populus* and *Salix*) but also on *Picea sitchensis* at low elevations.

***Nephroma resupinatum*** (L.) Ach. C; mainly on deciduous trees and shrubs (*Alnus*, *Populus* and *Salix*) and *Picea sitchensis* at low elevations.

****Nephroma sylvae-veteris*** Goward & Goffinet. R; on *Picea sitchensis* at Chilkoot L. State Recreation Area, *Sharnoff 1390.28*. A rare lichen thought to be exclusively associated with old growth forests and occurring in habitats transitional between the oceanic coast and the continental interior. Known from BC and n WA (Goward & Goffinet 1993). The taxonomic status of this species is uncertain, some consider it a rare form of *Lobaria oregana*.

***Nodobryoria oregana*** (Tuck.) Common & Brodo. R; corticolous on *Pinus contorta*; in low elevation open *Pinus contorta* peatlands. Old Tom's Creek drainage, Prince of Wales I. *1666 det. Brodo*.

***Normandina pulchella*** (Borrer) Nyl. I; on mosses on branches of trees and shrubs, or on other lichens; low elevations to subalpine. Easily over-looked due to its small size.

***Ochrolechia androgyna*** (Hoffm.) Arnold. On deciduous and coniferous tree bark, wood, rocks and on mosses and vegetation. In humid, forested habitats especially along lake shores and peatlands (Brodo 1991). Yakutat lowlands, *1592*.

***Ochrolechia arborea*** (Kreyer) Almb. On bark and wood of conifers and deciduous trees and shrubs. In open forests or along beaches, e.g. *Pinus contorta* and *Picea sitchensis* stands (Brodo 1991). Big Bay, w Baranof I., *2107*.

***Ochrolechia frigida*** (Sw.) Lynge. C; on soil and mosses in subalpine and alpine habitats.

-- **f. *thelephoroides*** (Th. Fr.) Lynge. C; primarily on subalpine and alpine rocks or soil, but also on bark or lignum in open forests at lower elevations.

+***Ochrolechia juvenalis*** Brodo. C; on conifer bark or lignum, and on *Alnus*; low elevation conifer forests. Big Bay, w Baranof I. *2141 det. Brodo*; Bear Ck, Mitkof I. *1846 det. Thomson;* LeConte Bay *267*. Known from BC s to CA (Brodo 1991).

***Ochrolechia laevigata*** (Räsänen) Vers. *ex* Brodo. C; smooth-barked, deciduous trees like *Alnus*, but also *Picea sitchensis*, *Pinus contorta* and *Tsuga heterophylla*. Mostly lowland *P. sitchensis/Alnus* stands but also in many coniferous forest types, especially along streams and beaches at low elevations.

***Ochrolechia oregonensis*** H. Magn. C; on *Picea sitchensis* and *Pinus contorta* bark or lignum; rarely on *Alnus*. *P. contorta* and deciduous/*P. sitchensis* forests; sea level to alpine.

+***Ochrolechia subpallescens*** Vers. C; on bark of *Populus*, *Alnus* and conifers; sea level to subalpine. Known from QCI s through CA in N Am (Brodo 1991).

***Ochrolechia subplicans*** (Nyl.) Brodo. Formerly *Pertusaria subplicans* and *P. hultenii*. See Brodo (1987) for discussion of the taxonomy, chemistry and ecology of this species.
**-subsp. *subplicans*.** On alpine rocks; Gastineau Peak near Juneau, *Brodo 26328*.
**-subsp. *hultenii*** (Erichsen) Brodo. On shoreline rocks; Aaron I. near Juneau, *Brodo 26399*.

***Ochrolechia szatalaënsis*** Vers. On bark or wood. Nw of Haines (Thomson & Ahti 1994) and Juneau, *Imshaug 28449A MSC*. See also Brodo (1991).

***Ochrolechia tartarea*** (L.) A. Massal. On rock at Port San Antonio, Baker I.; Heceta I.; and Shipley Bay, Kosciusko I. (Herre 1919). These reports need to be confirmed as *Ochrolechia* growing on rock were routinely grouped under the name *O. tartarea* until recently.

***Ochrolechia xanthostoma*** (Sommerf.) K. Schmitz & Lumbsch. On rocky soil in alpine and on *Salix* in riparian zone; Tawa Ck., Yakutat lowlands, *3396 det. Ryan*.

***Omphalina husdoniana*** (H.S. Jenn.) H.E. Bigelow. On a root wad on a peatland/ forest edge in the Windham Bay area at 400m, *Krieckhaus 3438 det. Ryan*.

+***Opegrapha rupestris*** Pers. On shore rocks, Prince of Wales I. (Herre 1919). Usually associated with moist limestone or calcareous schists (Purvis et al. 1992).

***Ophioparma lapponica*** (Räsänen) Hafellner & R.W. Rogers. C; on rocks in alpine habitats. Elbow Mtn, Thunder Mtn and near glacier terminus on shore rocks in LeConte Bay, mainland; Crystal Mtn., Mitkof I. *361*, *3265*, *3271*, *972*, *2030*.

***Pannaria pezizoides*** (Weber) Trevisan. C; on bark of deciduous trees and shrubs (*Alnus*, *Malus* and *Populus*) and *Picea sitchensis*, and mossy rocks; sea level to alpine.

***Parmelia hygrophila*** Goward & Ahti. C; on trees (*Alnus*, *Picea sitchensis*, *Pinus contorta* and *Populus*) in most low elevation forest types; also rare on base-rich rock. PNW endemic (Goward & Ahti 1983).

***Parmelia omphalodes*** (L.) Ach. On siliceous rock in open sites; Saxman village near Ketchikan (Krog 1968).

***Parmelia pseudosulcata*** Gyelnik. C; on conifers and *Populus* in most forest types; sea-level to subalpine.

***Parmelia saxatilis*** (L.) Ach. A; on rock in open sites; beaches to alpine. Also common on bark and lignum of conifers and deciduous shrubs (*Alnus*, *Malus*) in many forest types, particularly *Pinus contorta* peatlands and forest edges.

***Parmelia squarrosa*** Hale. C; on conifers and deciduous trees and shrubs, occasionally on rock; beaches and riparian habitats at lower elevations.

***Parmelia sulcata*** Taylor. A; on trees throughout, also infrequent on acid rock.

***Parmeliella triptophylla*** (Ach.) Müll. Arg. I; on deciduous trees and shrubs (*Alnus* and *Populus*); riparian. Unuk and Stikine R. *1024*, *456*, *1757*.

***Parmeliopsis ambigua*** (Wulfen) Nyl. C; same substrates and habitats as *P. hyperopta* but not as common and not as strongly associated with *Pinus contorta* peatlands.

***Parmeliopsis hyperopta*** (Ach.) Arnold. A; on coniferous and deciduous trees and shrubs, especially *Pinus contorta* peatlands and in mixed-conifer, deciduous riparian, and subalpine forests. Not common in *Tsuga heterophylla* or *Picea sitchensis* forest communities. Low elevation to subalpine.

***Parmotrema arnoldii*** (Du Rietz) Hale. I; on branches of conifers along marine beaches.

***Parmotrema chinense*** (Osbeck) Hale & Ahti. R; on branches of conifers along marine beaches. Sokoi Is., near Petersburg, *38*, *2596*.

***Peltigera aphthosa*** (L.) Willd. C; on soil, rocks, logs and stumps, and trunk bases of conifers and deciduous shrubs, often associated with mosses; sea level to alpine. Found most frequently on the mainland.

***Peltigera britannica*** (Gyelnik) Holt-Hartw. & Tønsberg. A; on soil, rocks, logs, stumps, and trunk bases of conifers and deciduous shrubs, often associated with mosses; in most forest types, except *Pinus contorta* open peatlands; low elevation to alpine.

- **cyanobacterial phototype**. I; on moss-covered logs, or bark of conifers in open to shady forests. Also collected on the AB Mountain Trail near Skagway, *Sharnoff 708.02*. See Goward et al. 1995) and Tønsberg & Holtan-Hartwig (1983) for differentiating phototypes of *Peltigera*.

***Peltigera canina*** (L.) Willd. I; occasionally seen in drier parts of the region. *P. membranacea*., a related, oceanic species, is much more common.

+***Peltigera cinnamomea*** Goward. I; on moss and mossy rocks and logs in open to somewhat sheltered inland forests in BC. Largely restricted to foothills and mountain habitats with long-lasting snow cover (Goward et al. 1995) Very similar to *P. membranacea* and possibly overlooked.

***Peltigera collina*** (Ach.) Schrader. A; primarily on trunks and branches of deciduous trees and shrubs (especially *Alnus*), also on mossy rocks and soil humus in deciduous or mixed *Picea* /deciduous forests in riparian zones; low elevations.

***Peltigera degenii*** Gyelnik. I; on soil humus, mossy rocks and mossy logs in open to somewhat sheltered forest sites at lower elevations. In mixed deciduous stands and mixed conifer stands. Not found in open peatlands or *Pinus contorta* forests.

***Peltigera didactyla*** (With.) J.R. Laundon. I; on soil, moss, logs, or trees in open sites.

***Peltigera elisabethae*** Gyelnik. R; on soil and mossy rock in open forests, also on

*Alnus* at beach fringe and on beach logs.

***Peltigera horizontalis*** (Hudson) Baumg. R; on moss-covered ground or shrubs. Hugh Smith L., Misty Fjords National Monument; Kadin I., mouth of Stikine R. *3473 det. Ryan, 1985 det. Brodo.*

***Peltigera lepidophora*** (Vainio) Bitter. R; on moss-covered rock in a mixed conifer forest, nw Revilla. I., *788 det. Thomson*; on young *Alnus*, Ohmer Ck., Mitkof I. In BC this species occurs on soil and moss in open sites and is more common in interior arid lands and wet interior forests (Goward et al. 1994b).

***Peltigera leucophlebia*** (Nyl.) Gyelnik. C; usually found growing with moss on soil or rock; in alpine habitats and near glacier termini.

***Peltigera malacea*** (Ach.) Funck. R; on soil and moss in open, drier forests, alpine ridges (Goward et al. 1994b) and shrubby vegetation. Yakutat (Thomson 1984).

***Peltigera membranacea*** (Ach.) Nyl. A; usually growing with mosses on soil (on the forest floor or open peatlands), rock, stumps and logs; most common in low elevation *Picea sitchensis*, *Tsuga heterophylla* and *Populus* forests.

***Peltigera neckeri*** Hepp *ex* Müll. Arg. I; with mosses on soils (mostly sandy) and mossy logs in forested habitats.

***Peltigera neopolydactyla*** (Gyelnik.) Gyelnik. A; on logs and stumps (usually associated with mosses), mossy rock, on humus on the forest floor, occasionally on bases of trunks or branches of conifers; primarily *Tsuga heterophylla* forests. Subalpine to alpine.

***Peltigera pacifica*** Vitik. I; on logs and stumps (usually associated with mosses), mossy rock, on humus on the forest floor, occasionally on bases of trunks or even branches of conifers. In various forest types at low elevations.

***Peltigera polydactylon*** (Necker) Hoffm. C; on logs and stumps (usually associated with mosses), mossy rocks or with humus in rock crevices, on humus on the forest floor, occasionally on bases of trunks or even branches of conifers and deciduous shrubs. Primarily found in *Picea sitchensis*, *Tsuga heterophylla* and mixed deciduous forests; sea-level to alpine. Widespread, but most common on the mainland.

+***Peltigera ponojensis*** Gyelnik. I; with mosses on glacial outwash, Mendenhall Glacier trail, *2809 det. Brodo*. On soil on the AB Mountain Trail near Skagway, *Sharnoff 1489.16*. In subalpine and alpine habitats in BC (Goward et al. 1994b).

***Peltigera praetextata*** (Flörke *ex* Sommerf.) Zopf. I; on soil (from humus to sand) or logs, with or without moss, in open forests and near marine beaches and mainland rivers. Low elevations.

***Peltigera rufescens*** (Weis) Humb. I; in BC on soil or moss in open, often somewhat exposed sites (Goward et al. 1994b). Granite Basin, near Juneau (Krog 1968); Sitka and Ketchikan (Thomson 1984).

***Peltigera scabrosa*** Th. Fr. A; on mossy logs, stumps and rocks, humus, occasionally on tree bases and conifer branches; primarily *Tsuga heterophylla* forests, sea level to alpine.

***Peltigera venosa*** (L.) Hoffm. I; on cut bank along Stikine R.; on liverwort-covered lava, Unuk R.; on moss-covered log, shore of Petersburg L.; at base of *Picea sitchensis* on the beach, *3375*, *2560*, *3197*, *753*; along road cuts.

***Pertusaria amara*** (Ach.) Nyl. Corticolous on hardwoods and conifers; infrequently saxicolous. Bear Ck, Mitkof I., *1850.*

***Pertusaria borealis*** Erichsen. C; on bark of *Picea sitchensis* and *Alnus* near beach edges and inland. Near Mendenhall Glacier, Juneau, *Viereck 8658 WIS*; on *Pinus contorta*, Petersburg, *Tønsberg 16578 BG*; and nw of Haines (Thomson & Ahti 1994).

***Pertusaria* cf. *bryontha*** (Ach.) Nyl. On wood in alpine; Elbow Mtn., mainland, *3264 det. Ryan.* This species is usually muscicolous, but our specimen keys here in Dibben (1980).

***Pertusaria dactylina*** (Ach.) Nyl. On rock, moss and *Tsuga mertensiana*; subalpine to alpine, *509 & 510 det. Ryan.*

***Pertusaria flavocorallina*** Coppins & Muhr. On *Alnus* and *Populus*, sea level to 30 m. Bank of Herbert R. n of Juneau and Yakutat (Tønsberg 1993).

***Pertusaria oculata*** (Dickson) Th. Fr. Among mosses on a vertical rock face, LeConte Bay shoreline, mainland, *371.* Subalpine and alpine in BC (Goward et al. 1994b).

***Pertusaria ophthalmiza*** (Nyl.) Nyl. C; on branches of *Alnus* at low elevations near rivers or marine beaches.

***Pertusaria sommerfeltii*** (Flörke *ex* Sommerf.) Fr. Typically on hardwoods in N Am (Dibben 1980). Mendenhall Valley (McCullough 1965).

***Pertusaria subambigens*** Dibben. C; on twigs and branches of *Picea sitchensis* and *Alnus* at low elevations, mainly near water edges, but also in mixed conifer and *Pinus contorta* open forests.

***Phaeophyscia ciliata*** (Hoffm.) Moberg. Usually on deciduous trees, also on conifers and rocks; Glacier Bay (Thomson 1963).

***Phaeophyscia endococcina*** (Körber) Moberg. On rocks and among mosses on rocks, rarely on tree bases; n Kuiu I. (Thomson 1984).

+***Phaeophyscia hirtella*** Essl. On *Alnus rubra* in riparian corridor; Unuk R., mainland, *470 det. Thomson.*

***Phaeophyscia orbicularis*** (Necker) Moberg. On beach logs above high tideline in the lower salt spray zone. Wrangell Narrows, Mitkof I., *3371 det. Ryan*, and Aaron I. in Lynn Canal (O'Clair et al. 1996).

***Phylliscum demangeonii*** (Moug. & Mont.) Nyl. On rocks at high tide mark at Zarembo Bay, Zarembo I. (Herre 1919).

***Physcia adscendens*** (Fr.) H. Olivier. R; on twigs of *Picea sitchensis.*

***Physcia aipolia*** (Ehrh. *ex* Humb.) Fürnr. var. *aipolia*. I; on *Populus* and *Salix* in low elevation, riparian habitats.

***Physcia caesia*** (Hoffm.) Fürnr. C; on rock and bark in open to somewhat sheltered sites from sea level to alpine habitats. One of the most common shoreline lichens, especially on rocks beneath bird perches (O'Clair et al. 1996).

***Physcia dubia*** (Hoffm.) Lettau. On base-rich rock in open sites in BC (Goward et al. 1994b). Juneau area (Krog 1968).

***Physcia stellaris*** (L.) Nyl. On deciduous and coniferous trees and shrubs, occasionally on rock or wood (Thomson 1963); Glacier Bay (Cummings 1904). This record should be checked as *P. stellaris* can be easily confused with the much more common *P. aipolia* (Thomson 1963). *P. stellaris* has also been reported from intermontane BC, where it is considered rare (Goward et al. 1992).

***Physcia tenella*** (Scop.) DC. On deciduous trees and shrubs Stikine R. valley, mainland, *3337.*

***Physconia muscigena*** (Ach.) Poelt. On rock and *Populus* bark along mainland river valleys and near salt water. Calciphilous; below bird perches and on limestones.

***Pilophorus acicularis*** (Ach.) Th. Fr. C; on siliceous rock outcrops, occasionally on wood or bark, in open to sheltered forests and shorelines; sea-level to subalpine.

***Pilophorus cereolus*** (Ach.) Th. Fr. R; on rock on AB Mountain Trail near Skagway, *Sharnoff 1489.05.*

***Pilophorus clavatus*** Th. Fr. I; on rocks; along lake edges, in open to sheltered forests and in subalpine and alpine habitats. *511*, *1224*, *3337.*

***Pilophorus nigricaulis*** Satô. I; on siliceous rock; low to subalpine and alpine elevations.

***Pilophorus robustus*** Th. Fr. R; on rock in n facing subalpine bowl among melting snow patches. Crystal Mtn., Mitkof I. *903.*

***Placopsis gelida*** (L.) Lindsay. A; on native rock, road fill and asphalt; sea level to alpine.

+***Placopsis roseonigra*** Brodo. Sitka and Juneau; *Brodo 26110* and *Ennis s.n.* Endemic to QCI and se AK (Brodo 1995b).

***Placynthium nigrum*** (Hudson) Gray. On calcareous rock; Waterfall Peak, mainland, *3235 det. Ryan.*

***Platismatia glauca*** (L.) Culb. & Culb. A; on conifers, less often on deciduous shrubs, in most forest types; low to subalpine elevations.

***Platismatia herrei*** (Imshaug) Culb. & C. Culb. A; on conifer trunks and branches in most forest types; low to, infrequently, subalpine elevations.

***Platismatia lacunosa*** (Ach.) Culb. & C. Culb. A; on branches of conifers and deciduous shrubs, in most forest types below the subalpine.

***Platismatia norvegica*** (Lynge) Culb. & C. Culb. A; on conifers and occasionally *Alnus* from low elevations to (infrequently) subalpine.

+***Plectocarpon lichenum*** (Sommerf.) D. Hawksw. Parasitic on *Lobaria pulmonaria.* (Thomson & Ahti 1994).

+***Polychidium dendriscum*** (Nyl.) R; on bark of conifers and deciduous shrubs.

***Polychidium muscicola*** (Sw.) Gray. On rock in splash zone. Staney I., near Prince of Wales I., *2582 det. Ryan.*

***Porpidia carlottiana*** Gowan. On rock. Usually exposed; along waterways in mountains or on seashore rocks. Pacific nw N Am endemic, common to hypermaritime localities on the w coast from OR to s central AK (Gowan 1989).

***Porpidia flavocaerulescens*** (Hornem.) Hertel & A.J. Schwab. C; on rock; in splash zone of marine beaches to alpine peaks.

***Porpidia lowiana*** Gowan. On rock on cliffs shaded by the forest canopy, on lake cliffs, on boulders in open slide area, low to mid elevations. Baranof I., Kupreanof I. and the mainland. *3115, 3171, 3364, 3354 &3339 det. Ryan.*

***Porpidia speirea*** (Ach.) Kremp. On alpine rock. Thunder Mtn., mainland, *669 det. Thomson.*

***Porpidia thomsonii*** Gowan. C and widespread; on exposed rock; marine shorelines and low elevation peatlands to subalpine and alpine habitats.

***Pseudephebe minuscula*** (Nyl. *ex* Arnold) Brodo & D. Hawksw. C; on rock and soil or moss-covered rock. Thunder Mtn, mainland and Crystal Mtn., Mitkof I. alpine; terminal moraine of Herbert Glacier, *2038 det. McCune*, *3215.*

***Pseudephebe pubescens*** (L.) Choisy. C; on alpine rocks and exposed glacial moraines.

***Pseudocyphellaria anomala*** Brodo & Ahti C; on tree branches (especially *Picea sitchensis* and *Populus*) and shrubs along marine beaches and mainland rivers.

***Pseudocyphellaria anthraspis*** (Ach.) H. Magn. I; on branches of *Picea sitchensis* and deciduous shrubs (*Alnus*, *Salix* and *Vaccinium*) along rivers or marine beaches.

***Pseudocyphellaria crocata*** (L.) Vainio. C; on branches of coniferous and deciduous trees and shrubs along rivers or marine beaches. Especially *Picea sitchensis* and *Alnus*, but also on *Populus*, *Malus*, *Tsuga heterophylla* and others.

+***Pseudocyphellaria rainierensis*** Imshaug. R; corticolous and lignicolous on coastal *Picea sitchensis*, *Tsuga mertensiana*, *Alnus* and *Malus*. On small marine islands: Sokoi Is., near Petersburg; Baird I., sw of Chichigof I.; Kadin I., mouth of Stikine R., *460*, *2767*, *3454*. A rare endemic, OR to AK.

***Psora decipiens*** (Hedwig) Hoffm. On alpine soils; Elbow Mtn., mainland, *3263 det. Ryan.*

***Psoroma hypnorum*** (Vahl) Gray. C; on rock, soil or bark (*Salix*, *Tsuga heterophylla* and *Vaccinium*) in open sites; low to subalpine and alpine elevations. At lower elevations, usually near fresh or saltwater beaches.

***Pyrrhospora cinnabarina*** (Sommerf.) Choisy. C; on fine branches of conifers in most forested areas; low elevations to subalpine.

***Ramalina* cf. *almquistii*** Vainio. Infrequently collected amphi-Beringian species of the high arctic and Aleutian Is. (Thomson 1984); *O'Clair 3381*. Small specimen.

***Ramalina dilacerata*** (Hoffm.) Hoffm. I; on *Alnus rubra* along the Mendenhall R, *1568*. On *Alnus* branch at Brotherhood Park in Juneau, *Sharnoff 742.24*.

***Ramalina farinacea*** (L.) Ach. C; on trunks and branches of *Picea sitchensis* and deciduous shrubs (*Alnus*, *Malus*) along marine beaches; rarely along rivers or on rock.

+***Ramalina inflata*** (Hook. f. & Taylor) Hook f. & Taylor subsp. *inflata*. I; on trunks and branches of *Alnus* along fresh and salt water beaches; at low elevations. These and other collections may be large sized *R. dilacerata*.

+***Ramalina* cf. *leptocarpha*** Tuck. R; on *Menziesia ferruginea* along the beach on Dog I. s of Ketchikan, *1879 det. Brodo*. This is a coastal w N Am species which may reach the n extent of its range in se AK.

***Ramalina menziesii*** Taylor. I; pendent from *Picea sitchensis* branches along salt water beaches, especially on peninsulas or small marine islands. Although this lichen occurs infrequently, when it does occur it is profuse, other *Ramalina* and *Usnea* may be present, and *Alectoria* will be absent. Hood Bay, Admirality I.; Shrine of St. Therese, Juneau; Cape Fanshaw, mainland; Table Bay, Kuiu I.; Schooner I. and Kah Sheets Bay, Kupreanof I. *1067*, *1906*, *2552*, *2722*, *3258.*

***Ramalina roesleri*** (Hochst. *ex* Schaerer) Hue. C; corticolous on trunks and branches of *Picea sitchensis*, other conifers, *Alnus* and *Salix* along marine beaches.

***Ramalina thrausta*** (Ach.) Nyl. C; on bark of tree trunks and branches, especially *Picea sitchensis*, along marine beaches.

***Rhizocarpon badioatrum*** (Flörke *ex* Sprengel) Th. Fr. On acid, alpine rocks. Thunder Mtn., mainland, *673 det. Thomson.*

***Rhizocarpon copelandii*** (Körber) Th. Fr. On exposed rock in splash zone just above high tide line at Kelp Bay on Baranof I. and the Wrangell Narrows. On alpine rock on Bear Claw Mtn., s Kupreanof I. and Cosmos Range and Elbow Mtn., mainland, *3134*, *3256*, *3270 det. Ryan.*

***Rhizocarpon disporum*** (Naegeli. *ex* Hepp) Müll. Arg. On rock above the trimline of the Taku Glacier in the Juneau Ice Field (Heusser et al. 1954). Occurring on acid or calcareous rocks in strong light (Thomson 1979).

***Rhizocarpon eupetraeoides*** (Nyl.) Blomb. & Forss. On acid rock. Unnamed peak w of Elbow Mtn., mainland, *3269 det. Ryan.*

***Rhizocarpon geminatum*** Körber. C; on acidic rocks, low to alpine elevations. Frequently on shoreline rocks in the salt spray zone (O'Clair et al. 1996).

***Rhizocarpon geographicum*** (L.) DC. C; on alpine rocks.

+***Rhizocarpon hensseniae*** Brodo. On alpine rocks; Gastineau Peak, 670 m elevation. Endemic to QCI and se AK (Brodo 1990).

***Rhizocarpon hochstetteri*** (Körber) Vainio. C; on acidic or basic rock; on shore rocks on w Baranof I. and just above tidal mud flats of the Stikine R; in alpine habitats in the Cosmos Range, mainland and Bear Claw Mtn, s Kupreanof I; *318*, *31586*, *3470 det. Ryan.* Also on Aaron I. in Lynn Canal (O'Clair et al. 1996).

***Rhizocarpon obscuratum*** (Ach.) A. Massal. On acidic rocks; in an open scrub forest at the warm springs by Baranof R., *3132 det. Ryan.* More common inland (O'Clair et al. 1996).

+***Rhizocarpon praebadium*** (Nyl.) Zahlbr. R; on alpine rocks. Thunder Mtn., n of the Stikine R., *521 det. Thomson.*

***Rhizocarpon superficiale*** (Schaerer) Vainio. On exposed, usually acidic, rocks (Thomson 1979). Klondike Goldrush National Historic Monument, near Skagway.

***Rinodina gennarii*** Bagl. C; strictly maritime, on acidic rocks in the salt spray zone (O'Clair et al. 1996).

***Rinodina sheardii*** Tønsberg. On trunks of *Alnus* on river banks; Herbert R. and Dotson Landing, Juneau vicinity (Tønsberg 1992).

***Schaereria corticola*** Muhr & Tønsberg. *On Alnus*. Bank of Herbert R., n of Juneau (Tønsberg 1993).

***Siphula ceratites*** (Wahlenb.) Fr. A; widespread in muskeg pools; lowlands to subalpine.

***Solorina bispora*** Nyl. R; on soil and rock on Mt. Roberts and Granite Basin in the Juneau area (Krog 1968).

***Solorina crocea*** (L.) Ach. C; on soil in seepage sites below late-lying snow patches at subalpine and alpine elevations.

***Solorina saccata*** (L.) Ach. I; on soil; low elevation to alpine.

***Solorina spongiosa*** (Ach.) Anzi. In BC this lichen is found on moist calcareous soil and moss in exposed subalpine and alpine localities (Goward et al. 1994b). Yakutat Bay (Cummings 1904).

***Sphaerophorus fragilis*** (L.) Pers. C; on alpine rocks.

***Sphaerophorus globosus*** (Hudson) Vainio and var. *gracilis* (Müll. Arg.) Zahlbr. A; on soil and bark (mainly conifers but also on *Populus* and deciduous shrubs) in all forest types from low elevation to alpine. *S. globosus* was the most frequently observed macrolichen in se AK forests. The var. *gracilis* intergrades completely with var. *globosus*.

***Stereocaulon alpinum*** Laurer. *ex* Funck. C; on moss and humus on gravel, on bare rock and on decomposing wood in exposed areas; low elevation (glacier termini) to alpine.

***Stereocaulon apocalypticum*** Nyl. On alpine rock; Cosmos Range, mainland, *3183 det. McCune*.

***Stereocaulon arenarium*** (Savicz) Lamb. C; on rock in exposed areas, in soil, and on other mosses and lichens; low elevation (glacier termini) to alpine. Also on lava flows.

***Stereocaulon botryosum*** Ach. C; on rock with or without mosses and on rock covered with thin layer of humus; in exposed areas sea level to alpine. On lava flows.

***Stereocaulon capitellatum*** H. Magn. On alpine rocks. Bear Claw and Sheridan Peaks, Kupreanof I. *3137*, *3140*, *3220 det. Ryan.*

***Stereocaulon condensatum*** Hoffm. On rock in alpine n of Stikine R., near BC border.

***Stereocaulon coniophyllum*** Lamb. C; on rock, with or without mosses. Our collections near mainland glacier termini at low elevations.

***Stereocaulon dactylophyllum*** Flörke. On mossy rock face along beach; Kruzof I., near Sitka, *2738 det. Thomson.*

***Stereocaulon glareosum*** (Savicz) H. Magn. On alpine rock; Horn Cliffs, near Petersburg, *3328 & 3329 det. Ryan.* On bare soil, frost boils and among mosses on acid soils; Skagway area (Thomson 1984).

***Stereocaulon grande*** (H. Magn.) H. Magn. C; on rock, usually associated with mosses. Broad habitat range includes rock faces, lava flows, crushed rock road base, beach logs and soil; sea level to alpine.

***Stereocaulon groenlandicum*** (E. Dahl) Lamb. On rock in road cut; Blue L. Rd, Sitka, *2212*; on lava, Blue R. lava flow, mainland, *748 det. Thomson.*

***Stereocaulon intermedium*** (Savicz) H. Magn. C; on rock, moss-covered rock or on thin humus layers over rock; splash zone of marine shorelines, open forests, alpine habitats.

***Stereocaulon myriocarpum*** Th. Fr. Granite Basin and the Shrine of St. Therese in the Juneau area (Krog 1968). Closely related to *S. tomentosum*, but with thinner, smoother tomentum and more developed cephalodia (Lamb 1977).

***Stereocaulon octomerum*** Müll. Arg. On moss-covered rock in subalpine habitats. Crystal Mtn, Mitkof I., *896 det. Thomson.*

***Stereocaulon paschale*** (L.) Hoffm. C; on bare rock or soil; can be associated with mosses; lowlands, subalpine and alpine.

***Stereocaulon pileatum*** Ach. On bedrock among mosses at LeConte Bay, mainland, *379 det. Thomson.*

***Stereocaulon rivulorum*** H. Magn. On ground, rock and moss-covered rock. Shore of Falls L., mainland; Cosmos Range alpine, mainland; Sheridan Peak, Kupreanof I.; *3178 & 3222 det. Ryan*, *3172.* This species is usually found below permanent snow banks and along flood banks of streams (Thomson 1984).

***Stereocaulon sasakii* var. *sasakii*** Lamb and **var. *tomentosoides*** Lamb. On soil and rocks. On basalt rock outcrop at Gallagher Ck., Chichagof I., *LaBounty 3331 det. Ryan*. On a gravel road near Petersburg, *Sharnoff 742.36*, in an open peatland near Juneau and a subalpine area on Harbor Mtn, Sitka; *Brodo 26182& 26085; O'Clair 26085 & 26182*. Also found near Hyder by E.G. Mayer. Similar in appearance to *S. tomentosum* but containing lobaric acid instead of stictic acid.

***Stereocaulon saviczii*** Du Rietz. On rock, on lava flows. LeConte Bay and Blue R. lava flow, mainland. *380 & 746 det. Thomson.*

***Stereocaulon saxatile*** H. Magn. C; on rock; low elevations to alpine.

***Stereocaulon spathuliferum*** Vainio. On organic soil and on beach rocks. Dry Pass, nw Chichagof I. and shore of Plotnikof L., s Baranof I.; *2159 & 2077 det. Wong.*

***Stereocaulon sterile*** (Savicz) Lamb *ex* Krog. On rock and moss-covered rock. Beach at Kanga Bay, w Baranof I.; shoreline of LeConte Bay, mainland. *382 det. Thomson*, *2144 det. Wong.*

***Stereocaulon subcoralloides*** (Nyl.) Nyl. On exposed rock face in splash zone above high tide line, near mouth of Kennel Cr., e Chichagof I. , *2778 det. Thomson.*

***Stereocaulon symphycheilum*** Lamb. On rock, soil, on lava flows; low elevations to alpine. LeConte Bay and Blue R. lava flow, mainland Crystal Mtn., Mitkof I., *383 & 749 det. Thomson*, *2045.*

***Stereocaulon tomentosum*** Fr. I; in soil among mosses. Meadow at Pogibshi Anchorage, n Baranof I.; second growth *Tsuga* forest, trail to Petersburg L., Kupreanof I., *882*, *2759.*

***Stereocaulon vesuvianum*** Pers. C; on rock and soil on lava flows, along lake shorelines and in alpine habitats.

***Sticta arctica*** Degel. R; intermingled with moss and other lichens on Mt. Roberts, Juneau area (Krog 1968).

***Sticta fuliginosa*** (Hoffm.) Ach. C; on *Populus*, *Alnus*, *Malus* and *Picea sitchensis* along beaches and rivers, especially on the mainland. Low elevations.

***Sticta limbata*** (Sm.) Ach. R; along beaches of small marine islands on conifers, hardwoods and shrubs (e.g. *Tsuga*, *Alnus*, *Malus*). Staney I., near Prince of Wales I.; small I. e of Pt. Vandeput, mainland; Sukoi Is. near Petersburg. *59*, *2587*, *2615*.

***Sticta weigelii*** (Ach.) Vainio **s. lato**. C; on *Alnus*, *Malus*, *Picea sitchensis* and *Thuja plicata* branches along beaches, lakes, streams and rivers; widespread at low elevations.

***Sticta wrightii*** Tuck. I; on *Picea sitchensis*, *Alnus*, *Populus* and *Salix* in *P. sitchensis* and mixed *Picea*/deciduous stands in floodplains of mainland rivers. (e.g. Patterson, Stikine, Unuk and Arnklen). *1016*, *1025*, *1642*, *3349*.

***Tephromela aglaea*** (Sommerf.) Hertel & Rambold. C; on acidic or slightly basic rocks, ranging from the salt spray zone on exposed beach rocks near Sitka (O'Clair et al. 1996) to alpine habitats.

***Thamnolia subuliformis*** (Ehrh.) Culb. C; on humus with other lichens and mosses; subalpine and alpine.

***Thamnolia vermicularis*** (Sw.) Ach. *ex* Schaerer. I; on humus with other lichens and mosses; subalpine and alpine.

***Thelotrema lepadinum*** (Ach.) Ach. On bark of hardwoods and conifers. *Picea/Tsuga* forest inland of Half Moon Bay, mainland; *Picea/Alnus* riparian area along Indian R. Trail, near Sitka; *Picea/Tsuga/Alnus* beach fringe at Blind Slough, Mitkof I. *1088*, *3093*, *3315 det. Ryan*.

***Toninia tristis*** (Th. Fr.) Th. Fr. On alpine soils. Thunder Mtn., mainland, *520 det. Thomson*.

***Trapelia*** (Choisy) sp. On rock outcrop in subalpine forest in the Missionary Range of Kupreanof I., *3334 det. Ryan*. Close to *T. coarctata* but with black, smaller apothecia.

***Trapeliopsis flexuosa*** (Fr.) Coppins & P. James. On slate rock. near Wrangell, AK (Herre 1919). Expected also on wood, plant debris and sandstone rocks (Purvis et al. 1992).

****Trapeliopsis pseudogranulosa*** Coppins & P. James. On *Tsuga heterophylla* bark. *Picea/Tsuga* forest inland of Half Moon Bay, mainland, *3089 det. Ryan*.

*****Tremella hypogymniae*** Diederich. Lichenicolous fungus on *Hypogymnia physodes*; nw of Haines, *Ahti 21415 det. Diederich (H)*. Previously reported in N Am from Ontario (Diederich 1996).

***Tremolecia atrata*** (Ach.) Hertel. On rock in the mainland alpine. Unnamed peak w of Elbow Mtn, mainland, *3259 det. Ryan*.

***Tuckermannopsis chlorophylla*** (Willd.) Hale. A; on coniferous and deciduous trees and shrubs in low elevation stands near water (beaches, lakes, rivers, streams).

***Tuckermannopsis subalpina*** (Imshaug) Kärnefelt. C; on shrubs and lower branches of *Tsuga mertensiana* in subalpine forests; on humic soils in high elevation peatlands and alpine habitats.

***Umbilicaria angulata*** Tuck. C; on rock; shorelines and lowland peatlands to alpine habitats. Hall Peak, n Kupreanof I.; Warm Springs Bay, w Baranof I.; LeConte Bay, mainland. *2755*, *3362*, *385 det. Ryan*.

***Umbilicaria arctica*** (Ach.) Nyl. On subalpine and alpine rocks. Crystal Mtn, Mitkof I., *2048 det. McCune*; Bear Claw Mtn, s Kupreanof I., *3144.*

***Umbilicaria cylindrica*** (L.) Delise *ex* Duby. On rock; Mt. Roberts, near Juneau (Krog 1968).

***Umbilicaria deusta*** (L.) Baumg. On acid rock in subalpine and alpine sites, especially in water channels on rock faces (Thomson 1984). Rowan Mtn., n Kuiu I. and edge of Swan L., mainland, *841, 3198.*

***Umbilicaria havaasii*** Llano. On rock in the mainland alpine; w of n fork Bradfield R., *Krieckhaus 3440 det. Ryan.*

***Umbilicaria hirsuta*** (Sw. *ex* Westr.) Hoffm. On exposed acid rock (Thomson 1984); Muir Glacier area (Cummings 1904).

***Umbilicaria hyperborea*** (Ach.) Hoffm. C; on rock; alpine and subalpine, to sea-level on moraines at glacial termini.

***Umbilicaria polyphylla*** (L.) Baumg. On exposed rock on Mt. Riley Trail, se of Haines, *Sharnoff 1389.26.*

***Umbilicaria proboscidea*** (L.) Schrader. C; on rock; alpine and lower elevations on fresh glacial moraines.

***Umbilicaria rigida*** (Du Rietz) Frey. On acid rock and bird perches (Thomson 1984). Known from Mendenhall Valley (McCullough 1965).

***Umbilicaria torrefacta*** (Lightf.) Schrader. C; on alpine rock but to sea-level near glacier termini.

***Umbilicaria vellea*** (L.) Hoffm. On open or shaded cliffs; Granite Basin near Juneau (Krog 1968).

***Umbilicaria virginis*** Schaerer. On alpine rocks. Crystal Mtn., Mitkof I., *2051 det. McCune.*

***Usnea cavernosa*** Tuck. On *Picea* nw of Haines (Thomson and Ahti 1994).

****Usnea chaetophora*** (Halonen et al. 1997). On *Picea sitchensis*, *Tsuga heterophylla* and small deciduous trees and shrubs along beach fringe, Staney I. near Prince of Wales I., and Shrine of St. Therese, Juneau. *2554 & 2589 det. Halonen.*

****Usnea* cf. *cornuta*** Körber. On beach fringe trees and shrubs; Staney I. near Prince of Wales I., *2590 det. Ryan.* Small specimens.

***Usnea filipendula*** Stirton. I; on coniferous trees and deciduous shrubs, especially along beaches. *1883 det. Ryan, 724 det. Halonen.*

****Usnea fragilescens* var. *mollis*** (Vainio) Clerc. I; on *Pinus contorta* in peatland on Dog I., s of Ketchikan, on trees along beach fringe at w Staney I. near Prince of Wales I. and at Cape Fanshaw, mainland. *2534, 2588 & 1865 det. Halonen.*

***Usnea glabrata*** (Ach.) Vainio. R; coastal forests. Known from Sitka National Monument (Krog 1968). This collection and those of the following two species should be re-examined. In the inland and maritime regions of BC, but not the hypermaritime (Halonen et. al. 1997) as here.

***Usnea glabrescens*** (Nyl. *ex* Vainio) Vainio. R; on trees. Sitka National Monument (Krog 1968). A hypermaritime and maritime species in BC (Halonen et al. 1997).

**Usnea hirta** (L.) F.H. Wigg. R; on trees; Indian R. Trail, Sitka (Krog 1968). A southern intermontane species in BC (Halonen et al. 1997).

**Usnea lapponica** Vainio. I-R on *Alnus*. Brotherhood Park, Juneau, *1554 det. Halonen*; and Sitka National Monument (Krog 1968).

**Usnea longissima** Ach. A; pendant on branches of conifers and deciduous shrubs; in deciduous stands, *Picea sitchensis*/deciduous stands, *Picea sitchensis*, mixed conifer or *Pinus contorta* stands; most common along beaches and riparian habitats.

**Usnea scabrata** Nyl. **s. lato.** On *Picea sitchensis* and *Alnus rubra* on small marine islands and peninsulas dominated by *Usnea*; *Alectoria* usually conspicuously absent. Collections include "Usnea prostrata" morphs. Shrine of St. Therese, Juneau; Pleasant Bay, Admirality I.; Gut I., mouth of Stikine R *58*, *2704*, *2555 det. Halonen*.

**Usnea substerilis** Stirton. On *Alnus rubra* in Brotherhood Park, Juneau, *1553 det. Halonen*. Also on *Picea* nw of Haines (Thomson & Ahti 1994).

+**Usnea trichodea** Ach. Pendent from coniferous trees, especially *Picea sitchensis*, and deciduous shrubs along the boundaries of lakes or along beaches. Hugh Smith L., Misty Fjord NM and Plotnikof L., Admiralty I. *1987*, *2183 & 2184 det. Ryan*. Some collections with red axes.

+**Verrucaria degelii** R. Sant. On littoral rock on sea cliff at top of Sunshine Cove, Auke Bay, *Brodo 26018*.

**Verrucaria epimaura** Brodo. On littoral rock, characteristically overgrowing *V. maura*. W side Lynn Canal, *Sharnoff 1487.16*. Recently described from coastal BC and Alaska (Brodo & Santesson 1997).

**Verrucaria maura** Wahlenb. A; on seashore rocks as a black band from the high intertidal and splash zones to lower salt spray zone. The most abundant maritime lichen in se AK (O'Clair et al. 1996).

**Verrucaria muralis** Ach. On calcareous rock at the Calder quarry, Prince of Wales I. (Herre 1919).

+**Verrucaria schofieldii** Brodo. On littoral rock; *Brodo 26366C*. Recently described; endemic to QCI and se AK (Brodo & Santesson 1997).

**Vestergrenopsis elaeina** (Wahlenb.) Gyelnik. R; near the terminus of the Mendenhall glacier on rock deglaciated about 25 years earlier, *Sharnoff 761.36*; Mendenhall V. (McCullough 1965);Glacier V, 20 km n of Juneau, *O'Clair 3387 det. Wong*.

**Vestergrenopsis isidiata** (Degel.) E. Dahl. On moss-covered rocks. Herbert Glacier terminus; Cosmos Peak, mainland; Sheridan Peak, Kupreanof I. *3246& 3450 det. Ryan*, *2860 det. Brodo;* and Mendenhall Valley (McCullough 1965).

**Xanthoria candelaria** (L.) Th. Fr. C; on rocks in the salt spray zone and on bark of trees along beaches (esp. *Picea sitchensis*). Best developed on shoreline rocks fertilized by bird droppings (O'Clair et al. 1996).

**Xanthoria elegans** (Link) Th. Fr. On beach rocks in the salt spray zone to alpine habitats, especially in high nitrogen environments beneath bald eagle and peregrine falcon nests, or rocks used as lookouts by marmots (O'Clair et al 1996).

**Xanthoria fallax** (Hepp) var. **fallax** Arnold **s. lato**. R; on bark in riparian zone.

Klondike Goldrush National Historic Park, *Atwood 18371a.*

***Xanthoria polycarpa*** (Hoffm.) Rieber. I; on twigs of *Picea sitchensis*, *Populus* and deciduous shrubs along beaches up to 200m.

***Xanthoria sorediata*** (Vainio) Poelt. On beach rocks; Gambier Bay, Admiralty I., *2541.*

***Xylographa opegraphella*** Nyl. *ex* Rothr. Strictly maritime, on stabilized driftwood and other wood exposed to the sea, often nitrogenized (Brodo 1984, 1992a). Eagle Beach, Lynn Canal (O'Clair et al. 1996).

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# LICHENS OF THE SPIRIDON PENINSULA, WESTERN KODIAK ISLAND, ALASKA, WITH OBSERVATIONS ON LICHEN COMMUNITIES

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## Abstract

One hundred twenty nine taxa of lichens are reported from western Kodiak Island, Alaska, where the lichen flora is little known. One species, *Porina lectissima* is new to Alaska. The lichen flora of western Kodiak Island falls into six ecological-geographic categories, with the majority of species falling into alpine-subalpine, coastal, and wet interior categories. Vegetation data from 266 relevés are classified into 31 community types using minimum variance clustering. Nine epigeaic and two epilithic community types had significant lichen components. Twenty-two epiphytic lichens from *Alnus crispa*, *Betula kenaica*, *Salix* spp., and *Populus trichocarpa* are enumerated from 28 relevés.

## Introduction

Situated along the northwestern border of the Gulf of Alaska, Kodiak Island (9,300 km$^2$), occupies an important biogeographical position (Fig. 1). The island has biogeographic relationships that radiate in three directions: westward along the Aleutian Islands, northward toward interior Alaska, and southeastward toward the temperate Pacific Coast and Rocky Mountain regions of North America (Vincent 1964).

This paper reports lichens collected on the Spiridon Peninsula, which is located in Kodiak National Wildlife Refuge on the west central coast of Kodiak Island. Hitherto the lichen flora of Kodiak Island has received only minor attention and there are no published reports for the Spiridon Peninsula. Previous reports for Kodiak Island are found in Cummings (1910), Degelius (1937), Gowan (1989), Hedrick (1936), Kärnefelt (1979), Krog (1969), Rothrock (1884), and Thomson (1984). There are no published studies of the lichen communities of Kodiak Island. The objectives of the present paper are to (1) record the lichens from a spectrum of habitats in the Chief Cove area, western Spiridon Peninsula, and (2) determine lichen species of high presence within the plant communities.

## Study area

The study encompasses about 5.2 ha of the Chief Cove area (54° 44'N, 153° 56'W) in the northwestern corner of the Spiridon Peninsula. The study area is dominated by rugged mountainous terrain, with rounded summits rising to 630 m, and rolling lowlands. The climate of the region is maritime. Based on climatic records from Larsen Bay (57° 32'N, 154° 00'W), located 20 km south of Chief Cove, the mean annual temperature is 4.4°C and the mean annual precipitation is 575 mm (Leslie 1989). Using an ecoclimatic-phytogeographical system, Tuhkanen (1984) included Kodiak Island in the middle boreal, hyperoceanic ($O_2$), perhumid region.

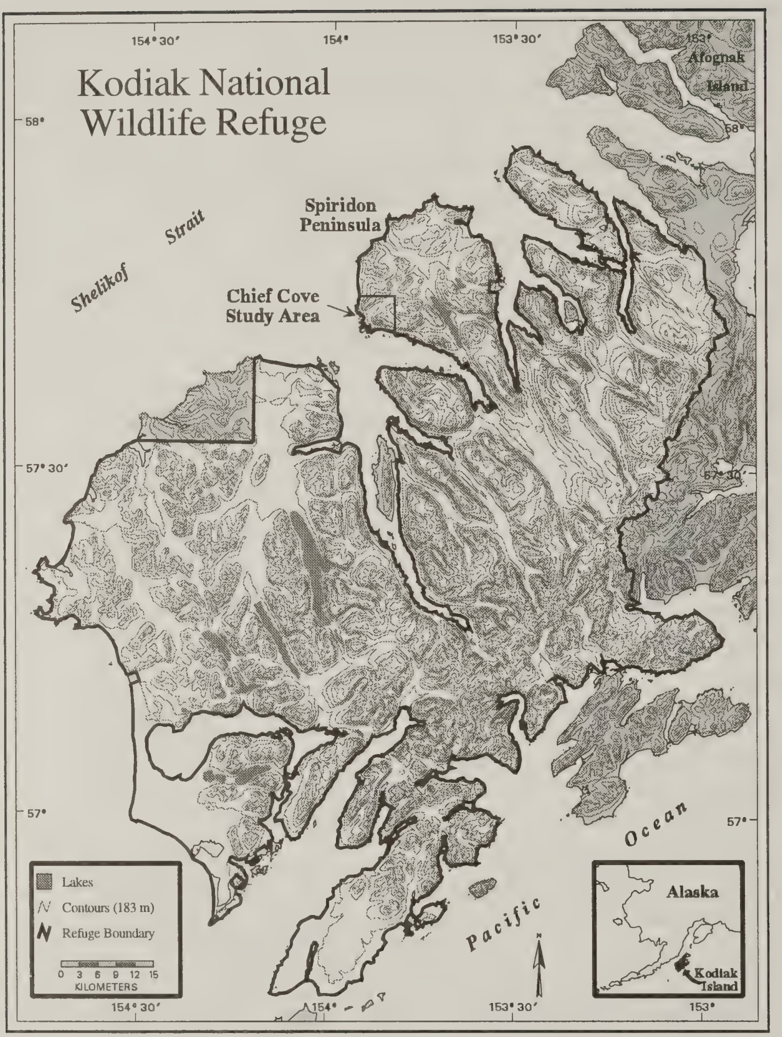

Figure 1. Location of the Spiridon Peninsula and the Chief Cove study area on Kodiak Island, Alaska.

Bedrock geology within the study area is characterized by stratified sedimentary rocks (Beikman 1980). The most widespread rocks are of Lower Cretaceous and Upper Jurassic ($KJ_3$) age. These rocks are a melange of flysch, greenstone, limestone, chert, granodiorite, greenschist, gabbro, and serpentenite. Upper Cretaceous (uK) rocks with graded beds of sandstone and slate occur within a small portion of the southeast corner of the study area.

The surficial geology of the Spiridon Peninsula is dominated by coarse rubbly deposits associated with steep-sloped mountains with high percentage of bedrock exposures (Karlstrom et al. 1964). The dominant soils are Dystric Cryandepts and Dystric Lithic Cryandepts (Rieger et al. 1979); these are Inceptisols formed in volcanic ash. The most recent ash fall occurred when Mount Katmai erupted in 1913, depositing approximately 30 cm of ash on the Spiridon Peninsula (Wilcox 1959). Griggs (1918) detailed vascular plant recovery following the eruption and included notes on some mosses but made no mention of lichens.

The vegetation of the region is described by Griggs (1936) but does not include lichen species. From my field observations, the vegetation of the Chief Cove area is lush with the herbaceous species of closed, lowland meadows attaining a height of 1-2 m. The vegetation of the study area may broadly be divided into three primary types: 1) forest communities of *Betula kenaica* and *Populus trichocarpa* are minor components of the lowlands, 2) thickets of *Alnus crispa*, *Rubus spectabilis*, *Salix* spp., and *Sambucus racemosa* and tall graminoid and forb meadows of *Calamagrostis canadensis*, *Epilobium angustifolium*, and *Geranium erianthum* predominate from lower through middle elevations, and 3) dwarf shrub heaths of *Empetrum nigrum*, *Rhododendron camtschaticum*, and *Arctostaphylos alpina* occur at upper elevations. Mires form a minor component and occur in isolated depressions and along streamlets.

The ten most frequently occurring vascular plants within the study area are listed in order of decreasing importance *Calamagrostis canadensis*, *Equisetum arvense*, *Epilobium angustifolium*, *Athyrium filix-femina*, *Angelica lucida*, *Heracleum lanatum*, *Trientalis europaea*, *Rubus spectabilis*, *Sanguisorba stipulata*, and *Veratrum viride*.

## Methods

### *Field studies*

Field studies were conducted during July and August 1990 with collections from 67 localities. All determinations were made by John W. Thomson. Voucher specimens are deposited in the University of Wisconsin Herbarium (WIS). Nomenclature follows Esslinger & Egan (1995).

The primary purpose of the work on the Spiridon Peninsula was to conduct a phytosociological study of the plant communities based on a set of 266 relevés. Plots were laid out in units of homogeneous vegetation so as to represent the totality of the environmental variation. Quadrat size was 100 $m^2$. Cover-abundance was estimated for vascular plants and lichens according to the 9-point ordinal scale of Westoff & van der Maarel (1973): 1, one or few individuals; 2, occasional and <5% cover of total plot area; 3, abundant and with very low cover, or less abundant but with higher cover; in any case <5% cover; 4, very abundant and <5% cover; 5, 5-12.5% cover; 6, 12.5-25% cover; 7, 25-50% cover; 8, 50-75% cover; and 9, 75-100% cover. During the course of the vegetation study, lichen collections were made in relevés; additional lichen collections were made outside the relevés as I travelled on foot from lower to upper elevations.

In addition, twenty-eight qualitative relevés were also made of the epiphytic lichen communities on four host taxa over a range of environmental conditions from lowlands to middle mountain slopes: *Alnus crispa*, *Betula kenaica* (=*B. papyrifera* var. *kenaica*), *Salix* spp. [*S. glauca*, *S. pulchra* (*S. planifolia* subsp. *pulchra*), and *S. alaxensis*], and *P. trichocarpa* (*Populus balsamifera* subsp. *trichocarpa*); sampling intensity was approximately proportional to the abundance of the woody species. An epiphytic relevé was the entire surface (base, trunk, or main stems as well as the crown and twigs) of an individual woody host species.

The major collection sites are listed below. Each site is followed by habitat information and elevation (m).

1. Moist *Empetrum nigrum-Salix arctica* heath, 630 m.
3. On *Alnus crispa* in *Alnus crispa-Calamagrostis canadensis* thicket, 24 m.
8. Dry *Festuca altaica-Salix arctica* dwarf shrub meadow, 396 m.
9. Very dry *Empetrum nigrum-Dryas integrifolia* barren, 463 m.
12. On *Betula kenaica* in moist *Betula kenaica-Athyrium filix-femina* coastal forest, 12 m.
14. On *Alnus crispa* in moist *Alnus crispa-Veratrum viride* thicket, 244 m.
15. Moist *Rosa nutkana-Athyrium filix-femina* open scrub, 290 m.
18. On *Alnus crispa* in moist *Alnus crispa-Veratrum viride* thicket, 256 m.
19. On *Salix pulchra* in moist *Salix glauca* thicket, 335 m.
31. On *Salix glauca* in *Salix glauca-Athyrium filix-femina* thicket, 30 m.
37. On *Salix alaxensis* in *Salix alaxensis* swamp thicket, 30 m.
39. On *Salix alaxensis* in *Salix alaxensis-Athyrium filix-femina* swamp thicket, 12 m.
40. On *Betula kenaica* in *Betula kenaica-Athyrium filix-femina* forest, 24 m.
41. *Betula kenaica-Calamagrostis canadensis* swamp forest, 30 m.
45. Same as #40 but at 35 m.
46. *Salix pulchra* in *Salix pulchra-Athyrium filix-femina* scrub, 35 m.
50. On *Alnus cripa* in *Alnus crispa-Rubus spectabilis* scrub, 259 m.
60. On *Populus trichocarpa* in open *Populus trichocarpa* forest, 3 m.
65. Epixylic on old salmon net drying rack, 1.2 m.
66. Epixylic on beached coastal log, 0.3 m.
68. On *Salix glauca* in *Salix glauca* thicket, 40 m.
70. Dry *Anemone narcissiflora-Arnica latifolia* low forb meadow, 591 m.
71. Dry *Empetrum nigrum-Salix stolonifera* lichen heath, upper NNW-facing upper mountain slope, 591 m.
72. Epilithic on pebbles in dry *Empetrum nigrum* fellfield, upper NNW-facing mountain slope, 567 m.
76. Dry *Empetrum nigrum-Loiseleuria procumbens* heath, 549 m.
77. Same as #76 but 561 m.
81. On *Salix bebbiana* in *Betula kenaica* forest, bench in coastal lowlands, 18 m.
88. On *Populus trichocarpa* in open *Populus trichocarpa* forest, 15 m.
90. On *Alnus crispa* in *Alnus crispa-Athyrium filix-femina* thicket, 18 m.

90À. On barnacle, sea level.

92. Same as #90 but 120 m.
97. On *Alnus crispa* in *Alnus crispa-Dryopteris austriaca* thicket, 381 m.
98. Moist *Empetrum nigrum-Hylocomium splendens* dwarf shrub heath, 463 m.
100. Very dry rock outcrop, 15 m.
102. On *Betula kenaica* in moist *Betula kenaica-Athyrium filix- femina* coastal forest, 37 m.
107. Same as #90 but 232 m.
113. Very dry rock outcrop on ridge crest of tor, 604 m.
118. Same as #90 but 250 m.
122. On *Alnus crispa* in moist *Alnus crispa-Veratrum viride* thicket, 29 m.
124. On *Betula kenaica* in moist *Betula kenaica-Calamagrostis canadensis* forest, 12 m.
126. Same as #90 but 12 m.
144. Dry *Empetrum nigrum-Loiseleuria procumbens* heath, 427 m.

151. Same as #88 but 30 m.
166. Epilithic in very dry escarpment grotto, 1.5 m.
167. Coastal very dry rock escarpment, 1.5 m.
168. Epilithic in coastal very dry rock escarpment grotto, 46 m.
169. Wet *Empetrum nigrum-Carex aquatilis* dwarf shrub mire, 286 m.
172. Moist *Salix pulchra-Lycopodium annotinum* thicket, 274 m.
182. On *Salix pulchra* in moist *Salix pulchra-Lycopodium annotinum* thicket, 162 m.
191. Moist *Festuca altaica-Solidago lepida* low meadow, 351 m.
194. Moist *Empetrum nigrum-Festuca altaica* hummocky heath, 381 m.
199. Moist *Angelica lucida-Festuca altaica* hummocky heath, 488 m.
200. Dry *Empetrum nigrum-Racomitrium* frost boil heath, 524 m.
201. On humus in dry scarcely vegetated fellfield, 518 m.
202. Epilithic on very dry rock tor, 610 m.
213. Dry *Cornus suecica-Festuca altaica* meadow, 396 m.
214. Dry *Rhododendron camtschaticum-Vaccinium vitis-idaea* heath, 433 m.
215. Dry *Empetrum nigrum-Racomitrium* heath, 555 m.
220. Moist *Geranium erianthum-Solidago lepida* meadow, 354 m.
223. Moist *Empetrum nigrum-Pleurozium schreberi* heath on ridge, 366 m.
246. Epilithic on very dry rock tor, 579 m.
247. Moist *Empetrum nigrum-Cladina* heath, 555 m.
256. Moist *Equisetum arvense* meadow, 140 m.
258. Moist *Salix barclayi* thicket, 134 m.
260. Wet *Equisetum arvense* meadow, 137 m.
262. Wet *Salix barclayi* thicket, 137 m.
263. *Epilobium angustifolium* meadow, 128 m.

Distributional categories are assigned to each taxon according to the ecological-geographic subdivisions of Noble et al. (1987) for British Columbia, supplemented by Goward et al. (1994), with an additional subdivision, **U**, for those species not in the Noble or Goward lists. Many of the lichens have combinations of the distributional categories. **A**, Alpine and Subalpine (high elevations throughout British Columbia, but especially north-central and northwest corner, primarily above timberline but including solitary stunted trees); **B**, Boreal (spruce region of northeast and north-central interior); **C**, Coastal Area (Queen Charlotte Islands, Vancouver island, Cascade Mountains strip on the adjacent mainland); **I(d)**, Dry Interior (semidesert, dry grasslands in central and southern interior, including the most open woodlands); **I(w)**, Wet Interior (forested areas in central interior and southern Rocky and Columbia mountains); **U**, Unclassified (species with distribution unknown; these are either under study, too poorly understood taxonomically for confidence in published maps, or not reported from British Columbia); and **W**, Widespread (present in many or most of the other locations).

### *Data analysis*

Numerical analysis of plant communities was accomplished with the classification methods of the MULVA-5 package (Wildi & Orlóci 1996) using a numerical solution to traditional phytosociological tabular classification proposed by Wildi (1989). The procedure involves a number of operational steps detailed by Wildi (see above). Outliers were detected using an absolute measure for the definition of composition isolation of a relevé, via a similarity index, the similarity ratio (based on normalized relevé vectors) of any relevé with its nearest neighbor. At a similarity ratio of 0.4, ten relevés were excluded. The resulting matrix, 256 relevés X 223 species (vascular plants and lichens), was submitted to multivariate classification analysis. For relevé classification, minimum variance clustering (Orlóci 1978) was performed.

TABLE 1. Comparison of geographic distribution patterns of the Spiridon Peninsula and Tuxedni Wilderness Area, Alaska and British Columbia. Values indicate the presence of each taxon occurring within each category; many are combinations of these. Percentage values are in parentheses. Key: A = alpine and subalpine; B = boreal; C = coastal; I(d) = dry interior; I(w) = wet interior; U = unclassified; W = widespread; n = total number of lichen taxa.

| Region | A | B | C | I(d) | I(w) | U | W |
|---|---|---|---|---|---|---|---|
| Spiridon | 50 | 18 | 44 | 9 | 32 | 18 | 18 |
| (n = 129) | (39) | (14) | (34) | (7) | (25) | (14) | (14) |
| Tuxedni | 77 | 42 | 93 | 23 | 70 | 6 | 31 |
| (n = 218) | (35) | (19) | (43) | (11) | (32) | (3) | (14) |
| BC | 165 | 59 | 553 | 116 | 288 | 127 | 46 |
| (n = 1039) | (16) | (6) | (53) | (11) | (28) | (12) | (4) |

Presence classes are: r, <3%; +, 3.1-10%; I, 10.1-20%, II, 20.1-40%; III, 40.1-60%; IV, 60.1-80%; V, 80.1-100%.

**Results**

*List of lichens*

One hundred twenty nine taxa of lichens were found on the western Spiridon Peninsula of Kodiak Island. Of these, 86 are new reports for Kodiak Island.

Distribution patterns for lichens from the Spriridon Peninsula are shown in relationship to Tuxedni Wilderness Area located in western Cook Inlet Alaska (280 km NNE of the Spiridon Peninsula; Talbot et al. 1992) and to British Columbia (Noble et al. 1987)(Table 1). Analysis of species distributions, in relation to ecological-geographic subdivisions of Noble et al. (1987), shows that Spiridon lichen taxa are most frequent in the alpine-subalpine, coastal, and wet interior subdivisions. This pattern is very similar to that of Tuxedni Wilderness Area. Many Spiridon lichen taxa, 29.4% (38) occur in more than one of Noble's subdivisions, but 20.1% (26) are entirely restricted to the coastal and 17.8% (23) to the alpine-subalpine categories.

In comparison to the lichen flora of British Columbia (Noble et al. 1987), the contribution of alpine-subalpine and boreal elements are higher for the Spiridon Peninsula and Tuxedni Wilderness. The dominant elements in British Columbia are coastal and wet interior.

The names of taxa not previously reported from Kodiak Island are indicated by asterisks. The name of each taxon is followed by a collection number which includes the site number (above) succeeded by a hyphen with an individual specimen number for the site. These are followed by boldface letters referring to the distribution pattern of Noble et al. (1987). Distributional subdivisions of a taxon present in more than one category are arranged alphabetically.

**Alectoria nigricans*, 71-19, 71-40, 113-15, 246-8. **A.**

*A. ochroleuca*, 246-26. Reported by Cummings (1910). **A.**

*Allantoparmelia almquistii*, 72-26, 202-7. Reported by Imshaug (1951). **W.**

**Amandinea punctata*, 12-24, 14-26, 18-22, 31-21, 39-27, 39-28, 40-27, 50-22, 50-25, 68-26, 81-34, 88-34, 88-39, 90-26, 92-27, 107-22, 107-28, 122-29, 151-33. **C.**

**Amygdalaria elegantior*, 167-4. **A, B.**

**Bacidia alaskensis*, 166-9, 167-2. **C.**

**Biatora albohyalina*, 12-31. **U.**

**B. vernalis*, 81-47, 107-30. **I(w).**

*Bryocaulon divergens*, 246-19. Reported by Cummings (1910) and Thomson (1984). **A, C.**

**Bryoria chalybeiformis*, 65-X-2. **A, C, I(w).**

**B. nitidula*, 200-17. **A.**

**Buellia disciformis*, 3-27, 12-23, 68-27, 92-25, 97-28, 118-23, 122-31, 124-31. **C.**

**Caloplaca verruculifera*, 167-1. In Alaska this species is known from the Aleutian Islands, St. Paul Island, and northwestern Alaska, but apparently this is the first report from Kodiak Island (Arup 1994). **C.**

**Cavernularia lophyrea*, 124-30. **C.**

**Cetraria ericetorum*, 113-X-7. **C, I(d), I(w).**

*C. islandica*, 71-17, 71-31A, 76-18. Reported by Cummings (1910) and Kärnefelt (1979). **A, I(d), I(w).**

**C. laevigata*, 1-34, 98-41, 201-X-1, 246-28, 247-24. **A, B.**

**C. muricata*, 71-31B, 71-37, 98-37, 113-X-6, 144-24. **C.**

*Cladina arbuscula*, 71-25, 76-10. Reported by Cummings (1910). **A, B, I(w).**

*C. mitis*, 1-29, 9-27, 71-23, 77-28, 144-17. Reported by Krog (1969) and Thomson (1984). **A, B, I(d), I(w).**

*C. rangiferina*, 1-39, 144-19, 247-14. Reported by Thomson (1984). **W.**

*C. stellaris*, 71-24. Reported by Cummings (1910) and Krog (1969). **A, B.**

**C. stellaris* var. *aberrans*, 247-13 (P+ yellow). **A.**

**Cladonia amaurocraea*, 199-32, 202-X-1. **A, B, I(w).**

*C. bellidiflora*, 24-X-12, 144-27. Reported by Thomson (1984). **A, C, I(w).**

**C. carneola*, 247-35. **W.**

**C. coccifera*, 1-34C, 71-29, 144-23, 167-13, 169-19, 200-21, 215-14, 223-X-5. **W.**

*C. coniocraea*, 12-36, 45-34, 92-28, 102-34. Reported by Degelius (1937) and Hedrick (1936). **B, I(w).**

*C. cornuta*, 58-X-1, 58-X-3, 65-X-4, 126-20, 223-X-1, 223-X-2, 223-X-4, 247-33A. Reported by Thomson (1984). **W.**

*C. deformis*, 223-X-3. Reported by Thomson (1984). **W.**

**C. ecmocyna* subsp. *intermedia*, 58-X-4. Reported by Thomson (1984) as the species. **A, B, I(w).**

*C. fimbriata*, 70-37, 194-11. Reported by Degelius (1937). **W.**

**C. gracilis* subsp. *gracilis*, 1-34, 71-20, 71-25A, 73-32, 76-16, 77-23, 98-36, 113-X-7A, 144-19A, 144-20A, 201-X-3, 214-34, 215-11, 247-26. **A, B, W.**

**C. macroceras*, 76-23. **A.**

**C. maxima*, 1-34B, 98-37A. **C.**

*C. scabriuscula*, 40-24. Reported by Degelius (1937) and Thomson (1984). **C, I(w).**

**C. thomsonii*, 1-32, 144-18. **U.**

**C. uncialis*, 71-26, 247-18. **W.**

**Collema ceraniscum*, 168-X-5. **A.**

**C. nigrescens*, 60-27, 151-36. **C.**

**C. undulatum* var. *granulosum*, 37-31, 37-33. **C.**

**Flavocetraria cucullata*, 113-X-5. **A, B.**

*Hypogymnia enteromorpha*, 124-27. Reported by Cummings (1910). **C, I(w).**

**H. subobscura*, 66-X-2, 66-X-3, 66-X-7. **A.**

**Lecanora albella*, 18-21, 46-22, 50-21, 79-22, 79-29, 96-22, 96-23, 96-27, 118-25. **U.**

**L. circumborealis*, 12-22, 12-30, 45-27, 45-31, 60-26, 81-42, 124-29. **C, I(w).**

**L. impudens*, 81-33, 81-35, 81-35, 88-31. **B.**

**L. orae-frigidae*, 65-X-1. This is a westward range extension from Demarkation Point, Alaska, and northward from the Queen Charlotte Islands, British Columbia (Thomson 1997). **C.**

**L. polytropa*, 71-X-1 (with *Lecidea lapicida*), 200-23. **W.**

**L. pulicaris*, 12-36A, 53-22, 81-46, 102-27, 111-22. Thomson (1997) reports this as a far northwestern record. **B.**

*L. varia*, 14-27, 50-28. Reported by Cummings (1910). **C.**

**L. xylophila*, 57-X-1, 57-X-2, 66-X-1. **C.**

*Lecidea carnulenta*, 39-23, 81-40, 102-28. J. W. Thomson (1997) reports this is probably a far northern record. **U.**

**L. lapicida*, 71-X-1. **C.**

**L. praenubila*, 113-7. **U.**

**Lecidella stigmatea*, 100-11A, 113-9, 202-8, 242-14. **C.**

**Leptogium saturninum*, 37-22. **C, I(w).**

**Lobaria linita*, 1-20, 70-7, 214-30. **A, C.**

*Melanelia commixta*, 113-3, 246-29. Reported by Cummings (1910). **A, I(w).**

**M. hepatizon*, 100-13, 100-16. **W.**

**M. septentrionalis*, 37-26A, 81-36, 81-45, 102-33, 124-28, 124-33. **B, I(w).**

*M. stygia*, 100-12. Reported by Cummings (1910). **A, I(d), I(w).**

**Mycoblastus alpinus*, 81-41, 100-20, 102-31, 113-11. **A, C.**

**M. sanguinaris*, 182-35. **C, I(w).**

**Nephroma arcticum*, 247-9. **A, I(w).**

**Ochrolechia frigida*, 9-24, 72-18, 77-22A, 113-12, 113-16, 202-13, 202-X-2, 246-9, 246-29A. **A.**

**O. frigida* fo. *thelephoroides*, 77-25, 246-17. **U.**

*O. suplicans* subsp. *hultenii*, 100-4, 200-20. Reported by Brodo (1988). **C.**

**O. subplicans* subsp. *subplicans*, 77-32. **C.**

**Ophioparma lapponica*, 100-23, 246-5. **A, I(w).**

*Parmelia omphalodes*, 100-3, 202-9. Reported by Cummings (1910), Krog (1969), and Thomson (1984). **I(w).**

*P. saxatilis*, 246-6, 246-20. Reported by Degelius (1937), Hedrich (1936), Krog (1969) and Thomson (1984). **W.**

*P. sulcata*, 12-32, 19-21, 37-27, 40-32, 45-26, 50-X-2, 65-X-3, 66-X-6, 81-48, 81-49, 88-X-3, 102-32, 124-26. Reported by Degelius (1937), Krog (1969) and Thomson (1984). **W.**

*Peltigera aphthosa*, 8-29, 126-17, 213-14. Reported by Cummings (1910), Degelius (1937), and Thomson (1984). **W.**

*P. canina sens. lato.*, 88-X-4, 126-18, 172-17. Reported by Cummings (1910), Degelius (1937), and Thomson (1984). **A, B, I(d), I(w).**

*P. collina*, 14-23, 37-26, 46-23, 60-29, 79-23, 88-33, 88-4, 151-22, 151-39, 192-21. Reported by Thomson (1984). **C, I(w).**

**P. didactyla*, 214-26. **W.**

*P. leucophlebia*, 1-31. Reported by Thomson (1984). **W.**

*P. malacea*, 15-14, 191-24, 220-23. Reported by Hedrick (1936) and Thomson (1984). **W.**

*P. membranacea*, 1-26, 39-22, 39-29, 41-17, 46-10, 70-10, 79-30, 122-26, 147-21, 182-14, 204-17, 213-13, 226-18, 253-12, 254-24, 256-14, 258-23, 260-13, 262-10, 263-13. Reported by Thomson (1984). **C, I(w).**

**P. scabrosa*, 247-32A. **A, B, I(d), I(w).**

**Pertusaria alpina*, 88-32. **B.**

**P. amara*, 107-23, 107-29. **C.**

**P. borealis*, 18-23, 39-26, 40-25, 45-30, 81-32, 102-30. **C.**

**P. bryontha*, 200-22. **U.**

**P. dactylina*, 77-22B, 144-25. **A.**

**P. panyrga*, 12-33, 71-21, 100-6, 100-10, 246-10. **A.**

**P. sommerfeltii*, 18-24, 90-29. **C.**

**P. subobducens*, 37-23, 215-16. **U.**

**P. suboculata*, 14-28, 53-23, 53-24, 79-21, 96-24, 97-22, 97-23, 97-25, 99-22, 111-23, 111-24, 118-24. **C.**

**Phaeophyscia hirtella*, 14-30. **C.**

**Physcia aipolia*, 37-29, 37-32, 79-28, 81-43, 88-35, 151-40. **C.**

**P. caesia*, 101-2, 167-3, 168-X-2. **W.**

*Platismatia lacunosa*, 100-2, 167-6. Reported by Cummings (1910) and Krog (1969). **C.**

**Porina lectissima*, 166-8. New to Alaska. **C.**

*Porpidia flavocaerulescens*, 100-5, 113-1, 202-10, 246-3. Non-sorediate; syn. *P. flavicunda* (Ach.) Gowan. Reported by Gowan (1989) and Gowan & Ahti (1993). **U.**

**Pseudephebe pubescens*, 72-15, 100-9, 113-6, 202-1A, 202-2, 215-17, 246-2. **A, I(d).**

*Psoroma hypnorum*, 144-29. Reported by Thomson (1984). **A, C, I(d), I(w).**

**Pyrenocollema halodytes*, 90A-1. **C.**

*Ramalina almquistii*, 66-X-5. Reported by Krog (1969). **U.**

*R. farinacea*, 37-21, 81-38, 81-50, 88-X-1 (salazinic acid strain; soralia K+), 88-X-2 (acid deficient strain), 107-27, 151-21. Reported by Degelius (1937) and Hedrick (1936). **B, C, I(w).**

**R. scoparia*, 168-X-1. **U.**

**Rhizocarpon anaperum*, 201-22, 201-23, 202-6. **U.**

**R. eupetraeoides*, 100-7, 100-11, 100-24, 113-5, 113-10, 202-3, 246-4. **A.**

**R. geminatum*, 101-3. **C.**

**R. geographicum*, 72-17, 113-18, 167-5, 202-15. **W.**

**Rinodina archaea*, 151-41. **C.**

**R. turfacea*, 9-25. **C.**

*Sphaerophorus fragilis*, 100-8, 100-15, 202-5, 202-18. Reported by Hedrick (1936). **A.**

*S. globosus*, 71-16, 113-14, 144-21, 202-12, 246-13. Reported by Krog (1969) and Thomson (1984). **A.**

*Stereocaulon alpinum*, 1-28, 10-38, 70-35, 71-18, 76-11, 98-32, 214-23, 247-10. Reported by Cummings (1910). **A, I(w).**

*S. arcticum*, 201-X-2. **U.**

**S. arenarium*, 113-2, 246-12. **A.**

*S. botryosum*, 113-17. Reported by Thomson (1984). **A.**

**S. paschale*, 77-20. **A, B, I(w).**

**S. rivulorum*, 144-20. **A.**

**S. saxatile*, 167-7. **A, B.**

**S. subcoralloides*, 100-21. **U.**

**Thamnolia subuliformis*, 71-31, 71-40A, 144-30, 247-23. **A.**

*T. vermicularis*, 9-23, 246-15. Repored by Krog (1969). **A.**

**Tremolecia atrata*, 202-4. **A.**

*Tuckermannopsis chlorophylla*, 66-X-4. Reported by Degelius (1937) and Thomson (1984). **A, C, I(w).**

**Umbilicaria angulata*, 113-20, 167-8. **A, C, I(w).**

*U. arctica*, 72-17. Reported by Thomson (1984). **A.**
**U. lyngei*, 100-1, 202-1, 246-1. **A.**
*U. proboscidea*, 113-4. Reported by Krog (1969) and Thomson (1984). **A.**
**Verrucaria maura*, 101-X-1. **C.**
*Xanthoria candelaria*, 151-35. Reported by Degelius (1937), Krog (1969), and Thomson (1984). **C, I(d), I(w).**
*X. elegans*, 101-1, 130-1. Reported by Thomson (1984). **W.**

*Lichen components of the vegetation*

Numerical-phytosociological analyses of the 266 vegetation plots identified 31 relevé-groups, or community types. Of these, eleven community types -- nine epigeaic and two epilithic -- contained lichen taxa that occurred in more than one relevé and only four contained a prominent lichen component (Tables 2 and 3). With the exception of these four community types, most of the lichens within the study area are relatively infrequent, not abundant, and occur scattered over the landscape.

Community-types richest in epigaeic lichens peaked in upper mountain slope habitats, particularly on *Empetrum nigrum-Oxytropis nigrescens* heaths (No. 1) of north-facing slopes (Table 1). Characteristic macrolichens with a presence of 60% or higher in these north-facing habitats included *Cladonia gracilis, C. coccifera, Cladina mitis, C. rangiferina, C. stellaris, Lobaria linita, Sphaerophorus globosus, Stereocaulon alpinum,* and *Thamnolia subuliformis,* while on south-facing upper slopes in the *Empetrum nigrum-Festuca altaica* heath (No. 2), only *Stereocaulon alpinum,* peaked in abundance. Lichens occurring over a wide range of upper to lower slope community types (Nos. 1-9) were from the genus *Peltigera* (*P. membranacea, P. aphthosa,* and *P. malacea*). *Peltigera membranacea* was the most widely distributed species.

Community types 1 and 2 of upper mountain slopes occur at mean elevations of 532 and 432 m; the soils of these communities have the thinnest A horizons (3.3 and 6.5 cm) and ash deposit layers (2.3 and 4.8 cm) of all communities. All other epigeaic communities range in mean elevation from 22 to 391 m, A horizon depths from 5.4 to 11.5 cm, and ash deposit layer depths from 9.8 to 14.5 cm. These data indicate that lichen species diversity is lowest in the low elevation community types 3 to 9, where ash deposit and A horizon layers are the thickest, and highest in the high elevation community types, where they are the thinnest.

The epigeaic lichen component of community types 12 through 31 was either absent or nearly absent; the names of these types are given in Table 4.

Two communities of epilithic lichens were identified: *Xanthoria elegans-Rhizocarpon geminatum* escarpment (No. 10) and *Pseudephebe pubescens-Rhizocarpon eupetraeoides* rock outcrop (No. 11)(Table 3). The first (No. 10) occurs on low-elevation coastal escarpments; the two primary species of this type are listed in the name. The second (No. 11) typically occurs along high elevation ridge tops on tors; common species include *Lecidella stigmatea, Porpidia flavicaerulescens, Pseudephebe pubescens, Rhizocarpon eupetraeoides, Sphaerophorus globosus,* and *Umbilicaria lyngei.*

The relationship of epiphytic lichens to their woody hosts are shown in Table 5. Two species, *Amandinea punctata* and *Ramalina farinacea*, occurred on all four hosts. Presence of some epiphytic lichens peaked on particular woody species. Thus, lichens with a presence >40% on only one or two hosts were *Amandinea punctata* on *Alnus crispa* and *Populus trichocarpa*; *Buellia disciformis* and *Pertusaria suboculata* on *Alnus crispa*; *Cladonia coniocraea, Lecanora circumborealis, L. pulicaris, Melanelia septentrionalis, Parmelia sulcata,* and *Pertusaria borealis* on *Betula kenaica*; *Peltigera collina* on *Salix* spp. and *Populus trichocarpa*; and *Collema nigrescens, Pertusaria sommerfeltii,* and *Physicia aipolia* on *Populus trichocarpa.*

TABLE 2. Synoptic table of macrolichens in epigeaic community types in western Kodiak Island, Alaska. Only lichens occurring in more than one relevé are shown. The first figure in a column indicates presence class, the second gives the mean cover class when the species is present (see Methods). Community types: 1, *Empetrum nigrum-Oxytropis nigrescens* heath; 2, *Emptrum nigrum-Festuca altaica* heath; 3, *Deschampsia beringensis-Equisetum arvense* meadow; 4, *Calamagrostis canadensis-Angelica genuflexa* meadow; 5, *Sanguisorba-stipulata Epilobium angustifolium* meadow; 6, *Angelica lucida-Carex macrochaeta* meadow; 7, *Alnus crispa-Dryopteris austriaca* thicket, 8, *Calamagrostis canadensis-Urtica dioica* meadow; and 9, *Betula kenaica-Calamagrostis canadensis* meadow.

| Community type | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Number of relevès | 9 | 14 | 10 | 12 | 16 | 17 | 28 | 13 | 11 |
| Mean elevation (m) | 1747 | 1419 | 330 | 463 | 857 | 1284 | 857 | 277 | 72 |
| Mean ash depth (cm) | 2.3 | 4.8 | 11.9 | 11.5 | 14.5 | 14.5 | 14.5 | 11.6 | 9.8 |
| North-facing upper mountain slopes | | | | | | | | | |
| *Sphaerophorus globosus* | IV 2 | . | . | . | . | . | . | . | . |
| *Thamnolia subuliformis* | III 2 | . | . | . | . | . | . | . | . |
| *Cladina stellaris* | III 2 | . | . | . | . | . | . | . | . |
| *C. arbuscula* | II 2 | . | . | . | . | . | . | . | . |
| *Cladonia uncialis* | II 2 | . | . | . | . | . | . | . | . |
| *C. subfurcata* | II 2 | . | . | . | . | . | . | . | . |
| *Cetraria islandica* | II 2 | . | . | . | . | . | . | . | . |
| *C. muricata* | II 2 | . | . | . | . | . | . | . | . |
| *Pseudephebe pubescens* | II 3 | . | . | . | . | . | . | . | . |
| *Umbilicaria arctica* | II 3 | . | . | . | . | . | . | . | . |
| North- and south-facing upper mountain slopes | | | | | | | | | |
| *Stereocaulon alpinum* | III 2 | III 2 | . | . | . | . | . | . | . |
| *Cladina rangiferina* | III 3 | II 2 | . | . | . | . | . | . | . |
| *C. mitis* | III 4 | + 2 | . | . | . | . | . | . | . |
| *Cladonia gracilis* | IV 3 | I 2 | . | . | . | . | . | . | . |
| *C. coccifera* | III 2 | + 2 | . | . | . | . | . | . | . |
| *Lobaria linita* | III 2 | II 3 | . | . | . | . | . | . | . |
| *Cetraria laevigata* | II 2 | + 1 | . | . | . | . | . | . | . |
| Widespread, upper to lower mountain slopes | | | | | | | | | |
| *Peltigera membranacea* | . | II 2 | II 2 | I 1 | I 1 | I 1 | r 1 | . | + 1 |
| *P. aphthosa* | II 2 | II 1 | . | . | II 2 | . | . | . | + 1 |
| *P. malacea* | . | . | . | . | II 2 | . | . | + 1 | . |

TABLE 3. Synoptic table of community types in western Kodiak Island, Alaska, with distribution of epilithic lichens within types. Only lichens occurring in more than one relevé are shown. The first figure in the column indicates presence class, the second gives the mean cover class when the species is present (see Methods). Community types: No. 10. *Xanthoria elegans-Rhizocarpon geminatum* escarpment, and No. 11. *Pseudephebe pubescens-Rhizocarpon eupetraeoides* rock outcrop.

| Community type | 10 | 11 |
|---|---|---|
| Number of relevés | 2 | 4 |
| Mean elevation (m) | 3 | 597 |
| *Xanthoria elegans* | V 7 | . |
| *Rhizocarpon geminatum* | V 4 | . |
| *Pseudephebe pubescens* | . | V 4 |
| *Rhizocarpon eupetraeoides* | . | V 5 |
| *Lecidella stigmatea* | . | V 4 |
| *Porpidia flavocaerulescens* | . | V 3 |
| *Umbilicaria lyngei* | . | IV 5 |
| *Sphaerophorus globosus* | . | IV 2 |
| *Melanelia commixta* | . | III 3 |
| *Parmelia omphalodes* | . | III 4 |
| *Stereocaulon arenarium* | . | III 2 |
| *Ophioparma lapponica* | . | III 2 |
| *Pertusaria panyrga* | . | III 2 |
| *Mycoblastus alpinus* | . | III 2 |
| *Alectoria nigricans* | . | III 2 |
| *Ochrolechia frigida* | . | III 2 |

## Discussion

Low representation of the dry interior ecological-geographic elements coupled with the high percentages of coastal and wet interior taxa in the floras of Tuxedni Wilderness Area and western Kodiak Island indicate that these elements extend northwestward from British Columbia to as far as Kodiak Island (Table 1). Thus, the maritime climate of western Kodiak Island and Tuxedni Wildersness Area is reflected in the lichen flora. The higher percentages of alpine-subalpine and boreal elements in their floras compared with British Columbia presumably reflects their more northern geographical location.

Compared to the lichen floras from other areas in western Alaska (Thomson & Sowl 1989; Talbot et al. 1991, 1992, 1997) where the total lichen floras ranged from 149 to 219 taxa, the total number of lichen taxa, 129 taxa, of the Chief Cove area is lower. Areally this comparison is valid only for Tuxedni Wilderness with 218 taxa (Talbot et al. 1992). Low species diversity in the Spiridon Peninsula may be a reflection of variation in sampling intensity. Effective lichen collecting time spent in the Spiridon Peninsula was about 40% less than in the other studies of Talbot et al. above.

TABLE 4. List of plant community types where an epigeaic lichen component is either absent or nearly absent. The number of releves comprising the type is shown in parentheses.

| No. | Community type |
|---|---|
| 12 | *Populus trichocarpa-Athyrium filix femina* forest (8) |
| 13 | *Salix glauca-Athyrium filix-femina* thicket (8) |
| 14 | *Salix pulchra/S. barclayi-Lycopodium annotinum* thicket (8) |
| 15 | *Sambucus racemosa-Claytonia sibirica* thicket (4) |
| 16 | *Rubus spectabilis-Calamagrostis canadensis* thicket (7) |
| 17 | *Vaccinium uliginosum-Empetrum nigrum* mire (3) |
| 18 | *Epilobium angustfolium-Lathyrus palustris* meadow (21) |
| 19 | *Epilobium angustifolium-Calamagrostis canadensis* meadow (16) |
| 20 | *Leymus mollis-Ligusticum scoticum* beach meadow (8) |
| 21 | *Senecio pseudoarnica-Leymus mollis* beach meadow (5) |
| 22 | *Lysichiton americanum-Claytonia sibirica* wet meadow (4) |
| 23 | *Equisetum arvense-Mimulus guttatus* wet meadow (5) |
| 24 | *Carex aquatilis/C. saxatilis* graminoid marsh (3) |
| 25 | *Equisetum fluviatile-Menyanthes trifoliata* forb marsh (2) |
| 26 | *Heuchera glabra-Campanula lasiocarpa* meadow (2) |
| 27 | *Potamogeton alpinum-Ranunculus trichophyllus* aquatic marsh (3) |
| 28 | *Nuphar polysepalum* aquatic marsh (3) |
| 29 | *Potentilla egedii-Stellaria humifusa* beach meadow (7) |
| 30 | *Puccinellia nutkaensis-Plantago maritima* beach meadow (3) |
| 31 | *Zostera maritima* seagrass meadow (2) |

Thick ash deposition, 30 cm, from the eruption of Mt. Katmai in 1913 may have had a marked effect on lichen diversity. In reconstructing the effects of the 1907 eruption of Ksudach volcano on the Kamchatka Peninsula, Grishin et al. (1996) showed that secondary succession dominated in ash deposits of 10 to 30 cm; they also showed that deposits of 10 to 20 cm eliminated lichens and mosses and but only reduced the number of dwarf shrubs and herbs. The thinnest ash deposits and the lushest lichens in the Chief Cove area were on upper mountain slopes. Assuming that 30 cm of ash was originally deposited evenly over the study area, presumably the ash deposits in the upper mountain areas were redistributed by wind and colluvial action to lower slopes resulting in thinner ash layers at higher elevation. Some of the lichen taxa present before the Katmai eruption may have survived in these alpine sites.

Lichen diversity and abundance may also be reduced by the lush growth of the vascular plants in the study area, shading lichens and blanketing them in litter. The relatively deep A soil horizon formed over the 86 years since the eruption of Katmai volcano suggests that litter accumulation in the area is significant.

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This paper is written as a tribute to John W. Thomson. For 20 years I have depended on John's expertise and generosity as he determined lichen collections from the national wildlife refuges of Alaska managed by the U.S. Fish and Wildlife Service. John's support kindled my enthusiasm and encouraged me to make extensive collections, which

TABLE 5. Occurrence of epiphytic lichens on four woody shrub and tree taxa in western Kodiak Island, Alaska. Lichen taxa are listed alphabetically. Key to host taxa: 1, *Alnus crispa*; 2, *Betula kenaica*; 3, *Salix* spp. (*Salix pulchra*, S. *glauca*, and *S. alaxensis*); and 4, *Populus trichocarpa*. Presence class: +, <10%; I, 10.1-20%; II, 20.1-40%; III, 40.1-60%; IV, 60.1-80%; 80.1-100%. Only lichens occurring in more than one relevé are shown.

| Woody vascular taxa<br>Number of relevés | 1<br>14 | 2<br>6 | 3<br>5 | 4<br>3 |
|---|---|---|---|---|
| *Amandinea punctata* | III | II | II | IV |
| *Biatora albohyalina* | . | I | I | . |
| *Buellia disciformis* | III | II | I | . |
| *Cladonia coniocraea* | + | III | . | . |
| *Collema nigrescens* | . | . | . | IV |
| *Lecanora albella* | II | II | II | . |
| *L. circumborealis* | . | III | . | II |
| *L. impudens* | . | I | . | II |
| *L. pulicaris* | I | III | . | . |
| *L. varia* | II | II | . | . |
| *Lecidea carnulenta* | . | II | I | . |
| *Melanelia septentrionalis* | . | III | I | . |
| *Mycoblastus alpinus* | . | II | . | . |
| *Parmelia sulcata* | . | V | II | . |
| *Peltigera collina* | + | . | III | V |
| *P. membranacea* | + | . | II | . |
| *Pertusaria suboculata* | III | . | . | II |
| *P. borealis* | + | IV | I | . |
| *P. sommerfeltii* | . | I | . | . |
| *Physcia aipolia* | . | . | II | IV |
| *Ramalina farinacea* | + | I | I | II |
| *Rinodina archaea* | . | . | I | II |

spanned vast distances from Attu Island of the Alaska Maritime National Wildlife Refuge (NWR) in the westernmost Aleutian Islands to Tetlin NWR in eastern Alaska; and from the Arctic NWR in the north to the Kenai NWR in the south central Alaska. The contribution to knowledge of the Alaskan lichen flora provided by John Thomson is unparalleled and unprecedented. We are all the richer for it.

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# ALPINE LICHENS FROM WASHINGTON STATE I. LICHENS FROM THE NORTHEASTERN OLYMPIC AND THE NORTHERN CASCADE MOUNTAINS

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## Abstract

Lichens were inventoried in the northeast Olympic and North Cascade Mountains. One hundred and thirty-three species of lichens have been identified from six study sites with an emphasis on macrolichens. One hundred seven species are listed for the Olympic sites, and one hundred four are listed for the North Cascade sites. Although both mountain ranges contain almost the same number of lichens, the richness varies from site to site. The individual Olympic sites display greater species richness than the North Cascades. Only *Vulpicida tilesii* was found solely in the Olympics. *Alectoria sarmentosa* subsp. *vexillifera*, *Umbilicaria arctica*, *U. cylindrica*, *U. deusta*, and *U. vellea* were found only at the North Cascades sites. Dry tundra sites at all locations contained more species than late snow-bank sites with mesic conditions.

## Introduction

Lichens are a major component of the vegetation of Washington's alpine areas, yet few studies have documented their diversity and distribution across the state. This is partially due to limited access to many alpine areas but also reflects the limited number of lichenologists exploring these areas. The Olympic and Cascade Mountains provide a wide variety of alpine habitats with high lichen diversity. For example, in some of the present study sites, lichens comprise over half the vegetation cover.

Alpine lichen collections from Washington are limited in scope and there are few rigorous studies of sites or locations. The first significant taxonomic paper was by Imshaug (1957) who worked on the alpine lichens of western United States and adjacent Canada. He discussed 61 macrolichens found from nine alpine locations in Washington. Later studies by Douglas (1973, 1974) and Douglas and Bliss (1977) focused on the North Cascade Mountains. Douglas' work presented lichens and mosses in the context of alpine plant communities. Ryan's (1985) work in the North Cascades provided a detailed study of lichens and documented species from both Chowder Ridge and Skyline Divide on Mount Baker. In the Olympic Mountains, Kunze (1980) examined lichen communities of Blue Mountain and Deer Ridge within the Olympic National Park for a limited number of species. Thomson (1984) included Washington state records in his treatment of arctic/alpine lichens. This document was extensive and based on his collections as well as those from other herbaria. More recently alpine lichens from the Olympics and North Cascades have been reported by Glew (1997, 1996b, 1993a,b), including the range extension of *Vulpicida tilesii* in the Olympic Mountain range of Washington (1994a).

Early works by Howard (1937, 1950), included records of alpine lichens for the state of Washington. Riley (1995) and Riley, McCune & Neitlich (1995) have further updated our alpine lichen records by the discovery of *Arctoparmelia incurva* (Pers) Hale and the range extension of *Usnea sphacelata* R. Br. in Washington. Regional studies have provided new records or range extensions of alpine lichens from the Northwestern United States (Hammer, 1995) and British Columbia, Canada (Goward et al, 1996).

This paper provides a taxonomic list and additional baseline data for Washington alpine lichens and emphasizes studies in the Olympics and North Cascades during the summers of 1990 - 1996. These preliminary findings emphasize macrolichens from these areas.

## Study Sites

**Northeast Olympic Mountains**: Three locations were examined in the Olympic Mountains: Elk Mountain and Deer Park (including Blue Mountain and Deer Ridge) in Olympic National Park, and a cirque south of Buckhorn Mountain in the Buckhorn Wilderness Area. Located between 47°30'N - 48°00'N and 123°00'W - 123°30'W, this portion of the state is rugged and relatively inaccessible by road (Figure 1). The alpine zone in this area of the Olympics ranges from 5,500 to 7,850 ft. (Tabor, 1987; U.S. Forest Service, 1987).

Geology: The Olympic Mountains resulted from uplifted rock material formed as the Pacific plate collided with the continental plate of North America. The parent materials of the northeast portion of these mountains are predominately sedimentary rock from the ocean floor and glacial deposits. Some areas also have basaltic oceanic crust, brought up to the surface through geological processes and white granite, transported by the Cordilleran ice sheets (Taber, 1987; Taber & Cady, 1978).

Climate: Alpine sites located in the northeast section of the Olympic Peninsula are influenced by a rain shadow effect from the mountains to the west and south. This area averages 125cm of precipitation each year, most falling as snow (Buckingham et al., 1995), making it more xeric than other parts of the peninsula. Their close proximity (20-22 km) to the Strait of Juan de Fuca and Puget Sound provides a maritime climate influence. The annual alpine temperature averages 0°C (Henderson, 1996).

General Vegetation: These sites are mainly dry tundra vegetation. Typical plants include *Agoseris glauca* (Pursh) Raf., *Solidago multiradiata* Ait., *Arenaria obtusiloba* (Rydb.) Fern, *Phlox diffusa* Benth., *P. hendersonii* (E. Nels.) Cronq., *Antennaria rosea* , *Lupinus lepidus* Doug., *Synthris pinnatifida* Wats., *Smelowskia calycina* (Steph.) C.A. Mey, *Salix nivalis* Hook., *Carex phaeocephala* Piper, *C. spectabilis* Dewey, *Luzula spicata* (L.) DC., *Festuca idahoensis* Elmer, and *F. ovina* var. *brevifolia* (R. Br.) Wats. with mosses and *Selaginella* spp.

**North Cascade Mountains**: Three sites were studied in the North Cascades. On the western slopes, Skyline Divide, on Mount Baker at 48°50'-51'N and 121°50'-51'W. On the eastern slopes, the Slate Peak and the Tatie Peak areas located at 48°44'-45'N and 120°41'-45'W (Figure 1). Elevation for these sites range from 6,000 to 7,000ft (Douglas, 1974; Alt & Hyndman, 1984).

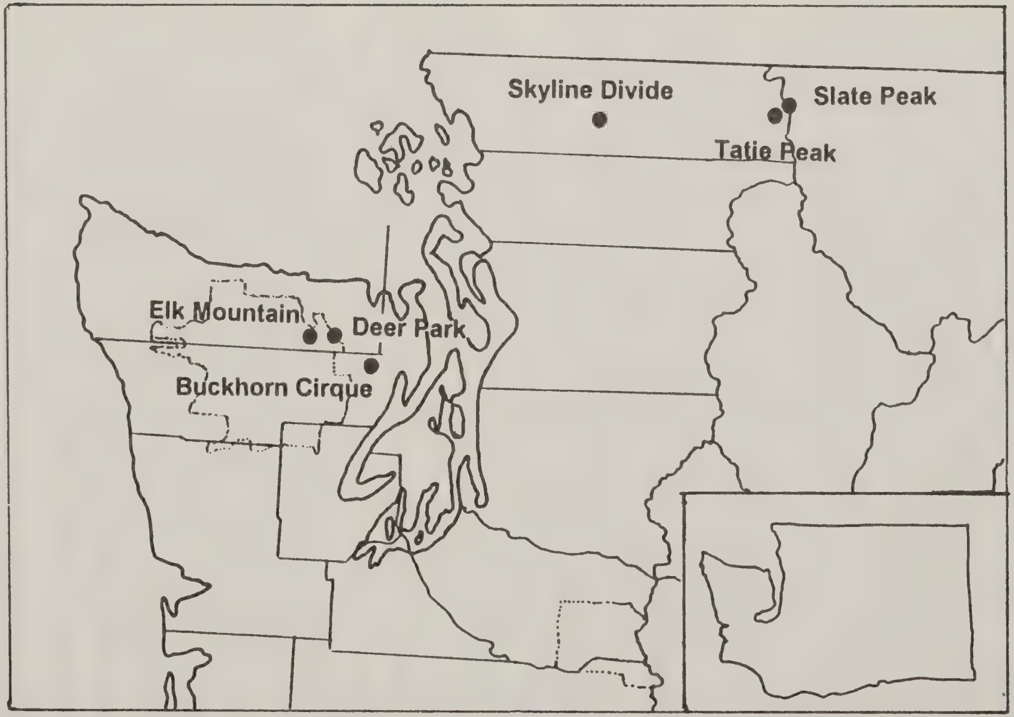

Figure 1. Map of lichen collection sites in the Olympic and North Cascade Mountains, Washington.

Geology: The North Cascades is composed of volcanic, sedimentary (sandstone, fossils, mudstone, glacial debris, and siltstone), and metamorphic rock (Taylor & Douglas, 1978; Alt & Hyndman, 1984; Stoffel & McGroder, 1990). Much of the eastern North Cascades resulted from uplifted and folded rock material that was later covered by glaciers (Alt & Hyndman, 1984).

Climate: Skyline Divide on the northwest slopes of Mount Baker is influenced by a maritime climate (Arno and Hammerly, 1990), being approximately 50 km from Puget Sound. Annual precipitation is very high, 300 cm/year (Franklin and Dyrness, 1988), highest of all alpine sites in this study. Average annual temperature is 0° C (Henderson, 1996).

The eastern slopes of the North Cascade Mountains is further inland by about 160 - 200 km, and exhibits a continental climate, but milder than that found in the great plains or Rocky Mountains. Compared to the other sites, winters are colder with fewer frost-free days, and summers are much warmer (Henderson et al., 1989). Average precipitation is 120 - 130cm/yr (Henderson, 1996), a high proportion falling as snow. Average annual temperature is -2.5° C (Henderson, 1996).

General Vegetation: Dry tundra vegetation contained the following plants: *Phlox diffusa, Saxifraga bronchialis* L., *Erigeron peregrinus* (Pursh) Greene, *Solidago multiradiata , Antennaria alpina* (L.) Gaertn., *Dryus octopetala* L., *Empetrum nigrum* L., and *Sedum lanceolatum* Torr., *Carex phaeocephala*, *C. spectabilis*, *Festuca ovina* var. *brevifolia*, *Poa* spp., mosses, and *Selaginella* spp.

On mesic sites, with late melting snow banks, the vegetation is made up of *Erigeron aureus* Greene, *Antennaria lanata* (Hooke) Greene, *A. rosea, Polygonum bistortoides* Pursh, *Veronica cusickii* Gray, *Luetkea pectinata* (Pursh) Kuntze, *Cassiope mertensiana* (Bong.) G. Don, *Phyllodoce empetriformis* (Sw.) D. Don, *P. glandulifora* (Hook.) Cov., *Kalmia microphylla* (Hook.) Heller, *Vaccinium deliciosum* Piper, *Carex nigricans* Retz., *C. spectabilis, Luzula piperi* (Cov.) Jones, *Festuca viridula* Vase., and mosses.

**General Overview of Study Sites**: Lichen communities fall into two major habitats: dry tundra and mesic sites (Glew, 1996a). The dry sites generally occur along ridges that are exposed and wind swept, resulting in relatively snow free environment. The south and southwest aspects have limited amounts of snow accumulation due to their almost constant exposure to the sun. Generally, the snow pack does not persist through the summer (Arno and Hammerly, 1990). Conditions in these areas tend to be harsh resulting in low vascular plant vegetation. Soils are very shallow with gravel and rocks a few centimeters beneath. Due to the steep slope of some of these areas, solifluction (soil movement) takes place when the snow melts. The mesic north and northeast facing slopes have snow accumulations that linger throughout the summer. Most of the moisture influencing the vegetation in these areas is from melt water originating from snow pack. They tend to be level and very stable, with dominant vascular plant vegetation. Summers are short, cool, and dry, barely giving the snow on northern slopes an opportunity to melt (Arno and Hammerly, 1990). However, the snow that does melt creates a very moist environment that, along with the predominance of ericaceous plants, has a very acidic humus and soil.

## Methods

Collections were made along transects using $0.25m^2$ quadrats, placed every 5m., and supplemented by general collecting at each site. Within the quadrat percent cover was recorded for each lichen species (Glew, 1996a, 1994b). A total of one thousand quadrats were sampled from the sites. Representative voucher specimens are deposited in the herbarium at the University of Washington (WTU). Taxonomic determinations were made following standard methods (Hale, 1979; James & White, 1985; McCune & Goward, 1995). Keys used were those of Breuss & McCune (1994 ), Dobson (1981), Goward, McCune, & Meidinger (1994), Hale (1979, 1990), Kärnefelt (1979), Lamb & Ward (1974), Laundon (1989), Llano (1950), Lohtander, K. (1994), McCune & Goward (1995), Orange (1995), and Purvis, et al (1992), Thomson (1979, 1984, 1987), Nomenclature follows that of Esslinger & Egan (1996).

## Results and Discussion

To date a total of 168 species have been identified from the six study sites (Table 1). For the northeast Olympic Mountain sites 128 species have been recorded. For the North Cascade Mountains, a total of 115 species have been documented to date. Forty-six lichens from this study were found only on the Olympic Mountain sites and 29 were found only in the North

Cascades, although other reports show that many of these species have been found in both mountain ranges. For the individual sites in the Olympics, 79 species are from Elk Mountain, 73 are from Deer Park, and 75 are from Buckhorn cirque. In the North Cascades, 78 species are from Skyline Divide, 66 species are from Slate Peak, and 49 are from the Tatie Peak area.

One lichen found at the Olympic sites is so far unknown from the North Cascade Mountains. *Vulpicida tilesii*, disjunct from the Rocky Mountains, has not been collected from the Cascade Mountains (Glew, 1994a).

Certain species of lichens are present only at the Olympic sites or are more common and widespread there. The species found only at the Olympic sites include: *Umbilicaria krascheninnikovii, Rhizoplaca melanophthalma, Ophioparma lapponica, Buellia geophila, Hypogymnia austerodes, Xanthoparmelia coloradoënsis* and *X. wyomingica* (Table 1). These lichens are known from Cascade locations other than the three study sites . Some have been documented by Ryan (1985) and Douglas (1974), such as, *Rhizoplaca melanophthalma*, which is commonly found in the Cascade Mountains and in eastern Washington on basaltic columns. Lichens occurring more frequently at the Olympic sites than the North Cascades sites as well include *Umbilicaria torrefacta, U. havaasii, Pseudephebe minuscula, Lecanora polytropa* and *Lecanora bicincta*. *Umbilicaria rigida* is frequently collected from exposed ridges in the Olympic Mountains. Its distribution includes arctic locations, and two other locations in Washington, one from the central Cascade Mountains (Thomson, 1984) and on one exposed ridge at Slate Peak, in the North Cascades (Glew, 1997, unpub).

Species of lichens that were found only at the North Cascades sites or were more common there include *Arthroraphis citrinella, Umbilicaria cylindrica, U. vellea*, and *U. arctica*, with *U. virginis* and *U. proboscidea* more common at these sites. *Dermatocarpon rivulorum* was only in subalpine meadows at Slate Peak and the Tatie Peak area in running streams resulting from snow melt. *D. rivulorum* was not observed at any of the alpine locations from the northeast Olympic Mountains.

Common lichen assemblages in alpine areas of the northeast Olympics include certrarioid lichens made up of *Cetraria ericetorum, C. islandica, C. muricatum* (occasionally *C. aculeatum*), *Flavocetraria cucullata, F. nivalis,* and *Thamnolia vermicularis* mixed with *T. subuliformis* (Glew, 1996b). These lichens are always found mixed with other alpine vegetation. Lichens found on the soil are *Cladonia carneola, C. macrophyllodes, C. ecmocyna, Ochrolechia upsaliensis, Peltigera rufescens, Stereocaulon alpinum, S. glareosum,* and *S. tomentosum*,. Many of the cladonias do not have podetia at these dryer sites. Frequent saxicolous species are *Pseudephebe pubescens, P. minuscula, Melanelia stygia, Caloplaca* spp., *Candelariella* spp., *Lecanora polytropa, Lecidea atrobrunnea,* and *Rhizocarpon geographicum s.l.* (Table 1).

Buckhorn cirque has the greatest number of fruticose lichens, mainly cetrarioid species. *Cetraria islandica* and *C. ericetorum* commonly occur and codominate in large patches up to 30 cm. across. *Flavocetraria cucullata* and *F. nivalis* also are in mixed patches with *F. cucullata* having the greatest cover. *Stereocaulon* spp. and *Cladina mitis* are mainly associated with graminoids appearing in patches ranging from 10 - 30 cm. Several *Umbilicaria* species were collected at this site (Table 1) with *Umbilicaria hyperborea* being the most common species. *Vulpicida tilesii* was only found at this Olympic site and not in the North Cascade Mountain sites. It was found in the cirque opposite the mid summer snow patches. This site has the highest lichen cover of all of the Olympic sites.

At Deer Park *Thamnolia* spp. (both *T. subuliformis* and *T. vermicularis*) are the most predominant lichens found in lichen communities. *Cladonia* species are the next most prevalent lichen group at this site. *Cetraria muricatum* is frequently found mixed with vegetation and the brown cetrarioid lichens. *Flavocetraria cucullata* is found in large patches mixed with grasses and sedges. *Umbilicaria rigida* is the most common umbilicate lichen found on rocks. The substrate at this site can be quite unstable, therefore preventing lichens from becoming established. Lichens were frequently associated with the other vegetation patches, entangled in their branches and leaves.

Elk Mountain lichen communities have the highest percent of saxicolous lichens, or about one third of the lichen cover found in the quadrats. Much of this is made up of the black macrolichens *Cornicularia normoerica, Melanelia stygia, Pseudephebe minuscula, P. pubescens, Umbilicaria hyperborea* (the most abundant umbilicate lichen), *U. krascheninnikovii, U. rigida*, and *U. torrefacta*, which can entirely cover the rocks. Half of the saxicolous species are crustose lichens. Lichen diversity on shale is not as great as sandstone, probably a result of the sandstone stripes being more stable than the shale.

Elk Mountain has many epiphytic and terricolous lichens. Along some areas next to rock stripes and on ridge tops, *Letharia vulpina* could be found growing amongst vascular plant vegetation and other epiphytic lichens. *Cetraria islandica* and *Flavocetraria cucullata* are the most common of the cetrarioid lichens seen at this site. *C. islandica* is commonly found along the edge of rock stripes, but still mixed with vascular plant vegetation. It may be that it is blown there by the high winds along the ridges. *Peltigera rufescens*, and occasionally *P. malacea* and *P. ponojensis*, are frequently found on the soil, especially where there has been a disturbance such as along the trail edge. In some mossy areas peltigeras could be found almost completely embedded in moss with only the upper tips exposed. This is also seen at Buckhorn cirque. Soil crusts such as *Ochrolechia upsaliensis* and *Lepraria cacuminum* can be repeatedly seen amongst the mosses, *Selaginella* spp. and on bare areas by plants.

Buckhorn cirque and Elk Mountain have the highest number of lichen species of the sites studied. For Elk Mountain, this is partly due to a combination of terrestrial vegetation and rock outcrops, providing a variety of substrates. Buckhorn cirque has very stable substrate which allows for the establishment of slow-growing lichens, such as soil crusts and saxicolous crustose forms. Deer Park's terrain is gravelly and less stable, reducing the diversity of lichens.

In the North Cascades mesic snow-bank communities of the Tatie Peak area, Skyline Divide, and Slate Peak, have a distinctive assemblage of lichens. These lichens generally do not occur in the more xeric tundra communities. There is greater diversity of cladonias, including *Cladonia bellediflora, C. squamosa, C. ecmocyna*, and *C. carneola*. Podetia are more developed than what is seen in the Olympics and mats cover larger areas. T*uckermannopsis subalpina* and *Solorina crocea* are found more frequently at these mesic sites, even though they are found at lower elevations into the montane zone. *Lepraria cacuminum* and *Leprocaulon subalbicans* regularly occur at the mesic sites. Deteriorating heathers, such as *Cassiope mertensiana, Phyllodoce empetriformis,* and *P. glandulifora* are commonly covered with patches of *Trapeliopsis granulosa.*

The mesic sites are at or barely above tree line, where alpine vegetation begins to integrate with the subalpine zone. This can be seen at sites, where *Cetraria islandica* and sometimes *C. ericetorum* begin to mix with populations of *Tuckermannopsis subalpina*. At these sites, *T. subalpina* is very robust and lobes develop the same size as *C. islandica*. Because the areas are exposed, *T. subalpina* acquires a darker brown color, but it is still paler than the dark forms *of C. islandica*. As the sites become more exposed and the ericaceous plants disappear, *C. islandica* and *C. ericetorum* become more frequent. At Slate Peak, on the ridge top trail, *T. subalpina* is the main cetrarioid lichen on the north and northeast facing slopes while on the south and southwest facing slopes, *C. islandica* and *C. ericetorum* dominate.

The exposed dry tundra communities of Skyline Divide and Slate Peak share many of the lichens seen from the northeast Olympic Mountains: the cetrarioid species, *Thamnolia subuliformis, T. vermicularis, Cladina mitis,* cladonias, stereocaulons, umbilicarias, *Peltigera rufescens, Lecidea atrobrunnea, L. cascadensis, Rhizocarpon geographicum*, and a variety of soil crusts where the substrate is more stable. At Skyline Divide *Cladina mitis* is widespread and abundant, even in the mesic sites at this location. *Flavocetraria nivalis* and *F. cucullata* are both at Slate Peak, but in small quantities. Only *F. nivalis* is found at Skyline Divide which is unusual because at all other dry tundra sites it is found with *F. cucullata* and less abundant. Ryan (1985) also noted the absence of *F. cucullata* on Skyline Divide and Chowder Ridge on Mount Baker. *Peltigera malacea* and *P. rufescens* are both found along the ridge at Skyline Divide *with P. malacea* being more frequent. *P. malacea* is commonly found growing epiphytically on *Empetrum nigrum*, *Cassiope mertensiana* and *Phyllodoce* spp. *P. rufescens* is always on soil.

## Conclusions

From this study 168 lichens have been identified from the alpine areas of the northeast Olympic Mountains and North Cascade Mountains. Of these, sixty-five percent are macrolichens and thirty-five percent are microlichens. Based on this study, the two mountain ranges have approximately the same number of species of lichens, but the Olympics sites have greater diversity than the sites from the North Cascades, with the exception of Skyline Divide. Those sites with a maritime influence, as in the Olympics and Skyline Divide, have a greater species richness than the sites on the eastern slopes of the North Cascade Mountains. In general, the dry tundra sites have greater species richness than the mesic snow bank sites. This may be the result of a larger variety of substrates in the dryer, exposed locations. Mesic sites are composed of lichen assemblages that are able to exist in more acidic soils. The moist substrate and generally shaded environment also allows for the development of ericaceous plants. Lichens such as *Tuckermannopsis subalpina*, *Solorina crocea*, and *Cladonia* spp. are commonly found in these locations. Some of the differences in richness between sites may relate to dispersal or subtle differences in habitat preferences.

In comparison with other studies of alpine lichens (see bibliography) the following similarities were observed. For the lichen species from this study that have currently been identified, 75 % have arctic affiliations (Thomson, 1979, 1984). Of these, 25% are strictly arctic/alpine. Eighty-five percent are found in the alpine or subalpine areas of Glacier National Park, Montana (Debolt & McCune, 1993). Fifty percent of the lichens found on the Beartooth Plateau in Montana and Wyoming (Eversman, 1995) also occur in alpine areas of the Washington sites. Ten percent of the lichens from this study are found at all six sites.

The type of site, mesic vs. xeric, along with other abiotic factors and vegetation, have a strong influence on the composition of lichens that are present (Glew, 1996a). For example, when macrolichens are examined from dry tundra sites at both Olympics and North Cascades locations, very similar types of assemblages are revealed. Also, cetrarioid lichens and *Thamnolia* spp. often occur throughout the dry, exposed ridge tops, but their abundance varies from site to site (Glew, in prep.). The major crustose species are commonly found at all sites where the rock substrate is similar.

An exception to the above situation are the umbilicate lichens where certain species seem to thrive only at one of the two alpine locations. This does not seem to be dependent on moisture, since the rock environment is exposed and dry on both sites. These differences may be related to glacial processes and remnant populations of species surviving the last ice sheet. *Vulpicida* *tilesii* also shares this disjunct distribution, being found in the Olympic and Rocky Mountains, but not in the Cascades (Glew, 1994a).

This overall study comprises a large number of collections covering a wide range of habitats that have not been previously examined. Approximately eighty percent of the specimens have been identified leaving twenty percent still to be examined. Therefore, further identifications will increase the number of species and unique lichens will be discovered. This study sampled a portion of the Olympic and Cascade Mountains. Further studies in these mountains will extend the distributions of alpine lichens and add to the number of lichens found in these areas.

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Table 1: Lichen species and site locations:
EM = Elk Mountain, BC = Buckhorn Cirque, DP = Deer Park,
SD = Skyline Divide, TP = Tatie Peak area, SP = Slate Peak.

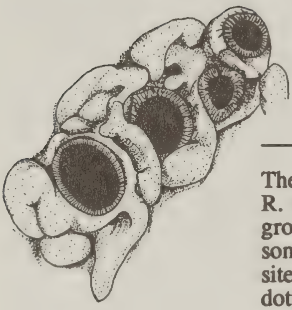
| SITE LOCATION | EM | BC | DP | SD | TP | SP |
|---|---|---|---|---|---|---|
| Acarospora fuscata (Schrader) Arnold | X |  | X | X | X |  |
| Ahtiana sphaerosporella (Mull. Arg.) Goward* |  | X |  |  | X | X |
| Alantoparmelia alpicola (Th. Fr.) Essl. | X |  |  | X |  |  |
| Alectoria nigricans (Ach.) Nyl. | X | X | X | X | X |  |
| Alectoria ochroleuca (Hoffm.) A. Massal. |  |  | X | X |  |  |
| Alectoria sarmentosa (Ach.) Ach.* |  |  | X | X |  |  |
| A. sarmentosa subsp. vexillifera (Nyl,) D. Hawksw. |  |  |  |  |  | X |
| Arthrorhaphis citrinella (Ach.) Poelt |  |  |  | X |  |  |
| Aspcilia candida (Anzi) Hue |  |  |  |  | X |  |
| Aspcilia caesiocinerea (Nyl. ex Malbr.) Arnold | X | X | X | X | X |  |
| Bellemerea alpina (Sommerf.) Clauzde & Roux |  |  |  | X | X |  |
| Bellemerea cinereorufescens (Ach.) Clauz. & Roux |  | X | X | X | X | X |
| Bellemerea subsorediza (Lynge) R. Sant. |  |  |  | X | X | X |
| Brodoa oroarctica (Krog) Goward | X | X | X | X | X |  |
| Bryoria chalybeiformis (L.) Brodo & D. Hawksw. | X | X | X | X |  |  |
| Bryoria fremontii (Tuck.) Brodo & D. Hawksw.* |  |  |  |  | X |  |
| Bryoria fuscescens (Geylnik) Brodo & D. Hawksw.* |  | X |  |  |  |  |
| Bryoria glabra (Mot.) Brodo & D. Hawksw.* |  |  | X |  |  |  |
| B. pseudofuscescens (Gyel.) Brodo & D. Hawksw.* |  |  | X |  | X |  |
| Bryoria trichodes (Michaux) Brodo & D. Hawksw.* |  |  | X |  |  | X |
| Buellia geophila (Flörke ex Sommerf.) Lynge |  | X |  |  |  |  |
| Caloplaca ammiospila (Wahlenb.) H. Olivier |  | X |  |  |  |  |
| Caloplaca dispersa (Pers.) Sommerf. |  |  | X |  |  |  |
| Caloplaca epithallina Lynge | X |  |  |  |  |  |
| Caloplaca jungermanniae (Vahl.) Th. fr. |  |  |  |  |  | X |
| Caloplaca lamprocheila (D.C) Flag. |  |  | X |  |  |  |
| Caloplaca saxicola (Hoffm.) Nordin |  |  | X |  |  |  |
| Caloplaca tiroliensis Zahlbr. | X | X | X |  |  |  |
| Candelariella aurella (Hoffm.) Zahlbr. |  |  | X |  |  |  |
| Candelariella terrigena Räsänen |  | X |  |  |  |  |
| Candelariella vitellina (Hoffm.) Müll. Arg. | X | X | X | X |  | X |
| Cetraria aculeatum (Schreber) Fr. | X | X |  | X |  | X |
| Cetraria ericetorum Opiz | X | X | X | X | X | X |
| Cetraria islandica (L.) Ach. | X | X | X | X | X | X |
| Cetraria muricatum (Ach.) Eckfeldt | X | X | X | X |  | X |
| Cladina arbuscula (Wallr.) Hale and Culb. | X |  |  |  |  |  |
| Cladina mitis (Sandst. ) Hustich | X | X | X | X | X | X |
| Cladonia bellidiflora (Ach.) Schaerer |  |  |  | X |  |  |
| Cladonia cariosa (Ach.) Spreng. |  | X |  |  |  |  |

| SITE LOCATION | EM | BC | DP | SD | TP | SP |
|---|---|---|---|---|---|---|
| Cladonia carneola (Fr.) Fr. | X |  | X | X | X |  |
| Cladonia chlorophaea (Flörke *ex* Sommerf.) Sprengel |  |  | X |  |  |  |
| Cladonia ecmocyna Leighton | X | X |  | X | X | X |
| Cladonia fimbriata (L.) Fr. |  |  |  |  |  | X |
| Cladonia gracilis (L.) Willd. | X |  |  |  |  |  |
| Cladonia macrophyllodes Nyl. | X | X | X | X |  |  |
| Cladonia pocillum (Ach.) Grognot | X |  | X |  |  |  |
| Cladonia pyxidata (L.) Hoffm. | X |  | X |  |  |  |
| Cladonia singularis Hammer |  |  |  | X |  |  |
| Cladonia squamosa Hoffm. |  |  |  | X |  |  |
| Cornicularia normoerica (Gunn.) Du Rietz | X |  | X | X |  | X |
| Dermatocarpon reticulatum H. Magn. |  | X |  |  | X | X |
| Dermatocarpon rivulorum (Arn.) Dalla Torre & Sarnth. |  |  |  |  | X | X |
| Diploschistes muscorum (Scop) Sant. |  |  |  | X |  |  |
| Flavocetraria cucullata (Bellardi) Kärnefelt & Thell | X | X | X |  |  | X |
| Flavocetraria nivalis (L.) Kärnefelt & Thell | X | X | X | X |  | X |
| Hypogymnia austerodes (Nyl.) Räsänen | X |  |  |  |  |  |
| Hypogymnia rugosa (G. Merr.) L. Pike* |  |  | X |  |  |  |
| Lecanora bicincta Ramond | X | X | X |  | X | X |
| Lecanora dispersa (Pers.) Sommerf. |  |  | X | X |  |  |
| Lecanora epibryon (Ach.) Ach. |  | X |  |  |  |  |
| Lecanora hagenii (Ach.) Ach. |  | X | X | X |  |  |
| Lecanora malaena (Hedl.) Fink | X |  |  |  |  |  |
| Lecanora polytropa (Hoffm.) Rabenh. | X | X | X | X | X | X |
| Lecidea atrobrunnea (Ramond *ex* Lam. & DC.) Schaer | X | X | X | X | X | X |
| Lecidea atromarginata H.Magn. |  |  |  |  |  | X |
| Lecidea cascadensis H. Magn. | X |  |  |  |  | X |
| Lecidea lapicida (Ach.) Ach. |  | X |  | X |  |  |
| Lecidea tessellata Flörke | X | X | X |  | X |  |
| Lecidella wulfenii (Hepp) Körber |  | X |  |  |  |  |
| Lecidoma demissum (Rutstr.)Gotth. Schneider & Hertel | X | X |  | X | X |  |
| Lepraria cacuminum (Massal.) Lohtander | X | X | X | X | X | X |
| Lepraria incana (L.) Ach. |  |  |  |  | X | X |
| Lepraria neglecta (Nyl.) Erichsen | X |  |  | X |  |  |
| Leprocaulon microscopium (Vill.) Gams ex D. Hawksw. |  |  |  |  | X |  |
| Leprocaulon subalbicans (Lamb) Lamb & Ward | X |  |  | X | X |  |
| Letharia columbiana (Nutt.) J.W. Thomson* |  | X |  |  | X |  |
| Letharia vulpina (L.) Hue | X | X |  |  | X |  |
| Lobaria linita (Ach.) Rabenh. |  |  |  | X |  |  |
| Megaspora verrucosa (Ach.) Haffelner & Wirth | X | X |  |  |  |  |
| Melanelia commixta (Nyl.) Thell | X | X |  | X |  | X |
| Melanelia disjuncta (Erichsen) Essl. | X | X |  |  |  |  |
| Melanelia exasperatula (Nyl.) Essl. | X |  |  | X |  |  |
| Melanelia hepatizon (Ach.) Thell |  | X |  |  |  | X |

| SITE LOCATION | EM | BC | DP | SD | TP | SP |
|---|---|---|---|---|---|---|
| Melanelia infumata (Nyl.) Essl. | X | | | X | | |
| Melanelia panniformis (Nyl.) Essl. | X | | | | | |
| Melanelia sorediata (Ach.) Goward & Ahti | X | X | | X | | X |
| Melanelia stygia (L.) Essl. | X | X | X | X | | |
| Mycobilimbia sabuletorum (Schreber) Hafellner | | X | | | | |
| Mycoblastus affinis (Schaerer) Schauer | | | | X | | |
| Mycoblastus sanguinarius (L.) Norman * | | | X | | | |
| Nodobryoria abbreviata (Müll. Arg.) Commons &Brodo* | | X | | | X | |
| Ochrolechia upsaliensis (L.) A. Mass. | X | X | X | X | | |
| Ophioparma lapponica (Räsänen) Hafellner & R. W. R | X | | X | | | |
| Pannaria pezizoides (Weber) Trevisan | | X | | | | |
| Parmelia saxatilis (L.) Ach. | X | | | X | | |
| Parmeliopsis ambigua (Wulfen) Nyl.* | | | | | | X |
| Parmeliopsis hyperopta (Ach.) Arnold* | | | X | | | X |
| Peltigera didactyla (With.) J.R. Laundon | X | | | | | |
| Peltigera kristinssonii Vitik. | X | | | | | |
| Peltigeran lepidophora (Vainio) Bitter | X | | X | | X | |
| Peltigera malacea (Ach.) Funck | X | X | | X | X | X |
| Peltigera ponojensis Gyelnik | X | | X | | | X |
| Peltigera praetextata (Flörke *ex* Sommerf.) Zopf | | | | | | X |
| Peltigera rufescens (Weiss) Humb. | X | X | X | X | X | X |
| Phaeophyscia sciastra (Ach.) Moberg | X | | | | | |
| Phaeorrhiza nimbosa (E. Fr.) Mayr. & Poelt | | X | | | | |
| Phylliscum demangeonii (Moug. & Mont.) Nyl. | | | | X | | |
| Physcia caesia (Hoffm.) Fürnr. | | | X | X | | |
| Physcia dimidiata (Ach.) Nyl. | | | X | | | |
| Physcia phaea (Tuck.) J.W. Thomson | X | | | | | |
| Physconia muscigena (Ach.) Poelt | X | X | X | X | | |
| Placynthiella uliginosa (Schrader) Coppins & James | X | X | | X | | X |
| Platismatia glauca (L.) Culb. & Culb.* | | | X | | | |
| Polychidium muscicola (Sw.) Gray | | X | | | | |
| Porpidia contraponenda (Arnold) Knoph & Hertel | | | | X | | |
| Porpidia thomsonii Gowan | | | | X | | |
| Protoparmelia badia (Hoffm.) Haffelner | | | | | X | X |
| Pseudephebe minuscula (Nyl. *ex* Arnold) Brodo & D. Hawksw. | X | X | X | | X | X |
| Pseudephebe pubescens (L.) Choisy | X | X | X | X | X | X |
| Psora globifera (Ach.) A. Massal. | | | | X | | |
| Psoroma hypnorum (Vahl) Gray | | | | | | X |
| Rhizocarpon bolanderi (Tuck.) Herre | X | | X | | | |
| Rhizocarpon disporum (Nägel *ex* Hepp) Müll. Arg | X | | | | | |
| Rhizocarpon distinctum Th. Fr. | | | | | | X |
| Rhizocarpon eupetraeum (Nyl.) Arnold | | | | | | X |
| Rhizocarpon geographicum (L.) DC. | X | X | X | X | X | X |

| SITE LOCATION | EM | BC | DP | SD | TP | SP |
|---|---|---|---|---|---|---|
| Rhizocarpon lecanorinum Anders | X |  | X |  |  |  |
| Rhizocarpon obscuratum (Ach.) A. Massal. |  |  |  | X |  |  |
| Rhizocarpon polycarpum (Hepp) Th. Fr. |  |  |  | X |  |  |
| Rhizoplaca chrysoleuca (Sm.) Zopf |  |  | X |  |  |  |
| R. melanopthalma (DC.) Leuckert & Poelt | X | X | X |  |  |  |
| Rimularia insularis (Nyl.) Rambold & Hertel | X |  |  |  |  |  |
| Solorina crocea (L.) Ach. |  | X |  | X | X | X |
| Sporastatia testudinea (Ach.) A. Massal. | X | X |  | X |  | X |
| Staurothele drummondii (Tuck.) Tuck |  |  | X |  | X | X |
| Staurothele fissa (Taylor) Zwackh |  |  |  |  |  | X |
| Stereocaulon alpinum Laur. *A115* Funck |  | X | X | X | X | X |
| Stereocaulon glareosum (Savicz) H. Magn. |  | X |  | X |  | X |
| Stereocaulon rivulorum H. Magn. |  | X |  |  |  |  |
| Stereocaulon tomentosum Fr. |  | X |  |  |  | X |
| Tephromela armeniaca (DC.) Hertel & Rambold |  |  |  |  | X |  |
| Thamnolia subuliformis (Ehrh.) Culb. | X | X | X | X |  | X |
| Thamnolia vermicularis (Sw.) Ach. *ex* Schaerer | X | X | X | X | X | X |
| Trapeliopsis granulosa (Hoffm.) Lumbsch |  |  | X |  | X | X |
| Tremolecia atrata (Ach.) Hertel |  | X |  | X |  |  |
| Tuckermannopsis chlorophylla (Willd.) Hale* |  |  | X |  |  |  |
| Tuckermannopsis merrillii (Du Rietz) Hale * |  | X |  |  | X | X |
| Tuckermannopsis subalpina (Imshaug) Kärnefelt * |  | X |  | X | X | X |
| Umbilicaria arctica (Ach.) Nyl. |  |  |  | X | X | X |
| Umbilicaria cylindrica (L.) Delise ex Duby |  |  |  |  |  | X |
| Umbilicaria decussata (Vill.) Zahlbr. | X |  | X | X |  | X |
| Umbilicaria deusta (L.) Baumg. |  |  |  | X |  |  |
| Umbilicaria havaasii Llano | X |  |  | X |  | X |
| Umbilicaria hyperborea (Ach.) Hoffm. | X | X | X | X | X | X |
| Umbilicaria krascheninnikovii (Savicz) Zahlbr. | X | X | X |  |  | X |
| Umbilicaria proboscidea (L.) Schrader |  |  | X | X |  | X |
| Umbilicaria rigida (Du Rietz) Frey | X | X | X |  |  | X |
| Umbilicaria torrefacta (Lightf.) Schrader | X | X |  | X |  |  |
| Umbilicaria vellea (L.) Hoffm. |  |  |  | X |  | X |
| Umbilicaria virginis Schaerer |  | X |  | X |  | X |
| Vulpicida tilesii (Ach.) J.-E. Matts. & M.J. Lai |  | X |  |  |  |  |
| Xanthoparmelia coloradoënsis (Gyelnik) Hale | X | X | X |  |  |  |
| Xanthoparmelia wyomingica (Gyelnik) Hale | X | X | X |  |  |  |
| Xanthoria elegans (Link) Th. Fr. | X | X | X | X | X | X |

* found in krummholz only



The **Rugged Crater Lichen** [*Diploschistes muscorum* (Scop.) R. Sant., Thelotremataceae] is a subtle species usually found growing over *Cladonia* spp. squamules and podetia (and sometimes over intergrown mosses) in sun-baked, exposed sites. In nature, this lichen appears like a felty, grey, black-dotted mass, but microscopic examination reveals a grey nodular thallus pitted with concave, rough-edged, black apothecia. Mature asci contain four large, dark, muriform ascospores. Typical habitats in the Catskill Mountains of New York are fallen logs or glacial erratics covered with *Cladonia*. Drawn (ca. x30) by Robert Dirig from material found on *Cladonia* at the Albany Pine Bush, New York, an extensive inland sand plain.

*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
IN HONOR OF JOHN W. THOMSON.
EDS: M. G. GLENN, R. C. HARRIS, R. DIRIG & M. S. COLE.
MYCOTAXON LTD., ITHACA, NY. 1998.

# LICHENS OF GRANITIC PEAKS IN THE BITTERROOT RANGE, MONTANA AND IDAHO, USA

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ABSTRACT. Lichens on the high peaks and ridges of the Bitterroot Range are of particular interest because the Bitterroot Range lies near the eastern edge of the peninsula of oceanic influence into western Montana. The crest of the Bitterroot Range lies at the top of the huge Idaho Batholith, the largest mass of granite within the relatively maritime region of western Montana. A total of 218 species of lichenized fungi were found, distributed among 80 genera. *Lecidea syncarpa*, new to North America, is a common species in the Rocky Mountains. A species close to *Diplotomma alboatrum* is described in detail. It occurs on vertical rock surfaces and beneath sheltered overhangs. A key is given for sterile white crusts on soil or moss in the alpine. *Lecanora swartzii,* new to North America, also occurs beneath overhanging rocks.

## INTRODUCTION

Only a handful of lichen studies have been published for alpine areas of the northern Rocky Mountains in Montana, Idaho, and adjoining British Columbia and Alberta. Imshaug's "Part I" describing alpine macrolichens of the western states (Imshaug 1957) gave high hopes for a "Part II" which never arrived. Recent lichen floras (Goward and McCune 1994, McCune and Goward 1995) included alpine macrolichens, but the crustose alpine lichens have been included only in floristic works for a few areas (e.g. DeBolt and McCune 1993, Eversman 1995). A comparison of the list in this paper with the few papers including alpine lichens from the Cascade Range (e.g. Douglas 1974, Ryan 1985) will show that the alpine areas of the Rockies and the Cascades have many differences. The most useful comprehensive keys for alpine crusts in the northern Rockies remain, therefore, Thomson (1979), Bird (1970), and McCune (1997).

The species list presented in this paper probably represents less than half of the total alpine lichen flora of the northern Rockies. I base this guess on the combination of our ignorance and inclusion of only granitic rocks in this study. The present paper includes a list of species, ecological notes, extended descriptions of selected species, a key to whitish sterile crustose species, and a briefly annotated checklist.

## STUDY AREA

The high peaks and ridges of the Bitterroot Range lie near the eastern edge of the peninsula of oceanic influence into western Montana (McCune 1984). The crest of the Bitterroot Range lies at the top of the huge Idaho Batholith, the largest mass of granite within the relatively maritime region of western Montana. Most of the other high ranges in western Montana are primarily of sedimentary rock, with notable exceptions in the Anaconda Range and the Beartooth Plateau. Most of the granites in the Idaho Batholith are granodiorite and quartz monzonite (Ross 1963).

Climatic data are unavailable for the high mountains of the Bitterroot Range. Summers are warm yet short and often have prolonged dry periods. During the rest of the year precipitation is frequent, though often in small amounts. Snowfields often persist well into July although wind exposed ridges and peaks are relatively snow free through the winter.

All collecting sites reported here are on peaks and ridges over 2000 m in elevation. This study includes the highest peak in the Bitterroot Range, Trapper Peak, at 3080 m. The major collecting sites (Table 1, Figure 1) are all non forested. They range from broken subalpine forests to true alpine communities with no trees even in spots with adequate soil. Many of the sites had krummholz or scattered small trees around the edges. All of the sites are extremely rocky and many have almost no soil development.

Table 1. Primary collecting sites at elevations over 2000 m, in order of increasing elevation (States: MT=Montana, ID=Idaho).

| Site | Elev., m | State | County | Lat. | Long. |
|---|---|---|---|---|---|
| Bear Cr. Overlook | 2165 | MT | Ravalli | 46°23' | 114°17' |
| Skookum Butte | 2195 | MT | Missoula | 46°39.5' | 114°23' |
| Castle Rock | 2350 | MT | Ravalli | 45°53' | 114°27' |
| Big - Sweathouse divide | 2500 | MT | Ravalli | 46°28' | 114°14' |
| Grave Peak | 2520 | ID | Idaho | 46°23.5' | 114°44' |
| Ingomar Peak | 2590 | MT | Ravalli | 46°13' | 114°25' |
| Salmon Mt | 2624 | ID | Idaho | 45°37' | 114°50' |
| Lolo Peak | 2750 | MT | Lolo | 46°40' | 114°15' |
| Little St. Joseph Peak | 2753 | MT | Ravalli | 46°36' | 114°13' |
| Canyon Peak | 2755 | MT | Ravalli | 46°15' | 114°21' |
| Sweeney Peak | 2780 | MT | Ravalli | 46°39' | 114°13' |
| St. Mary's Peak | 2845 | MT | Ravalli | 46°31' | 114°14' |
| El Capitan | 3043 | MT | Ravalli | 46°01' | 114°24' |
| Trapper Peak | 3080 | MT | Ravalli | 45°53.5' | 114°18' |

Figure 1. Major collecting sites (triangles) and location of study area. Small squares are towns. The Montana-Idaho border is shown by a dotted line.

## METHODS

Each site was visited on only one day, with the exception of St. Mary's Peak which was visited twice. Collecting effort was fairly uniform across the sites, except for less time spent at Bear Creek overlook. Vouchers were collected for most species at most sites, but some common species were simply recorded without collecting. Approximately 1000 collections were made. Vouchers are primarily in the author's herbarium and OSC, with smaller numbers in WIS. Nomenclature mainly follows Esslinger and Egan (1995).

## RESULTS AND DISCUSSION

### Biodiversity

A total of 218 species in 80 genera were found. This total is much smaller than that of the alpine lichens of the Rocky Mountains because calcareous substrates are not represented in this study. The list given below is, however, fairly typical of siliceous alpine sites in the Rocky Mountains.

A few species are conspicuous by their absence. *Evernia divaricata* and *Dactylina madreporiformis* are common on the high granitic areas of the Beartooth Plateau in southern Montana and northwestern Wyoming, but these species are apparently absent from the Bitterroot Range. *Dactylina arctica* is common in the Canadian Rockies but still has not been found in the Rocky Mountains in the U.S. *Umbilicaria proboscidea* is another species common in the Canadian Rockies but apparently absent in the Bitterroot Range. *Cornicularia normoerica* is fairly frequent in the Cascade Range of Oregon and Washington, but is very rare in Montana, where it is not known south of Glacier Park (DeBolt and McCune 1993; McCune and Goward 1995).

Given the elevation range included in this study (2000-3080 m), one might expect a number of species to be restricted to one end or the other of this range. Certainly the low elevation sites include more species requiring woody substrates. A few species occurred only at the highest sites, for example, *Dactylina ramulosa*, *Sporastatia polyspora*, and the possibly undescribed black-fruited *Caloplaca*.

### Alpine Habitats in the Bitterroots

Extensive alpine fellfields occur in only a few areas, one of the largest being on Lolo Peak. Alpine communities in the Bitterroot Range are mostly small, local, and poorly developed. This derives from several factors: elevation, topography, and snow, as described below. Elevations are rather low (compared to the Beartooth Plateau) for developing alpine communities at this latitude. Most of the sites had peripheral small trees. The peaks and ridges are steep and very rocky, with little soil development, greatly restricting the potential for terricolous lichen development. Snowpacks are deep in many microsites, excluding all but a few lichens tolerant of prolonged burial by snow.

Combining these factors results in many alpine lichens being restricted to a very narrow habitat on many of the peaks: cliff ledges and short slopes near the crest of peaks on the northwest side. This is the intersection of the most favorable areas on two independent gradients: the temperature gradient, with alpine lichens favoring cooler northerly aspects, and the wind/snowpack gradient, with lichens favoring the windswept western faces. Thus the best alpine lichen development in the Bitterroot Range is usually near the crest of northwestern slopes, combining cool temperatures and low snow accumulation. Because of the steep topography, the terricolous alpine lichen communities are often restricted to cliff ledges just off the NW side of the summits.

## Communities Beneath Overhangs

Lichens beneath sheltered overhangs and cliff faces often formed complex mixtures of interesting species. Some of these species are in the *Lecanora rupicola* group. Examination of this group in light of Leuckert and Poelt (1989) has refined our understanding of this group. *L. swartzii* (Ach.) Ach., new to North America, is quite distinct morphologically from the rest of the group, having almost stalked areoles and apothecia. It was found at four locations (Castle Rock, Ingomar Peak, Little St. Joseph Peak, and Skookum Butte, in all cases beneath overhangs. *L. rupicola* sens. str. turns out to be essentially absent from the northern Rockies, most of the previous reports actually being *L. bicincta*. West of the Cascade crest the pattern reverses and *L. rupicola* is much more common than *L. bicincta* but occasionally (Siskiyou Mountains) they co-ocur. All three taxa in Europe have two or more subspecies differing in chemistry (Leuckert and Poelt 1989), but I found it difficult to assign the North American specimens to subspecies based on spot tests.

*Lecanora swartzii* is a component of the distinctive community that grows beneath overhanging rocks. Other species restricted to this habitat are *Lecanora pringlei, Fuscidea praeruptorum*, and the *Diplotomma* species discussed below. Curiously, the two *Lecanora* species and the *Fuscidea* have very similar growth forms, being stalked areolate to almost fruticose. *L. argopholis*, when growing in this habitat, also assumes this growth form. Surely these are extremely stable habitats where longevity can be obtained by adopting a growth form that allows thickening in place rather than rapid lateral expansion.

***Lecidea syncarpa*** Zahlbr. Verh. Zool.-Bot. Ges. Wien. 68:10. 1918.
Syn.: *Lecidea gneissicola* Zahlbr. Ann. Mycol. 17:235. 1919.
*Lecidea saxosa* R. A. Anderson (nomen nudum)

*Lecidea syncarpa* is a fairly common species in the Rocky Mountains. This taxon was tentatively described as a new taxon, "*L. saxosa*", by Roger Anderson (1964) but this description was never formally published. In correspondence Dr. Anderson mentioned that he had found this to be synonymous with the European *L. syncarpa.* This fact is noted in Hertel (1995). This species is apparently poorly known and rare even in Europe. The following description is based on notes sent to me by Dr. Anderson, along with my own observations on variability.

**Thallus** to 15 cm diam., rimose areolate to areolate or subsquamulose, brown, pale brown, or yellowish brown, less often greenish tinged; **areoles** to 2-3 mm diam., usually contiguous, occasionally somewhat dispersed, sometimes whitish or blackish edged; **prothallus** black or nearly so (occasionally whitish in spots), often conspicuous between the areoles or at the thallus margin, but occasionally not apparent.

**Apothecia** lecideine, black or somewhat whitish pruinose, to 3 mm diam., usually sessile to slightly elevated above the areoles; **disc** initially concave or flat, later convex; **margin** thin to somewhat thick, usually persistent except in strongly convex apothecia; **exciple** bluish green or olivaceous at the edge, pale or hyaline within or greyish-cloudy from crystals of norstictic acid, forming K+ rusty crystals; **hymenium** 45-55(60) $\mu$m high, I+ blue-green, the asci I+ red brown; **epihymenium** blue green or olivaceous; **subhymenium** hyaline or nearly so; **hypothecium** brownish or pale brown; **ascospores** 8-13 x 3-5(7) $\mu$m, simple, 8/ascus; **conidia** not seen.

**Chemistry**: Cortex I+ blue, K+ red, P+ yellow, C-; Medulla I+ blue or purple, K-, P-, C-. Contains norstictic acid (TLC).

**Taxonomy**: This member of the *Lecidea atrobrunnea* group is easily recognized its typically pale brownish, K+ red thallus and I+ blue medulla. For a description of the European material see Hertel (1970).

**Distribution**: Rocky Mountains in North America from western Montana south to Colorado and Utah; also in Europe (Austria, Spain).

**Ecology**: The substrate is typically siliceous rock, but occasionally this species is found on calcareous rock. It is usually in the subalpine to alpine zones in exposed to somewhat sheltered sites, but extends down into cool steppe communities (e.g. the Idaho location below).

**Representative Specimens Seen**: USA. COLORADO: Clear Creek County, N-facing slope between Squaw Mt. and Chief Mt., 39°41'N 105°30'W, 3440 m, *Anderson 5426, Lich. Western N. Amer. No. 38*; Summit County, North Star Mtn. near Blue Lake Reservoir, T8S R78W S3, 3600-3900 m, *Anderson 9160.* IDAHO: Custer County: Lost River Range, above Bear Creek, 43°49'N

113°28'W, 2200 m, *McCune 19734*; Fremont County, E of Henrys Lake, 44°38'N 111°18'W, 2100-2700 m, *Anderson 10246*. MONTANA: Gallatin County: Madison Range, ridge above Beaver Creek, 45°10'N 111°22'W, 2835 m, *McCune 15757*; Ravalli County: Bitterroot Range, summit of El Capitan, 46°01'N 114°24'W, 3043 m, *McCune 13067.* WYOMING: Park County: Beartooth Plateau, 44°59'N 109°26'W, 3150 m, *McCune 19894*. (all specimens in herb. McCune).

**Additional Locations**: Roger Anderson provided me with location data for the following additional states and counties, but I have not seen the specimens. COLORADO: Boulder, Garfield, Grand, Hinsdale, Larimer, Mesa, Ouray, Pitkin, San Juan, and San Miguel Counties. UTAH: Duchesne County (Uinta Mts.). WYOMING: Carbon County (Snowy Range Pass).

***Diplotomma*** sp.

**Thallus** indistinct, becomming verruculose to bullate, the verrucules or areoles typically 0.1 to 1.0 mm diam., dull olive brownish but in one case grayish pruinose.

**Apothecia** lecideine, 0.3-0.7(1.0) mm diam.; **disc** initially flat but soon convex to hemispherical, black, often lightly but distinctly pruinose; **exciple** soon disappearing as the disk becomes convex, brown in section, the edge about 50 $\mu$m thick; **hymenium** ca. 125 $\mu$m high, not inspersed with oil drops; **epihymenium** brown, with superficial hyaline to yellowish granules; **hypothecium** brown; **ascospores** 16-19 x 7-10 $\mu$m, submuriform to muriform, with about 4 transverse walls and 1-2 longitudinal partitions, greyish to brown, 8/ascus; **conidia** not seen.

**Chemistry**: No lichen substances known; spot tests negative except hymenium, hypothecium, and exciple amyloid (I+ blue).

**Taxonomy**: Only two saxicolous *Diplotomma* species are known from the Rocky Mountains. *D. alboatrum* has muriform spores while the norstictic-deficient chemotype of *D. venustum* (= *D. epipolium*) has 3-septate spores. The species reported here is in the *D. alboatrum* group. That species typically occurs on calcareous rock, has a whitish thallus, and often a pseudothalline margin. The Montana material is close to descriptions of *D. ambiguum*. *Diplotomma ambiguum* was recently synonymized under *D. alboatrum* (as *Buellia alboatrum* in Nordin 1996). Nordin considered *D. ambiguum* to be an epruinose form occurring on siliceous coastal rocks in Scandanavia. Because of the complex taxonomic history and extremely variable morphology of *D. alboatrum*, a satisfactory disposition of the material from Montana must await the North American revision of this group by Anders Nordin.

The specimens are sometimes confused by associated *Amandinea punctata*. This species and the *Diplotomma* are sometimes intricately intermixed. The *Amandinea* has a thinner and usually more prominent exciple (about 20 $\mu$m thick), lacks the superficial granules on the epihymenium, and has two-celled spores. Both the *Amandinea* and *Diplotomma* can grow on a similar thallus, so that it is likely that the *Amandinea* is parasitic on either the *Diplotomma* or the underlying *Lecanora bicincta*.

*Diplotomma ambiguum* is in the North American checklist based on Imshaug’s (1951) monograph, material which is K+ red, and should be referred to *D. chlorophaeum*, according to Noble (1982). This can also be considered to be the norstictic acid chemotype of *D. alboatrum*.

**Distribution**: I have seen similar specimens only from western Montana in the northern Rocky Mountains. The Californian records (Imshaug 1951) are another species (see preceding paragraph).

**Ecology**: The thallus may arise on the thallus of other lichens or on bare rock. So far it is known exclusively from near-vertical siliceous rock surfaces and beneath sheltered overhangs. Typical associates are *Lecanora bicincta*, *Amandinea punctata* (see under Taxonomy), *Fuscidea praeruptorum,* and *Lecanora pringlei* and, in one case, *Xanthoria candelaria*. *Lecanora pringlei* and *F. praeruptorum* are likewise restricted to a similar habitat and are probably good indicator species for the possible presence of this *Diplotomma*.

**Specimens Seen**: USA. MONTANA: Missoula County, Bitterroot Range, summit of Skookum Butte, 46°39.5’N 114°23’W, 2195 m, on vertical rock beneath overhang, 14 July 1981, *McCune 11616* (OSC, SASK, herb. McCune); north end of Sapphire Range, north slope of University Mountain, 46° 52’N 113° 57’W, 1035 m, on cliffs surrounded by talus and broken forests of *Pseudotsuga* and *Larix occidentalis*, September 1993, *McCune 21151* (OSC).

## Species List

Species were found in both Idaho and Montana unless only one state or the other is indicated by "Id" or "Mt". Because collecting sites in Montana outnumbered those in Idaho by 6:1, most of the species reported only from Montana probably also exist in the alpine of the Bitterroot Range in Idaho.

*Acarospora chlorophana sensu lato*
*Acarospora fuscata*
*Acarospora schleicheri* Mt
*Acarospora thamnina* Mt
*Ahtiana sphaerosporella* Mt
*Alectoria sarmentosa* Mt
*Alectoria vexillifera* Mt
*Allantoparmelia alpicola* Mt
*Amandinea punctata*
*Arthroraphis citrinella*
*Aspicilia caesiocinerea*
*Aspicilia cinerea* Mt
*Aspicilia desertorum ?*
*Aspicilia supertegens ?*
*Bellemerea alpina*
*Bellemerea cinereorufescens*
*Biatora vernalis* Mt
*Brodoa oroarctica*
*Bryonora castanea* Id
*Bryonora pruinosa* Mt
*Bryoria chalybeiformis* Mt
*Bryoria fremontii* Mt
*Bryoria pseudofuscescens* Mt
*Buellia papillata*
*Buellia retrovertens*
*Caloplaca cinnamomea* Mt
*Caloplaca epithallina* Mt
*Caloplaca jungermanniae*

*Caloplaca saxicola* Mt
*Caloplaca stillicidiorum* Mt
*Caloplaca tiroliensis* Mt
*Caloplaca sp.* (black fruited, on bryophytes) Mt
*Candelariella terrigena*
*Candelariella vitellina*
*Carbonea vitellinaria*
*Catapyrenium cinereum* Mt
*Catapyrenium daedaleum* Mt
*Cetraria cucullata* Mt
*Cetraria ericetorum* ssp. *reticulatum*
*Cetraria hepatizon*
*Cetraria islandica* Mt
*Cetraria merrillii* Mt
*Cetraria nivalis* Mt
*Cetraria pinastri* Mt
*Cetraria platyphylla* Mt
*Cladonia borealis*
*Cladonia carneola* Mt
*Cladonia cervicornis* (with morphology of *C. macrophyllodes* but lacking atranorin by TLC)
*Cladonia chlorophaea* Mt
*Cladonia ecmocyna* Mt
*Cladonia fimbriata* Mt
*Cladonia macrophyllodes*
*Cladonia ochrochlora* Mt
*Cladonia pocillum*
*Cladonia pyxidata* Mt
*Cladonia sulphurina* Mt
*Coelocaulon aculeatum*
*Coelocaulon muricatum*
*Cystocoleus ebeneus* Id
*Dactylina ramulosa* Mt
*Dermatocarpon intestiniforme* Mt
*Dermatocarpon reticulatum* Mt
*Diploschistes muscorum*
*Diplotomma* cf. *ambiguum* (see text) Mt
*Diplotomma penichrum* (normally a species of low to middle elevations but also occasionally in the subalpine) Mt
*Ephebe solida* (on seepage lines over rock) Mt
*Fuscidea praeruptorum* (see text under "overhangs"; containing alectorialic and barbatolic acids and unknowns by TLC; prothallus paler gray than European specimens I have seen; apothecia not found)
*Hydrothyria venosa* (spring in subalpine forest not far below ridgetop; see McCune 1984) Mt
*Hypogymnia austerodes* Mt
*Hypogymnia imshaugii*
*Hypogymnia metaphysodes* Mt
*Hypogymnia "montana"* (see McCune & Goward 1995)
*Hypogymnia physodes* Mt
*Hypogymnia tubulosa* Mt
*Lecanora argopholis* (see text; overhangs) Mt
*Lecanora beringii* Mt
*Lecanora bicincta* (see text)
*Lecanora cenisea*
*Lecanora circumborealis*
*Lecanora impudens* Mt
*Lecanora intricata*
*Lecanora marginata* Mt
*Lecanora novomexicana* (the *thomsonii* morph) Mt
*Lecanora polytropa*
*Lecanora pringlei* (see text; overhangs) Mt
*Lecanora swartzii* (see text; overhangs) Mt
*Lecanora umbrosa* Mt
*Lecanora zosterae* Mt
*Lecidea atrobrunnea*
*Lecidea auriculata*
*Lecidea fuscoatra*
*Lecidea lactea* Id
*Lecidea plana*
*Lecidea praenubila* Mt
*Lecidea syncarpa* (see text) Mt

*Lecidea tessellata*
*Lecidella elaeochroma* Mt
*Lecidella patavina* Mt
*Lecidella stigmatea* Mt
*Lecidella wulfenii* Mt
*Lecidoma demissum* Mt
*Lepraria cacuminum*
*Lepraria neglecta*
*Leprocaulon subalbicans*
*Leptochidium albociliatum*
*Leptogium lichenoides*
*Leptogium subaridum* (Salmon Mt., Idaho; extremely isidiate, forming a compact tuft over *Grimmia;* medulla similar to that of *L. magnussonii*) Id
*Letharia columbiana* Mt
*Letharia vulpina* Mt
*Lobaria linita* (rare, Grave Peak only; see McCune 1984) Id
*Massalongia carnosa* Mt
*Megaspora verrucosa* Mt
*Melanelia disjuncta*
*Melanelia elegantula* Mt
*Melanelia infumata* Mt
*Melanelia panniformis* Mt
*Melanelia sorediosa* Mt
*Melanelia stygia* Mt
*Melanelia subelegantula* Mt
*Melanelia subolivacea* Mt
*Melanelia tominii* Mt
*Miriquidica garovaglii* Id
*Miriquidica griseoatra* Mt
*Miriquidica leucophaea* Mt
*Mycobilimbia fusca* Mt
*Nodobryoria abbreviata*
*Nodobryoria subdivergens* Mt
*Ochrolechia androgyna* Mt
*Ochrolechia inaequatula*
*Ochrolechia upsaliensis* Mt
*Ophioparma lapponicum*
*Pannaria pezizoides* Id
*Pannaria praetermissa* Id
*Parmelia omphalodes* ssp. *pinnatifida* Mt
*Parmelia omphalodes* Mt
*Parmelia saxatilis*
*Parmeliopsis ambigua* Mt
*Peltigera aphthosa*
*Peltigera canina*
*Peltigera collina* Mt
*Peltigera didactyla* Mt
*Peltigera kristinssonii* Mt
*Peltigera lepidophora* Mt
*Peltigera leucophlebia*
*Peltigera malacea*
*Peltigera ponojensis*
*Peltigera rufescens* Mt
*Peltigera venosa* Mt
*Phaeophyscia sciastra* Mt
*Phaeorrhiza nimbosa* Mt
*Physcia dubia*
*Physcia phaea* Mt
*Physconia enteroxantha* Mt
*Physconia muscigena*
*Physconia perisidiosa* Mt
*Placynthiella oligotropha* Sometimes dominant on soil on solifluction lobes but also common on many other microsites. Mt
*Placynthiella uliginosa*
*Platismatia glauca* Mt
*Polychidium muscicola* Id
*Polysporina simplex*
*Porpidia glaucophaea* auct. (see Gowan 1989)
*Porpidia crustulata* Mt
*Protoparmelia badia*
*Pseudephebe minuscula*
*Pseudephebe pubescens* Mt
*Psora nipponica* Mt
*Psoroma hypnorum*
*Pyrrhospora elabens* Mt
*Rhizocarpon disporum* Mt
*Rhizocarpon eupetraeum* Mt
*Rhizocarpon geminatum* Mt
*Rhizocarpon geographicum*
*Rhizocarpon grande*

*Rhizocarpon hochstetteri* Mt
*Rhizocarpon macrosporum* Mt
*Rhizocarpon polycarpum* Id
*Rhizocarpon pusillum* Mt
*Rhizocarpon riparium*
*Rhizocarpon superficiale* Mt
*Rhizoplaca melanophthalma* Mt
*Rimularia insularis* Mt
*Rinodina archaea* Mt
*Rinodina mniaraea* Id
*Rinodina turfacea* Mt
*Solorina crocea*
*Sporastatia polyspora*
*Sporastatia testudinea*
*Staurothele areolata* Mt
*Stereocaulon alpinum* Mt
*Tephromela aglaea* Mt
*Tephromela armeniaca*
*Thamnolia subuliformis*
*Trapeliopsis granulosa* Mt
*Umbilicaria angulata* Id
*Umbilicaria decussata* Mt
*Umbilicaria deusta*
*Umbilicaria havaasii* Mt
*Umbilicaria hyperborea*
*Umbilicaria krascheninnikovii*
*Umbilicaria lambii* Mt
*Umbilicaria phaea* Mt
*Umbilicaria torrefacta* Mt
*Umbilicaria vellea*
*Umbilicaria virginis*
*Verrucaria* sp. Mt
*Xanthoparmelia coloradoensis*
*Xanthoparmelia lineola* Mt
*Xanthoria candelaria* Mt
*Xanthoria elegans* Mt
*Xanthoria sorediata* Mt

## Key to Sterile White Alpine Crusts on Soil or Moss

Species included were found in or near the study area. Bracketed species were not found in the study area but are likely to be found there or nearby in the future. In many cases these species occur on soil or moss over rock. The *Lepraria* species are poorly known in North America and will require considerable revision.

1a Thallus minutely fruticose
  2a Thallus corticate, C+ red, K-, P-. Thallus warty sometimes becoming coralloid, usually with spiny extensions
    [***Ochrolechia frigida***]
  2b Thallus ecorticate, C-, K+ yellow or deep yellow, P+ yellow or orange
    3a Thallus P+ deep yellow turning orange (thamnolic acid and atranorin); phyllocladia poorly developed and blending onto pseudopodetia; widespread, common in many open habitats
      ***Leprocaulon subalbicans***
    3b Thallus P+ pale yellow or P- (atranorin and rangiformic acid); phyllocladia and pseudopodetia well developed and differentiated (typically the thallus is so well developed that it would not be keyed here); uncommon
      [***Leprocaulon gracilescens***]

1b Thallus crustose

  4a Thallus P+ yellow, deep yellow, orange-red, or pale orange

    5a Thallus P+ yellow or P+ deep orange, K+ yellow, C-

      6a Thallus P+ yellow (alectorialic acid); thallus smooth, superficially appearing corticate but actually not

      ***Lepraria neglecta***

      6b Thallus P+ deep yellow turning deep orange (thamnolic acid + atranorin); thallus fuzzy, obviously ecorticate

      ***Leprocaulon subalbicans*** (see above)

    5b Thallus P+ pale orange, K-, C+ red (gyrophoric acid + unknown substance); thallus warty, grading to fine granules but not forming discrete soralia

    ***Ochrolechia inaequatula***

    [The P reaction of *O. inaequatula* is unlike the rich oranges from stictic, norstictic, and thamnolic acids; instead it is a dull, pale orange, but nevertheless a distinct reaction.]

  4b Thallus P+ pale yellowish or P-

    7a Thallus C+ red, KC+ red, K-

      8a Soredia not in discrete soralia but rather with a warty thallus grading into small granules; thallus P+ pale orange

      ***Ochrolechia inaequatula*** (see above)

      8b Soredia in discrete soralia or the soralia fusing into a continuous, finely sorediate crust; thallus P- (gyrophoric acid only)

      ***Ochrolechia androgyna***

    7b Thallus C-, KC- or KC+ yellow, K- or K+ yellow

      9a Thallus K+ yellow, containing atranorin

        10a Thallus margin indistinctly to distinctly lobed; thallus containing rangiformic acid plus traces of other fatty acids

        [***Lepraria borealis***]

        10b Thallus margin diffuse or obscurely lobed; thallus containing porphyrillic and fatty acids, usually roccellic acid); both powdery and granular forms are known; cortex lacking; very common in exposed alpine and subalpine sites; widespread

        ***Lepraria cacuminum***

      9b Thallus K-, atranorin lacking, forming large, corticate warts, never forming a powdery or finely granular thallus; widespread and common

      ***Ochrolechia upsaliensis***

      [Although not usually sterile, juvenile, sterile colonies of *Ochrolechia upsaliensis* are occasionally found; these are KC-, C- or C+ yellow]

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# LICHENS OF GRAND TETON NATIONAL PARK, WYOMING

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ABSTRACT: Two hundred twenty-one lichen species in 72 genera were identified from collections made in 1995 in Grand Teton National Park. Previous reports included four species not encountered in 1995. Nearly half the species (49%) were saxicolous, mostly on granitic substrates; 24% of the species were corticolous or lignicolous, 9% were terricolous, and the remainding species were on other substrates (decaying wood, plant debris, moss, litter, other lichens). Crustose species were 43% of the total number; 33% were foliose, 16% were fruticose, and 8% were squamulose. The lichen species and their distribution reflect the cold continental climate of the park, vegetation patterns, fire history, and perhaps human use of the valley part of the park.

Lichens are valuable indicators of air quality (Stolte, et al., 1993; Gries, 1996) and, since they grow slowly, of ecological stability and integrity (Hale, 1974, 1983; Ladyman & Muldavin, 1996; Wetmore & Bennett, 1996). An inventory of species present is considered mandatory for establishing baseline information for monitoring of atmospheric and terrestrial quality (Nash, et al. 1993). A few key areas of ecological interest in the northern Rocky Mountains near Grand Teton National Park have been investigated: Glacier National Park (Debolt & McCune 1993), the Swan Valley in northwestern Montana (McCune, 1982), Yellowstone National Park, (Eversman, 1990), alpine meadows of the Beartooth Plateau (Eversman, 1995), and the Anaconda-Pintler Wilderness Area, Montana (St. Clair & Newberry, 1993), The National Park Service has catalogs of known lichen species from 93 national park units, but had recorded only 18 species from Grand Teton National Park (Wetmore & Bennett, 1996).

The major objective of lichen study in Grand Teton National Park was to determine species present as a first step in identifying those that are sensitive to air pollution and other stresses. A secondary objective, not included in this paper, was the tissue analysis of species of *Bryoria, Usnea* and *Letharia* for element content.

Previously published collections of lichens in Grand Teton National Park include those of Imshaug (1957) who identified ten species from three sites 3000-3422 m on the east face of the Teton Range and Oswald (1966) who reported 13 species from glacial moraines on the valley floor. Mahaney (1975) measured lichen growth relative to glaciation at 3100 m; he observed that within 75-150 m of a glacier, on rock that had been free of ice for about 100 years, *Lecanora novomexicana* and *Lecidea atrobrunnea* reached maximum diameters of 8 mm. On rock free of ice for about 1000 years, the surfaces had 20-25% lichen cover; four species (*Aspicilia* sp., *Lecanora novomexicana, Lecidea atrobrunnea,* and *Rhizocarpon geographicum* ) formed thalli 132 mm, 126 mm, 143 mm, and 52 mm respectively. Spence (1981) listed ten lichen species (eight saxicolous, one terricolous, one muscicolous) near glaciers at 2865-3120 m; he observed that lichens were absent on moraines with slopes of 20-50°, and that *Stereocaulon alpinum* along with *Xanthoria elegans* on moss preceded growth of any saxicolous lichen. Sites snow-free about 100 years had mosses but no lichens.

**Park Description.** Grand Teton National Park is in northwest Wyoming joined to adjacent Yellowstone National Park to the north by the John D. Rockefeller Parkway; its western boundary, the top of the Teton Range, borders Idaho. The elevation rises sharply from 2030 m in Jackson Hole to over 4150 m on Grand Teton Peak. The east slopes of the Teton Range were designated a national park in 1929; it was enlarged in 1950 to include more of Jackson Hole in which are located former and currently operating dude and cattle ranches. The park extends about 55 km north to south, and 34 km east to west, with irregular boundaries. The climate is continental. Annual precipitation in the northern part of the valley (Jackson Lake Dam) is about 62 cm, mostly as snow; the southern part (Jackson, Wyoming) receives about 41 cm (NOAA, 1995). Average annual temperature is about 3°C. In some years, snow remains on the ground all summer at higher elevations.

Glacial features such as moraines, hanging valleys, cirques, alpine lakes, ice fields and small glaciers are conspicuous in the park. The steep east-facing slopes of the Teton Range are dissected by ice- and water-cut canyons. The core rock types are granite, gneiss and schist with overlying calcareous layers visible mostly on the west side of the Teton Range and at the northern and southern tips of the range. The northern part has volcanic rocks of the same nature as on the adjacent Yellowstone Plateau.

**Plant Communities.** The valley floor, a gravelly outwash plain, is dominated by sagebrush *(Artemisia tridentata* Nutt, *A. cana* Pursh) and grasses; some areas are highly disturbed by grazing by cattle, horses, elk, and bison. Blue spruce (*Picea pungens* Engelm.) is abundant with cottonwoods (*Populus balsamifera* L., *P. angustifolia* James) along the Snake River. The dominant species on moraines is lodgepole pine (*Pinus contorta* Dougl. *ex* Loud) (Oswald, 1966); successional species are subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and occasional Engelmann spruce (*Picea engelmannii* Parry *ex* Engelm.) on wetter sites and Douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco) on drier sites. Oswald (1966) observed that all stands on moraines were less than 200 years old; older individual Douglas fir trees had fire scars. None of his sites have burned since 1966, although fires have occurred in other locations. In adjacent Yellowstone National Park, the time between successive fires on a site is 150 to 400 years (DeSpain 1990); the assumption is made that the fire cycle is similar in Grand Teton National Park. On the mountain slopes, a rather straightforward elevational series of trees is Douglas fir, usually with lodgepole pine on the lower slopes, above which Engelmann spruce-subalpine fir forests extend to timberline, where whitebark pine (*Pinus albicaulis* Engelm.) is also present. Uppermost tree stands are usually krummholz islands. Peaks above timberline are generally steep and unstable; meadows with tall grasses and herbs are in more level sites. Aspen (*Populus tremuloides* Michx.) forms extensive stands on moraines and on the lower Teton Range slopes; conifers are in the understory of many aspen groves. The communities reflect a combination of climatic, edaphic, and biologic processes, and contain three major species, lodgepole pine, Douglas fir, and aspen, that are well adapted to fire (Whitlock, 1993).

**Methods**. From early July to October 1995, more than 2000 lichen specimens were collected from all substrates from 37 sites in Grand Teton National Park considered to represent all vegetation communities present, following guidelines by Smith, et al. (1993). Collections were made from sagebrush-grassland, lodgepole pine, Douglas fir, Engelmann spruce-subalpine fir, alpine, and riparian blue spruce-cottonwood communities. The highest peaks in the Tetons (Grand Teton, Mount Moran, Mount Teewinot) were not included in this study because their ascent requires technical climbing skills. For identification I used standard morphological and chemical techniques (Bird, unpublished keys; Brodo & Hawksworth, 1977; Culberson, 1972; Goffinet & Hastings, 1994; Goward, et al., 1994; Laundon, 1989,1992; McCune, unpublished key; McCune and Goward, 1995; Ryan & Nash, 1991, 1993; Thomson, 1967, 1979, 1984; Timdal, 1986; Wetmore, 1967, 1994, 1996.), and current nomenclature (Dorn, 1984; Esslinger & Egan, 1995).

**Collection Locations.** Areas from which lichens were collected July through September, 1995, are arranged in approximate order from north to south in the Teton Range, then north to south in Jackson Hole (Figure 1). Sites 1c, 7b, 8a, and 23 are calcareous; other sites are granitic (granites, schist, gneiss).
**Teton Range.** 2052- 4173m. **1a.** Wilcox Point, west side of Jackson Lake. 2060m. 43°59'N, 110°43'W. Moist spruce-fir. **1b**. Moose Creek. 2100m. 43°58'N, 110°44'W. Lodgepole pine and willow. **1c.** Webb Canyon, SE base of Owl Peak. 2200m. 43°58'N, 110°45'W. Calcareous rock. **2.** Waterfalls Canyon. 2000-2424m; 43°55'N, 110°44'W. Granitic rock, gneiss, schist. Aspen, spruce, Douglas fir. Fire in 1974 in part of canyon. **3a**. Paintbrush Canyon. 2425m; 43°48'N, 110°47'W. Granitic rock. Aspen, Engelmann spruce, Douglas fir. **3b.** Holly Lake. 2812 m. 43°48'N, 110°48'W. **3c.** Paintbrush Divide. 2880 m. 43°47'N, 110°49'W. Exposed granitic rock. **4a.** Cascade Creek Canyon, west side of Jenny Lake. 2056-2400 m. 43°45'N, 110°48W'. Granitic rock. Aspen, Douglas fir, spruce. **4b**. Below Schoolroom Glacier. 2600-3030 m. 43°44'N, 110°51'W. Exposed granitic rock outcrops and talus; lodgepole pine, spruce. **5a**. Lupine Meadows. 2061-2400m. 43°45N', 110°44'30". Lodgepole pine, Douglas fir. Granite boulders. **5b.** Surprise Lake. 2520 m. 43°44'N, 110°47'30". Exposed granitic rock. **5c**. Amphitheater Lake. 2545 m. 43°44'N, 110°48'W. Exposed granitic rock. **6a.** Phelps Lake trailhead. 2030-2212 m. 43°39'N, 110°48'W. Lodgepole pine, Douglas fir. **6b**. Phelps Lake, northwest end. 2090m. 43°39'N, 110°49'W. Quartz-rich granitic outcrop. **6c.** Phelps Lake, WSW side. 2060 m. 43°38'N, 110°49W'. Moist spruce stand at mouth of Open Canyon. **7a.** Granite Canyon mouth. 1940-2100 m. 43°37'N, 110°50'W. Aspen, Douglas fir; granitic boulders. **7b**. Top of Granite Canyon. 3000-3152 m. 43°37N', 110°51'W. Calcareous outcrops and soils. **8a**. Rendezvous Peak (top of tram, Teton National Forest), upper slopes. 3030 m. 43°36'N, 110°52'30"W. Alpine and krummholz subalpine fir and spruce. Calcareous dolomite outcrops and loose rock. **8b**. Lower slopes of Rendezvous Peak. 2800 m. 43°36'N, 110°53'W. Granitic rock. Douglas fir, lodgepole pine.
**Jackson Hole and Gros Ventre Range. 9.** Rockefeller Parkway/ Park Boundary, east of Steamboat Mountain. 2224-2318 m. 44°03'N, 110°41'W. From spruce and willow to Douglas fir, lodgepole pine. **10.** Moose Island, Jackson Lake. 2055 -2061 m. 43°56'N, 110°38W. Sandy soil, granitic rock. Lodgepole pine, Douglas fir, subalpine fir. **11**. Pilgrim Creek, floodplain and moraine SSE of Pilgrim Mountain. 2100-2121 m. 43°56'N,

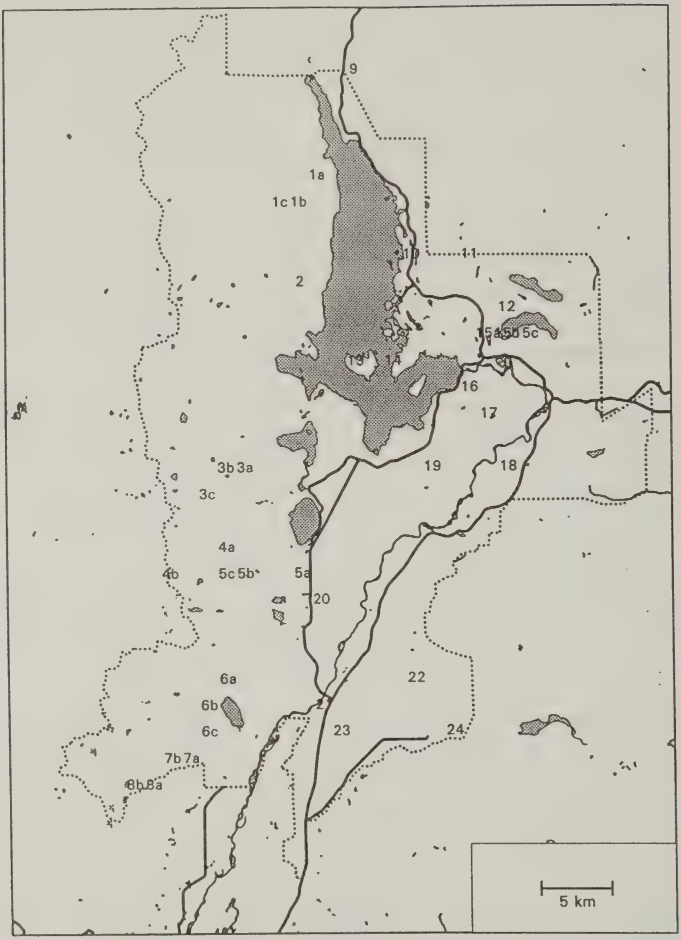

Figure 1. Grand Teton National Park and the collecting sites. Boundaries of the park are represented by the dotted line. The mottled areas are lakes, with Jackson Lake the largest. Sites 1a-8b are in the Teton Range. The heavy lines represent major roads. The Snake River runs east from Jackson Lake, then northeast to southwest through the valley floor.

110°35'W. Gravelly floodplain with cottonwoods. Lodgepole pine on moraine. **12.** Grand View Point. 2109-2218m; 43° 54'N, 110°33'30"W. Douglas fir with rhyolite cliffs. **13.** Elk Island, east half, Jackson Lake. 2048-2076m. 43°52'N, 110°41'W. Lodgepole pine, Douglas fir, young subalpine fir, grass. **14.** Hermitage Point, east shore of Jackson Lake. 2053-2060 m; 43°51-54'N; 110°37-38'W. Lodgepole pine, Idaho fescue, sagebrush. **15a.** Emma Matilda Lake, near Christian Pond. 2100 m. 43°52'30"N, 110°34'W. Lodgepole pine, sagebrush. **15b**. Douglas fir, spruce on south side of lake. 2061-2100 m. 43°53'N, 110°33'W. **15c**. Overlook, south side of lake. 2100m. 43°52'30"N, 110°33W. Granitic outcrop. **16.** Signal Mountain, south and east slopes. 2302-2348 m. 43°51'N, 110°35W. Granitic. Douglas fir, aspen; sagebrush on lower slopes. **17.** Cow Lake - Cattlemen's Bridge area. 2050 m. 43°50-51'N, 100°34'W. Rhyolite cliff. Lodgepole pine, subalpine fir; big sagebrush. **18.** Snake River, west side. 2030m. 43°48'N, 110°33'W. Sandy soil; used by elk and bison. Spruce, cottonwood. **19.** Potholes. 2070 m; 43°48'N, 110°47'W. Loose gravelly disturbed soil. Sagebrush-grassland; invading lodgepole pine. **20.** Timbered Island, moraine. 2050m. 43°43'N, 110°43'W. Lodgepole pine, Douglas fir, spruce. **21**. Snake River Bend. 1955 m. 43°39'N, 110°43'W. Sandy soil. Blue spruce, cottonwood. **22.** Ditch Creek. 2040m; 43°40'N, 110°38'W. Gravelly alluvial soil. Sagebrush-grassland. **23**. Blacktail Butte. 2300 m; 43°38'N, 110°42'W. Calcareous. Douglas fir, aspen. **24.** Kelly Warm Springs, Kelly Peak. 2024-2109m; 43°38'N, 110°36'W. Willow, sagebrush-grassland to aspen, subalpine fir, lodgepole pine.

## Results and Discussion

Two hundred sixteen species were identified from over 2000 collected specimens. Ninety-six species (43%)., were crustose; 72 species (33%) were foliose, 35 (16%) were fruticose, and 17 (8%) were squamulose. One "pin lichen" (*Chaenotheca furfuracea)* was collected. Nearly half of the species (108) were from rock substrates, mostly granitic; 44 species (19%) were corticolous, 20 (9%) were terricolous; 8 (4%) were lignicolous, and the remaining 41 species (19%) were on decaying wood, plant debris, litter and other lichens. *Catillaria chalybeia, Chaenotheca furfuracea, Peltigera ponojensis, P. retifoveata,* and *Solorina bispora* had not been previously identified from this immediate area

**Rock Communities**. Several species grew on granitic rock surfaces throughout the park: the most common and abundant of these were *Aspicilia caesiocinerea, Bellemerea cinereorufescens, Caloplaca fraudans, C. holocarpa* and *Candelariella aurella* that were also on bark, *Rhizocarpon geographicum, R. riparium, Xanthoria fallax,* and *X. sorediata*. The occurrence of *Pseudephebe pubescens* and species of *Umbilicaria* was less than expected on the granitic boulders and outcrops in comparison to similar substrates on the Beartooth Plateau and Yellowstone Park. The highest windswept ridges visited were calcareous, which is perhaps one explanation. It might also be a function of not sampling some of the highest granitic peaks, or of deep-lying snow that bury the boulders and soil most of the year; the growing season may not be long enough to allow lichen establishment of foliose species (Benedict, 1991; Walker, et al., 1993). Expected *Brodoa oroarctica* and *Pseudephebe pubescens,* reported previously from Grand Teton National Park (Imshaug, 1957), were not collected.

At the top of Rendezvous Peak and Granite Canyon, calcareous sites, and near Schoolroom Glacier, the rock is in smaller pieces and does not appear stable. Lichen cover was relatively sparse, perhaps reflecting the instability, or perhaps indicating conditions either too dry or too snow-covered for much lichen growth. The major species on calcareous rock above 3000 m were *Xanthoria elegans* and *Staurothele drummondii; Collema fuscovirens* and *C. polycarpon* occurred only on calcareous rock in relatively moist sites.

**Soil Communities.** The major lichens observed on the soil in Jackson Hole, the valley floor, were *Cladonia cervicornis, Peltigera malacea* and *P. rufescens*. Expected well-developed soil crust communities with several species of *Psora, Collema, Catapyrenium,* and perhaps *Buellia elegans*, similar to those in Montana (Eversman & Schanz 1997), Idaho (Kaltenecker & Wicklow-Howard, 1994) and Utah (Anderson & Rushforth 1976) were not found. This is perhaps due to one or more of these factors: inadequate sampling, very porous gravelly soils (Oswald, 1966) that do not hold adequate moisture, or historically heavy use by grazing animals (bison, elk, cattle and horses).

Alpine species of *Cetraria, Vulpicida, Thamnolia,* and *Dactylina* identified from sites in Yellowstone National Park (Eversman, 1990), the Beartooth Plateau (Eversman 1996), Glacier National Park (Debolt & McCune 1993) and Colorado and New Mexico (Egan 1971) likewise were not found in the alpine sites visited. The upper slopes of the Teton Range are steep and jagged, with very little development of broad meadow surfaces such as those in Yellowstone Park and the Beartooth Plateau. Instability of rock and soil on the steep slopes apparently does not allow for an adequate soil surface for development of fruticose lichen communities. Where more level surfaces do occur in the Teton Range, they tend to be wet alpine meadows with dense grass-sedge communities that probably out-compete lichens. The species found only on calcareous alpine soils were *Collema tenax, Solorina bispora,* and *Toninia sedifolia*. Imshaug (1957) reported *Cladonia coccifera* from an alpine granitic site.

**Wood and Bark Communities.** All of the species on wood and bark are characteristic of boreal forests in this region. The arboreal lichens show characteristics in common with distribution in Yellowstone National Park (Eversman, 1990): few fruticose species and the same curious paucity of species of the genus *Hypogymnia* found abundantly in conifer forests in Montana north of Yellowstone Park. Only five species of *Hypogymnia* from five sites were collected, and they are not hearty specimens. They were all from moist Douglas fir or spruce sites, suggesting that low relative humidity in most forest communities of Grand Teton National Park inhibits growth of *Hypogymnia* and fruticose species. Lichens grow mostly on tree bases and branches rather than on the trunks. Subalpine fir with its smooth bark tends to have more lichen growth than Douglas fir, spruce, or lodgepole pine.

In addition to the 42 species collected from bark in 1995, Oswald (1966) also reported *Candelaria concolor* and *Usnea glabrata* from conifer bark on comparatively low-elevation moraines.

**Lichens reported from Grand Teton National Park.** Nomenclature follows Esslinger and Egan (1995); substrates and site locations are included. Sites 1c, 7b, 8a and 23 are calcareous; all the others are granitic.

*Acarospora fuscata*. Rock. 4b, 6b, 12, 16
*A. glaucocarpa*. Rock. 1b, 6a, 8a, 23
*A. heppii*. Calcareous rock. 1c
*A. smaragdula*. Rock. 2, 7b, 8a, 16, 17, 19

*Amandinea (Buellia) punctata.* Bark ,wood. 5b, 8a, 13, 15b, 18
*Arthonia glebosa.* Soil. 3a
*Aspicilia calcarea.* Rock. 1c, 19
*A. candida.* Rock. 7a, 8a, 15a, 16
*A. caesiocinerea.* Rock. 1c, 2, 3a, 3b, 3c, 4a, 4b, 6a, 6b, 7a, 7c, 8a, 8b, 13, 16, 17, 19, 20, 22
*A. cinerea.* Rock. 2, 5b, 6b, 6c, 7a, 8b, 9, 11, 16, 19, 20, 24
*A. supertegens.* Rock. 6a
*Bellemerea alpina.* Rock. 5b, 6a, 7a, 8a.
*Bellemerea cinereorufescens.* Rock. 1c, 2, 3a, 4a, 6a, 6b, 7a, 9, 14, 16, 20
*Brodoa oroarctica* (Imshaug, 1957)
*Bryoria fremontii.* Conifer bark. 1a, 2, 5a, 7a, 7b, 9, 10, 11, 13, 14, 15a, 15b, 23
*B. fuscescens.* Conifer bark. 1a, 1c, 2, 5b, 6a, 6b, 6c, 7a, 7b, 10, 11, 13, 14, 15a, 15b, 16, 18, 20, 22
*B.. glabra.* Conifer bark. 7a
*B. lanestris.* Conifer bark. 1c, 10, 12, 13
*Buellia erubescens.* Wood. 6c, 6b, 7a, 11, 12, 15a, 15b, 18, 23
*Caloplaca atroalba.* Rock. 15a, 23
*C. citrina.* Bark, rock. 1a, 7a, 13
*C. epithallina.* Crustose lichens. 4a, 6a, 6c, 7a
*C. flavovirescens.* Rock. 4b, 6b, 15c
*C. fraudans.* Rock. 1c, 2, 6a, 6b, 8a, 11, 12,13,14, 16, 19, 22
*C. holocarpa.* Rock, bark. 4a, 6a, 8a, 10, 12, 13, 15b, 15c, 19, 22, 23
*C. jungermanniae.* Rock. 8b, 12, 13, 15a, 15c
*C. pinicola.* Wood. 7b
*C. saxicola.* Rock. 8a, 15b, 16, 24
*C. sideritis.* Rock. 2, 6a
*C. tiroliensis.* Plant debris. 9, 15c
*C. vitellinula.* Rock. 6a, 7a, 7b, 12
*Candelaria concolor* (Oswald, 1966)
*Candelariella aurella.* Rock, bark. 1b, 1c, 5b, 6a, 7a, 7b, 7c, 8a, 11, 12, 13, 20
*C. canadensis.* Moss on soil. 2
*C. vitellina.* Bark, on *Aspicilia*. 6a, 6b, 7a, 7b, 12, 13, 15b, 20
*C. xanthostigma.* Litter, moss. 6a, 7b, 12, 15b, 23
*Catapyrenium cinereum.* Soil. 7b, 8a, 15a
*C. norvegicum.* Rock. 8a
*C. squamulosum.* Rock. 6a, 7b, 8a
*Catillaria chalybeia.* Rock. 14
*Chaenotheca furfuracea.* "Pin lichen", mossy wood. 4a
*Chrysothrix chlorina.* Mossy soil and rock. 2, 6a, 7a, 11, 16, 18, 23
*Cladonia cariosa.* Soil, litter. 5c, 6a, 7a, 9, 10, 13, 14, 15a, 24b
*C. carneola.* Fruticose, wood. 5a, 10, 13, 14, 16, 18
*C. cenotea.* Decaying logs, litter on soil. 2, 9, 14, 20
*C. cervicornis* subsp. *cervicornis.* Soil, litter. 1a, 1c, 4a, 9, 10, 11, 13, 14
*C. cervicornis* subsp. *verticillata.* Soil, litter. 5a, 10, 13, 15a, 18
*C. chlorophaea.* Soil, litter. 1a, 1c, 2, 3a, 4a, 5a, 6a, 6b, 7a, 9, 11, 13, 15c, 18, 19, 20
*C. coccifera.* (Imshaug, 1957)
*C. coniocraea.* Mossy, decaying wood. 1a, 2, 3a, 6a, 9, 11, 12, 13, 15b, 15c, 18, 19

*C. decorticata*. Soil. 1a, 6c, 14
*C. deformis*. Decaying logs, litter on soil. 2, 5b, 15b
*C. ecmocyna* subsp. *ecmocyna*. Soil. 13
*C. fimbriata*. Decaying logs, litter. 1a, 2, 3b, 4a, 5a, 5b, 6a, 6b, 7a, 7b, 9, 10, 11, 13, 14, 15a, 15b, 15c, 16, 17, 18, 19, 20, 22, 23
*C. gracilis*. Litter on soil. 15a.
*C. norvegicum*. Mossy soil. 4a, 10
*C. ochrochlora*. Decaying logs, litter. 1a, 5
*C. pocillum*. Mossy soil, litter. 1b, 3, 5c, 7b, 7c, 9, 13, 15c, 22, 23
*C. pyxidata*. Soil, litter. 2, 3, 4a, 4b, 5b, 6a, 7a, 7b, 10, 13, 15a, 15c, 18, 20, 24
*C. rei*. Soil, litter. 1a, 2, 5b, 7b, 9, 10, 15c, 20
*C. subulata*. Litter on soil. 2, 5a, 9
*C. sulphurina*. Decaying logs. 2, 5a, 6a, 6c, 7a, 9, 10, 11, 12, 13, 14, 18, 19, 20 24
*C. transcendens*. Decaying logs, litter. 2, 5a
*C. verruculosa*. Soil. 2, 19
*Coelocaulon aculeatum*. Soil. 3, 4b
*Collema fuscovirens*. Rock, soil. 1c, 6b
*C. polycarpon*. Calcareous rock. 1c, 23
*C. tenax*. Soil. 7b
*Cyphelium tigillare*. Wood. 3c, 5b
*Dermatocarpon luridum*. Rock. 4a, 7a
*D. miniatum*. Rock. 2, 4b, 6b, 7a, 12, 15c, 16
*D. moulinsii*. Rock. 4a, 4b, 6b, 7a
*D. reticulatum*. Rock. 2, 3b, 4a, 6a, 6b, 6c, 7a, 8a, 16
*D. rivulorum*. Rock. 4b, 15c
*Dimelaena oreina*. Rock. 6a, 6c
*Diploschistes muscorum*. Moss. 4b
*D. scruposus*. Rock. 4a
*Endocarpon pulvinatum*. Rock. 1c, 7b
*Farnoldia (Lecidea) jurana*. Rock. 3b
*Fuscopannaria leucophaea*. Moss. 6c
*F. praetermissa*. Moss. 6b
*Hypocoenomyce scalaris*. Wood. 13
*Hypogymnia austerodes*. Bark. 1a, 6c
*H. farinacea*. Conifer bark. 6a
*H. imshaugii*. Conifer bark. 6a
*H. physodes*. Conifer bark. 7b
*H. tubulosa*. Conifer bark. 18
*Lecania nylanderiana*. Calcareous rock. 1c
*Lecanora albescens*. Rock. 20
*L. allophana*. Bark. 1a, 6a, 7b, 13
*L. argopholis*. Rock. 3a, 3c, 4a, 6a, 6b, 12, 15a
*L. cenisia*. Rock. 5a, 6b, 7a, 11, 15c
*L. crenulata*. Rock. 1b, 7a
*L. dispersa*. Rock. 12
*L. epibryon*. Plant debris. 23
*L. garovaglii*. Rock. 4b, 6a, 6b, 6c, 11, 12, 16, 24
*L. hagenii*. Bark. 1a, 6a, 7a, 10, 12, 13, 15a, 16, 24

*L. marginata.* Rock. 2, 7a, 8a, 9, 19, 23
*L. muralis.* Rock. 6a, 6b, 7a, 15c, 14, 16
*L. nigromarginata.* Rock. 16, 17
*L. novomexicana.* Rock. 4a, 4b, 6a, 6b, 7a, 8, 12, 20
*L. polytropa.* Rock. 1b, 2, 3a, 3c, 4a, 5b, 6a, 6b, 9, 12
*L. pulicaris.* Bark. 5b, 6c, 7a
*L. rugosella.* Bark. 16
*L. rupicola.* Rock. 2, 3a, 7a, 12, 16
*L. subrugosa.* Bark. 7a, 7b, 11
*L. varia.* Bark. 3b, 6a, 6b, 7a, 7b, 8a, 15a, 20
*Lecidea atrobrunnea.* Rock. 2, 3a, 3b, 3c, 4a, 4b, 6a, 6b, 7a, 7b, 9, 12, 20, 22
*L. auriculata.* Rock. 3a, 3b, 7b, 19
*L. elabens.* Wood. *1a,* 7a, 7b, 12
*L. plana.* Rock. 2, 6a
*Lecidella euphorea.* Wood, bark. 1a, 2, 5c, 6a, 6b, 6c, 7a, 7b, 8a, 12, 13, 18, 24
*L. stigmatea.* Crustose, rock. 6a, 8a, 14, 19
*Lempholemma polyanthes.* Rock. 6b
*Lepraria cacuminum.* Mossy rock, soil. 3a, 3b, 3c, 4a, 5c, 6a, 6b, 7b, 11, 15a, 15c
*Leptogium cyanescens.* Rock. 1c, 6b
*L. saturninum.* Rock. 1c, 4b, 6a, 6b, 6c, 7a, 7b
*Letharia columbiana.* Conifer bark. 4a, 9, 11, 13
*L. vulpina.* Conifer bark. 1a, 1b, 1c, 2, 3a, 4a, 5a, 5b, 6b, 6c, 7a, 7b, 9, 10, 11, 12, 13, 14, 15b, 15c, 16, 18, 20, 23
*Lobothallia alphoplaca.* Rock. 6a, 6b, 7a, 15a
*Melanelia disjuncta.* Rock. 6a
*M. elegantula.* Bark. 3c, 7a, 7b, 8a, 11, 12, 13, 15a, 18, 21, 23, 24
*M. exasperatula.* Bark. 1a, 3, 5b, 6a, 6b, 7a, 7b, 8b, 11, 12, 13, 15a, 15b, 16, 18, 20, 23
*M. infumata.* Rock. 7a, 8b, 12, 16, 23
*M. sorediata.* Rock. 6a, 6b, 6c
*M. stygia.* Rock. 3c, 7a, 4b, 16
*M. subelegantula.* Bark. 5a, 6a, 6b, 7a, 12
*M. subolivacea.* Bark. 6a, 6b, 7a, 7b, 13, 15b, 16, 23
*Nephroma parile.* Mossy soil, litter. 3c, 5b, 5c, 6c, 6b, 7a
*Pannaria pezizoides.* Soil. 4a
*Parmelia sulcata.* Bark. 4a, 6a, 7a, 15b
*Parmeliopsis ambigua.* Conifer bark at base of trees. 1a, 1c, 3b, 4a, 5a, 6c, 7a, 7b, 11, 12, 13, 14, 15a, 15b, 15c, 16, 17, 18, 19, 20, 23
*P. hyperopta.* Wood. 1a, 15a
*Peltigera aphthosa.* Moist soil, litter. 1a, 4a, 5a, 5b
*P. canina.* Soil, litter. 2, 4a, 5a, 7b, 9, 15a, 16, 20, 23
*P. didactyla.* Soil, moss. 2, 5a, 5b, 6a, 9, 13, 20, 24
*P. kristinsonii.* Soil, moss. 2, 7a
*P. malacea.* Soil, moss. 1a, 5b, 6b, 7a, 10, 13, 14, 19, 23
*P. membranacea.* Soil, litter. 1a, 1c, 15b
*P. neckeri.* Soil, litter. 14
*P. polydactylon.* Soil, litter. 1a, 1c
*P. ponojensis.* Soil, litter. 9, 20
*P. praetextata.* Soil, litter. 6b, 20

*P. retifoveata*. Soil, litter. 1a, 13, 15, 17, 19, 21
*P. rufescens*. Soil, litter. 1a, 1b, 1c, 2, 3a, 3c, 4a, 5c, 6b, 7a, 7b, 8a, 9, 10, 11, 12, 13, 15a, 17, 18, 19, 20, 21, 22, 23, 24
*P. venosa*. Soil, litter. 3a, 4a, 5a, 6a
*Phaeophyscia decolor*. Rock, mossy rock. 4a, 5a, 6a, 6b, 6c, 7a, 8b
*P. nigricans*. Rock. 6c
*P. sciastra*. Mossy rock. 5a, 6a, 16, 23
*Physcia adscendens*. Bark. 6a, 6b, 6c, 7a, 7b, 10, 15a, 15b, 17, 24
*P. aipolia*. Bark. 6b, 6c
*P. biziana*. Rock. 6a, 6b, 23
*P. caesia*. Rock. 2, 4a, 6a, 6b, 6c, 16
*P. callosa*. Rock. 4a
*P. dimidiata*. Mossy rock. 16, 23
*P. dubia*. Bark, mossy rock. 5b, 6a, 6b, 7a, 8b, 12, 113, 14, 5a, 15b, 15c, 16, 23
*P. phaea*. Mossy rock. 3, 4a, 6a, 6b, 6c, 16
*P. stellaris*. Bark. 6b
*Physconia muscigena*. Mossy rock. 6b, 7c, 23
*Placynthiella uliginosa*. Mossy rock. 14
*Pleopsidium (Acarospora) chlorophanum*. Rock. 5b, 7a, 8a, 16
*Polychidium muscicola*. Moss on rock. 7a
*Polysporina (Sarcogyne) simplex*. Rock. 4b
*Porpidia crustulata*. Rock. 3a, 5a, 9
*P. macrocarpa*. Rock. 5b, 7b, 12, 22
*Protoblastenia rupestris*. Calcareous rock. 1c
*Protoparmelia badia*. Rock. 19, 24
*Pseudephebe minuscula*. (Imshaug, 1966)
*P. pubescens*. Rock. 6a
*Psora decipiens*. Soil. 4b, 7b, 22
*P. globifera*. Rock. 2, 6a, 14, 15c, 16, 17
*P. himalayana*. Rock. 4a, 15c, 16
*P. montana*. Rock. 7a, 8a, 15a
*P. nipponica*. Rock crevices. 16
*P. tuckermanii*. Rock, soil. 7a, 21, 23
*Psoroma hypnorum*. Mossy soil 3a, 3c, 9, 16
*Pyrrhospora (Lecidea) elabens*. Wood. 1a, 3, 7b, 11, 18
*Rhizocarpon disporum*. Rock. 3a, 4a, 4b, 5a, 6a, 6b, 7a, 16
*R. geminatum*. Rock. 3b, 5b, 6a, 6b, 6c, 16
*R. geographicum*. Rock. 2, 3c, 4a, 4b, 6a, 6c, 7a, 8b, 13, 15c, 20
*R. grande*. Rock. 6c
*R. riparium*. Rock. 1 c, 2, 3a, 3b, 4b, 5b, 6a, 6b, 9, 12, 15c, 16
*Rhizoplaca chrysoleuca*. Rock. 4a, 5a, 6a, 6b, 6c, 7a, 16
*R. melanophthalma*. Rock. 4b, 6a, 6b, 6c, 8b, 12, 15b, 16, 19
*Rimularia insularis*. On *Lecanora rupicola*. 2, 3a, 7a, 12, 16
*Rinodina annulata*. Bark. 23
*R. archaea*. Wood, bark of deciduous trees. 6a, 7b, 15a
*R. bischoffii*. Rock. 7b, 9
*R. calcigena*. Usually calcareous rock. 1c, 7a, 8a
*R. exigua*. Bark of alder. 6a, 19

*R. milvina*. Rock. 2
*R. pyrina*. Bark. 1a, 1b, 15a, 20
*Solorina bispora*. Alpine calcareous soil. 8a
*S. crocea*. Soil. 5b
*Sporastatia testudinea*. Rock. 3c
*Staurothele drummondii*. Rock. 1c, 2, 6b, 7b, 8a, 12, 16, 23
*S. fissa*. Rock. 2, 4a, 5b, 7b, 8a, 23
*Stereocaulon alpinum*. Soil. 2
*Toninia sedifolia*. Alpine calcareous soil. 8a
*Trapeliopsis granulosa*. Wood, organic soil. 3c, 6a, 15a, 15b
*Tuckermannopsis chlorophylla*. Conifer branch. 6a
*U. hyperborea*. Rock. 3c, 4a, 4b, 5c, 6a, 6b, 7a
*U. kraschenninikovii*. Rock. 6b, 8b, 11, 16
*U. torrefacta*. Rock. 6a
*U. vellea*. Rock. 4a, 5b
*U. virginis*. Rock. 3, 4b, 8b
*Usnea lapponica*. Bark. 1a, 1c, 2, 5, 6a, 6c, 7a, 7b, 10, 12, 13, 15a, 16, 22
*U. substerilis*. Bark. 1c, 2, 4a, 5a, 6b, 7a, 7b, 8a, 11, 13, 14, 15a, 15b, 15c, 18, 20, 21, 23
*Verrucaria caerulea*. Rock. 5b
*Verrucaria compacta*. Rock. 16
*V. fuscella*. Rock. 1c, 6b, 8a, 16
*V. nigrescens*. Rock. 1c
*V. glaucovirens*. Rock. 1b, 6a, 6b, 6c, 8a, 24
*Vulpicida pinastri*. Base of conifer trees. 4a, 6a, 6b, 18
*Xanthoparmelia coloradoensis*. Rocky soil. 15a
*Xanthoparmelia cumberlandia*. Rock. 3, 4b, 6a, 6b, 16
*X. lineola*. Rock. 4b, 6a, 6b, 6c, 7a
*X. plittii*. Rock. 6b,16
*X. subdecipiens*. Rock. 2, 6a, 6c, 7a, 11
*X. wyomingica*. Soil. 4b
*Xanthoria elegans*. Foliose, rock. 2, 4b, 5b, 6a, 6b, 7b, 8a, 8b, 12, 16, 23
*X. fallax*. Bark, moist rock. 6b, 6c, 7a, 7b, 7c, 10, 11, 13, 15a, 15b, 15c, 16, 18,21, 22, 23, 24
*X. polycarpa*. Bark. 1a, 6a, 7b, 10, 13, 15a, 15b, 23, 24
*X. sorediata*. Rock. 2, 4a, 4b, 5b, 6a, 6b, 6c, 7a, 8a, 15a, 19

The cold dry continental climate, the steep slopes of the peaks and the fire history of Grand Teton National Park affect the vegetation patterns, including lichens. It was expected that fewer species of lichens would grow in this park compared with areas with Pacific influence (DeBolt & McCune, 1993; McCune 1982); however, Grand Teton National Park, as well as Yellowstone National Park immediately north, remain undercollected. Further excursions into the alpine would add significantly to the knowledge of the lichen flora of this region.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
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# THE LICHEN FLORA OF STONY PASS, AN ALPINE TUNDRA SITE IN SOUTHWESTERN COLORADO

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## ABSTRACT

Sixty-eight species in 41 genera are reported for Stony Pass, a high elevation alpine tundra site in the San Juan Mountains of southwestern Colorado. *Candelariella reflexa*, *Collema ceraniscum*, and *Dermatocarpon lorenzianum* are reported as new species records for the state of Colorado. The lichen flora at Stony Pass is dominated by species from the Arctic floristic element. The overall percentage of Arctic Element species at Stony Pass (78%) is most similar to the alpine lichen floras at Lake Peak (84%) and Sierra Blanca Peak (76%) in north-central and south central New Mexico respectively. However, Stony Pass shares more total species in common with Mt. Audubon in north central Colorado (40/68). This pattern suggests that the contribution of the Temperate Element to alpine tundra sites differs significantly from site to site; while the Arctic Element, in general, tends to be more homogenous from site to site.

Keywords: lichens, alpine tundra, San Juan Mountains, Colorado

## INTRODUCTION

**Previous work-** In the past, the lichens of southwestern Colorado have not been extensively researched. However, in recent years lichenological work in the region has been conducted in connection with the establishment of a lichen air quality biomonitoring program and baseline in the San Juan-Rio Grande National Forest (St. Clair et al. 1996). Other areas of Colorado, including several sites along the Front Range, have been studied. Early reports on Colorado lichens include, Willey (1874), J. Müller (1895), and Fink (1935). Weber and Shushan (1955) described several important components of Colorado alpine tundra lichen communities including several species in the following genera, *Cetraria, Cornicularia, Dactylina*, and *Thamnolia*. In 1957 Imshaug collected alpine macrolichens throughout western North America, reporting forty-nine species for Colorado. In the mid 1960s, Weber (1965) published a review of the Colorado representatives of the lichen family Pannariaceae; while Anderson (1964) completed an extensive inventory of the lichen genus *Lecidea* in Rocky Mountain National Park. In 1969 Egan described the lichen flora of Mount Audubon, a prominent Front Range Peak in the Colorado Rockies; and in 1971 he studied three additional alpine tundra sites in New Mexico: La Cal Basin, Lake Peak, and Sierra Blanca Peak. In 1973 Gough examined distribution patterns of corticolous cryptogams (lichens and bryophytes) on selected conifer substrates at several locations in St. Vrain Creek Valley in the Front Range; and in 1978 Flock examined the effects of snow cover and soil moisture on the distribution of lichens and bryophytes on an alpine tundra ridge in the Indian Peaks area of the Colorado Rockies. With data collected from the same general area Komárková (1979) published an extensive phytosociological survey which included some information about lichen community structure. In 1980, Fields studied distribution patterns of lichens found on the sub alpine forest floor in Rocky Mountain National Park; and Peard (1983) examined the distribution of non-crustose lichens on the trunks of Rocky Mountain Juniper in Boulder County, Colorado. In 1969 Shushan and Anderson published the first catalog of Colorado lichens, this list included 521 taxa in 88 genera; this list was updated in 1992 by Weber and Wittmann. In spite of all the lichenological research in the state of Colorado, very little work has been done in the southwestern quadrant of the state. This study provides the first detailed information about alpine tundra lichens in southwestern Colorado.

**Study site-** Stony Pass is a high mountain Pass in the San Juan Mountains of southwestern Colorado (Figure 1). Between 1875 and 1882 Stony Pass was the only major supply route into the mining community of Silverton. The pass was replaced as a supply route in 1882 when the Denver-Rio Grande Railroad from Durango was completed. The pass is located in San Juan County, in the San Juan-Rio Grande National Forest. Elevation at the pass is approximately 3840 m. The pass is above timberline and has a typical alpine tundra type vascular plant community, including *Acomastylis rossii, Bistorta bistortoides, Castilleja occidentalis, Phacelia sericea, Potentilla pulcherrima, Rydbergia grandiflora, Salix arctica, Salix reticulata, Selaginella densa, and Trifolium attenuatum.* Stony Pass consists of a complex of shallow, well drained soils (cobbly loam) with rocky outcrops on mountain slopes and ridges. Rock formations in the area are volcanic dominated by rhyolite and tuff. Average annual precipitation is 85-115 cm; average annual air temperature is -3 to 1° C; and the average frost-free period is less than 40 days.

## MATERIALS AND METHODS

**Collection, identification, and deposition of specimens-** An area of approximately 25 hectares in and around the pass proper was systematically searched for lichens. Specimens were collected from soil, rock, moss, and detritus.

Specimens were identified using standard lichen keys, taxonomic treatises and by making comparisons with herbarium material. Standard chemical spot tests, and where necessary, thin-layered chromatography techniques were used to finalize species identifications. All specimens are deposited in the Herbarium of Nonvascular Cryptogams at Brigham Young University (BRY) in Provo, Utah.

**Organization of species list-** Each species is followed by relative abundance and substrate information, as well as collection and herbarium numbers (Larry St. Clair's collection numbers were used for this paper). Our scale of relative abundance is rare < common < abundant. Assignment of relative abundance categories is based on the following criteria: rare = 1-2 encounters, common = 3-9 encounters, and abundant >10

Fig. 1. Map showing location of Stony Pass in southwestern Colorado.

10 encounters. Only one collection is cited for each species. Nomenclature follows Esslinger and Egan (1995).

## RESULTS

Sixty-eight lichen species in 41 genera are reported for Stony Pass, San Juan County, Colorado. *Candelariella reflexa*, *Collema ceraniscum*, and *Dermatocarpon lorenzianum* are reported as new state records for Colorado. Following is an alphabetical list of all lichen species collected at Stony Pass.

ACAROSPORA AMERICANA. Common on volcanic rock. BRY C-31658 (St. Clair 7773).
ASPICILIA CAESIOCINEREA. Common on volcanic rock. BRY C-31647 (St. Clair 7762).
ASPICILIA DESERTORUM. Common on volcanic rock. BRY C-31635 (St. Clair 7750).
BRODOA OROARCTICA. Common on volcanic rock. BRY C-31625 (St. Clair 7740).
CALOPLACA AMMIOSPILA. Rare on moss over soil. BRY C-31664 (St. Clair 7779).
CALOPLACA CINNABARINA. Common on volcanic rock. BRY C-31642 (St. Clair 7757).
CALOPLACA EPITHALLINA. Common, as an epiphyte on saxicolous lichens. BRY C-31653 (St. Clair 7768).
CALOPLACA MODESTA. Rare on volcanic rock. BRY C-31610b (St. Clair 7725b).
CANDELARIELLA AURELLA. Rare on detritus. BRY C-31626 (St. Clair 7741).
CANDELARIELLA REFLEXA. Rare on moss over soil. BRY C-31619 (St. Clair 7734).
CANDELARIELLA XANTHOSTIGMA. Rare on moss over soil. BRY C-31663 (St. Clair 7778).
CATAPYRENIUM CINEREUM. Common on soil. BRY C-31609 (St. Clair 7724).
CETRARIA ACULEATA. Abundant on soil. BRY C-31597 (St. Clair 7712).
CETRARIA ERICETORUM. Abundant on soil. BRY C-31587a (St. Clair 7702a).
CETRARIA ISLANDICA. Common on soil. BRY C-31587b (St. Clair 7702b).
CLADONIA POCILLUM. Common on soil. BRY C-31655 (St. Clair 7770).
CLADONIA PYXIDATA. Rare on moss over soil. BRY C-31615 (St. Clair 7730).
COLLEMA CERANISCUM. Rare on soil. BRY C-31604 (St. Clair 7719).
COLLEMA CRISTATUM. Rare on soil. BRY C-31646 (St. Clair 7761).
DACTYLINA MADREPORIFORMIS. Abundant on soil. BRY C-31586 (St. Clair 7701).
DERMATOCARPON LORENZIANUM. Rare on volcanic rock. BRY C-31617 (St. Clair 7732).
DERMATOCARPON MINIATUM. Common on volcanic rock. BRY C-31624 (St. Clair 7739).
DERMATOCARPON RETICULATUM. Common on volcanic rock. BRY C-31603 (St. Clair 7718).
DIPLOSCHISTES MUSCORUM. Abundant on soil. BRY C-31593 (St. Clair 7708).
FLAVOCETRARIA NIVALIS. Abundant on soil. BRY C-31588 (St. Clair 7703).
LECANORA ARGOPHOLIS. Common on volcanic rock. BRY C-31607 (St. Clair 7722).
LECANORA HAGENI. Common on detritus. BRY C-31595 (St. Clair 7710).
LECANORA PHAEDROPHTHALMA. Common on volcanic rock. BRY C-31628 (St. Clair 7743).
LECANORA POLYTROPA. Abundant on volcanic rock. BRY C-31639 (St. Clair 7754).
LECANORA RUPICOLA. Abundant on volcanic rock. BRY C-31611 (St. Clair 7726).
LECANORA NOVOMEXICANA. Abundant on volcanic rock. BRY C-31640 (St. Clair 7755).
LECIDEA ATROBRUNNEA. Abundant on volcanic rock. BRY C-31606 (St. Clair 7721).
LECIDEA LEUCOTHALLINA. Rare on volcanic rock. BRY C-31618 (St. Clair 7733).
LECIDEA RUFOFUSCA. Rare on detritus. BRY C-31634 (St. Clair 7749).
LECIDEA TESSELLATA. Common on volcanic rock. BRY C-31623 (St. Clair 7738).
LECIDELLA STIGMATEA. Common on volcanic rock. BRY C-31613 (St. Clair 7728).
LECIDOMA DEMISSUM. Rare on soil. BRY C-31666 (St. Clair 7781).
LOBOTHALLIA ALPHOPLACA. Common on volcanic rock. BRY C-31648 (St. Clair 7763).
MEGASPORA VERRUCOSA. Rare on detritus. BRY C-31645 (St. Clair 7760).

OCHROLECHIA UPSALIENSIS. Abundant on soil. BRY C-31594 (St. Clair 7709).
PELTIGERA NECKERI. Rare on moss. BRY C-31662 (St. Clair 7777).
PELTIGERA PRAETEXTATA. Common on moss over soil. BRY C-31667 (St. Clair 7782).
PHAEOPHYSCIA NIGRICANS. Rare on moss/detritus over soil. BRY C-31656 (St. Clair 7771).
PHAEORRHIZA NIMBOSA. Common on soil. BRY C-31592 (St. Clair 7707).
PHAEORRHIZA SAREPTANA. Rare on detritus. BRY C-31657 (St. Clair 7772).
PHYSCIA DUBIA. Common on volcanic rock. BRY C-31612 (St. Clair 7727).
PHYSCONIA MUSCIGENA. Abundant on soil. BRY C-31591 (St. Clair 7706).
PLEOPSIDIUM CHLOROPHANUM. Abundant on vertical rock surfaces (volcanic). BRY C-31622 (St. Clair 7737).
PROTOPARMELIA BADIA. Common on volcanic rock. BRY C-31616 (St. Clair 7731).
PSEUDEPHEBE MINUSCULA. Common on volcanic rock. BRY C-31649 (St. Clair 7764).
PSORA DECIPIENS. Common on soil. BRY C-31665 (St. Clair 7780).
RHIZOCARPON GEOGRAPHICUM. Abundant on volcanic rock. BRY C-31608 (St. Clair 7723).
RHIZOPLACA CHRYSOLEUCA. Abundant on volcanic rock. BRY C-31600 (St. Clair 7715).
RHIZOPLACA MELANOPHTHALMA. Abundant on volcanic rock. BRY C-31602a (St. Clair 7717a).
SOLORINA BISPORA. Rare on soil. BRY C-31669 (St. Clair 7784).
SPORASTATIA TESTUDINEA. Abundant on volcanic rock. BRY C-31652 (St. Clair 7767).
STAUROTHELE AREOLATA. Common on volcanic rock. BRY C-31632 (St. Clair 7747).
STEREOCAULON RIVULORUM. Rare on moss over soil. BRY C-31605 (St. Clair 7720).
TEPHROMELA ARMENIACA. Common on volcanic rock. BRY C-31651 (St. Clair 7766).
THAMNOLIA SUBULIFORMIS. Abundant on soil. BRY C-31585 (St. Clair 7700).
UMBILICARIA DECUSSATA. Common on volcanic rock. BRY C-31660 (St. Clair 7775).
UMBILICARIA HYPERBOREA var. HYPERBOREA. Abundant on volcanic rock. BRY C-31599 (St. Clair 7714).
UMBILICARIA VIRGINIS. Common on volcanic rock. BRY C-31598 (St. Clair 7713).
XANTHOPARMELIA COLORADOËNSIS. Abundant on volcanic rock. BRY C-31630 (St. Clair 7745).
XANTHOPARMELIA CUMBERLANDIA. Common on volcanic rock. BRY C-31602b (St. Clair 7717b).
XANTHOPARMELIA WYOMINGICA. Common on soil or over small rocks and soil. BRY C-31590 (St. Clair 7705).
XANTHORIA ELEGANS. Abundant on volcanic rock. BRY C-31629 (St. Clair 7744).
XANTHORIA SOREDIATA. Rare on volcanic rock. BRY C-31610a (St. Clair 7725a).

## DISCUSSION AND CONCLUSIONS

**Species distribution patterns-** The lichen flora at Stony pass is diverse and well-developed. Stony Pass is dominated by Arctic Element species (78%); with Temperate Element species comprising the balance of the flora. In comparing the lichen flora at Stony Pass with other alpine tundra sites in the Rocky Mountains, Stony Pass shares the most total species in common with Mt. Audubon in north central Colorado (40 out of 68 species). However, in terms of the degree of domination by Arctic Element species the flora at Stony Pass is more similar to two sites in north central and south central New Mexico (Lake Peak and Sierra Blanca Peak). The total contribution of Temperate Element species at most Rocky Mountain alpine tundra sites seems to be somewhat unique from site to site. For example, three sites in New Mexico (La Cal Basin, Lake Peak and Sierra Blanca Peak) share only 5-6 species in common, while Mt. Audubon and Stony Pass share only 2-3 species in common with the three New Mexico sites. The contribution of Temperate Element species to a given alpine tundra site tends to be the most important factor influencing the degree of similarity between any two sites. Overall, the Arctic Element of Rocky Mountain alpine tundra lichen floras tends to be more homogenous across sites.

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# CORTICOLOUS LICHENS OF CAPITOL REEF NATIONAL PARK AND ADJACENT AREAS OF FISHLAKE NATIONAL FOREST, UTAH, U.S.A.

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## ABSTRACT

Forty-six species of corticolous lichens in 21 genera are reported for Capitol Reef National Park and two adjacent sites in Fishlake National Forest. Seven typically saxicolous species were collected from juniper lignum and doug fir lignum and bark. Eleven species are listed as new species records for the state of Utah.

Keywords: corticolous lichens, Capitol Reef National Park, Colorado Plateau, Utah

## INTRODUCTION

**Previous work-** The lichen flora of Utah and specifically the Colorado Plateau is poorly known. Lichenological investigations in Utah began with Tuckerman's collections which included 27 species and 8 varieties (Tuckerman 1871). Fink (1919) reported four species and Magnusson (1954) named several new species from various locations in Utah. Flowers (1954) compiled the first checklist of Utah lichens, listing 127 species in 27 genera. Imshaug (1957) collected several high elevation sites in Utah and reported 14 species. Nielsen (1960) collected and studied the lichens of the central portion of the Wasatch Mountains and reported 42 species and two varieties in 17 genera with 33 new species records for Utah. Anderson and Rushforth (1977) published the first of several studies on cryptogamic soil crusts in Utah listing 17, mostly terricolous species, in 11 genera. Nash and Sigal (1981), as part of an air quality biomonitoring survey commissioned by the National Park Service for Zion National Park, reported 159 lichen species in 53 genera (four were new state records). St. Clair (1984) studied lichen community structure along an alpine tundra ridge in the Uinta Mountains of northeastern Utah and reported 66 lichen species, 16 of which were new records for the state. Newberry (1991) in describing the lichen flora of the Uinta Mountains reported 291 taxa in 95 genera. A comprehensive review of Utah lichens, based on species reports in 44 papers, yielded a total of 318 species and 11 varieties in 85 genera (St. Clair et al. 1991). Newberry and St. Clair (1991) and St. Clair et al. (1995) reported an additional 117 species in 50 genera for the Utah flora, increasing the total number of lichen taxa reported for the state to 435.

Corticolous lichens have been studied throughout intermountain western North America including: Zion National Park, in southern Utah (Nash and Sigal 1981;

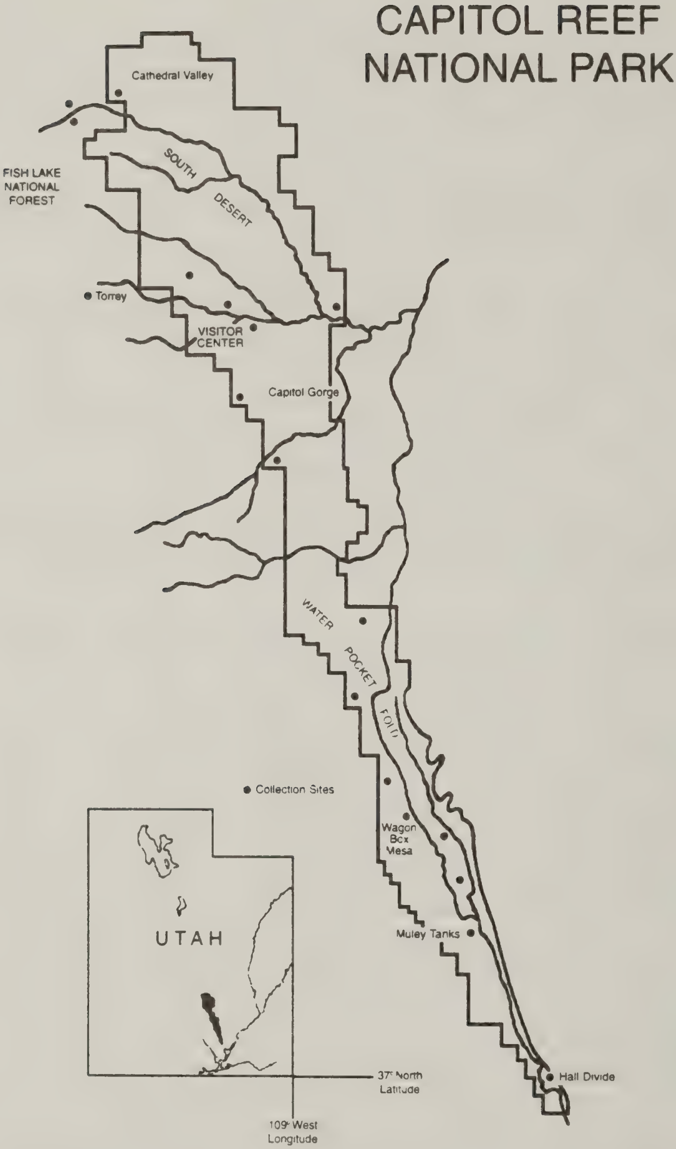

Fig. 1. Map of collection sites in Capitol Reef National Park and Fishlake National Forest, Utah.

Rushforth et al. 1982; St. Clair et al. 1986); southeastern Arizona (Darrow 1950; Weber 1963); the Rocky Mountain Front Range, Colorado (Gough 1975; Peard 1983); west-central Canada (Jonescu 1970); Snake River Plain (Rosentreter 1990); and Navajo National Monument, northeastern Arizona (Nebeker and St. Clair 1984; Rushforth et al. 1984; St. Clair et al. 1986). However, very little is known about the corticolous lichens of the Colorado Plateau.

**Study area-** Capitol Reef National Park is located in south-central Utah approximately 220 km southeast of Salt Lake City in portions of Emery, Sevier, Wayne and Garfield counties (Figure 1). The park was originally established in 1937 as a national monument encompassing the pioneer town of Fruita. In 1971, the monument was enlarged and designated a national park.

Capitol Reef National Park is in the arid, upland portion of the Colorado Plateau. Precipitation varies considerably from month to month with August being the wettest month, averaging 2.71 cm, and January and February the driest months at 0.71 cm. Annual average precipitation is 17.42 cm with most of the moisture falling during infrequent late afternoon summer thunderstorms (Brough et al. 1983).

Habitat patterns within the park have yielded several distinctive vegetation types (Welsh 1993). Large portions of the park are dominated by pinyon pine (*Pinus edulis* Engelmn.) and Utah juniper (*Juniperus osteosperma* (Torr.) Little). Lower elevation areas along the southern boundary of the park, support mixed sagebrush (*Artemisia* spp.), while middle elevation areas contain cliff-rose (*Purshia mexicana* (D. Don) Welsh), singleleaf ash (*Fraxinus anomala* Torr. *ex.* Wats.), and dwarf mountain mahogany (*Cercocarpus intricatus* Wats.). Ponderosa pine (*Pinus ponderosa* Lawson), fremont mahonia (*Mahonia fremontii* (Torr.) Fedde), and various grass species are common at sites above 2000 m. Fremont cottonwood (*Populus fremontii* Wats.) occurs commonly along washes. Riparian habitats were not particularly rich in lichen species a phenomenon which may be due to frequent, violent flooding. Some lichens; however, were found on wild plum (*Prunus domestica* L.) which has escaped cultivation and now occurs along the Fremont River.

We also collected two additional sites in Fishlake National Forest, in an area immediately adjacent to the northwest boundary of the park. Engelmann spruce (*Picea engelmannii* Parry *ex*. Engelmn.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), quaking aspen (*Populus tremuloides* Michx.), doug fir, (*Pseudotsuga menziesii* (Mirbel) Franco) and various shrub species dominate these two sites.

## MATERIALS AND METHODS

**Collection, identification and deposition of specimens-** Lichen specimens were systematically collected from the bark and wood of all tree and shrub species at each collection site. The distribution of collection sites was designed to reflect the range of vascular plant community types in the park. The two collection sites in Fishlake National Forest were included because of their proximity to the park and the fact that they represent an additional vascular plant community type (mixed spruce-fir forest)

Specimens were identified using standard lichen keys, taxonomic treatises and by making comparisons with herbarium material. Standard chemical spot tests, and where necessary, thin-layered chromatography techniques were used to finalize species identifications. All specimens are deposited in the Herbarium of Nonvascular Cryptogams at Brigham Young University (BRY) in Provo, Utah.

**Organization of species list-** Relative abundance, substrates, collection sites, and herbarium and collection numbers are listed after each species. Our scale of relative abundance is rare < common < abundant. Assignment of relative abundance categories is based on the following criteria: rare = 1-2 encounters, common = 3-9 encounters, and abundant >10 encounters. Only one collection is cited for each species. Nomenclature follows Esslinger and Egan (1995).

## RESULTS

Forty-six species of corticolous lichens in twenty-one genera are reported for Capitol Reef National Park and two adjacent sites in Fishlake National Forest. *Arthonia exilis, Caloplaca microphyllina, Caloplaca ulmorum, Catapyrenium acarosporoides, Catapyrenium tuckermanii, Lecania fuscella, Pertusaria saximontana, Phaeophyscia cernohorskyi, Physciella melanchra, Physciella nepalensis,* and *Stenocybe major* (a non-lichenized Ascomycete) are reported as new species records for Utah.

Following is an alphabetical list of all corticolous lichen species collected in Capitol Reef National Park and adjacent sites in Fishlake National Forest. Species marked with an asterisk are new state records.

AMANDINEA PUNCTATA. Common on bark and lignum at several sites in the park. BRY C22431 (Yearsley 0001).

*ARTHONIA EXILIS. Rare on lignum at Bitter Creek Divide in the park. BRY C22393 (Yearsley 0002).

ASPICILIA CINEREA. Abundant on lignum from several sites in the park. BRY C22225 (Yearsley 0003). We have collected this species at various sites on the Colorado Plateau; however, a definite species designation has been difficult. We have listed it as *Aspicilia cinerea*, which is typically saxicolous, because our material seems to fit best into that general group. A review of the pertinent literature suggests that our material may be very similar to the European lichen *Aspicilia lignicola.*

BUELLIA ERUBESCENS. Common on lignum and bark at Desert Overlook in Fishlake National Forest, as well as two sites in the park. BRY C22429 (Yearsley 0004).

CALOPLACA ARIZONICA. Common on bark and lignum at several sites in the park. BRY C22399 (Yearsley 0005).

CALOPLACA CERINA. Common on bark or lignum at two sites in the park as well as Elkhorn Campground in Fishlake National Forest. BRY C22401 (Yearsley 0006)

CALOPLACA HOLOCARPA. Rare on bark and lignum at Elkhorn Campground in Fishlake National Forest. Also collected near the Willow Tanks site in the park. BRY C22504 (Yearsley 0007).

*CALOPLACA MICROPHYLLINA. Rare on bark and lignum at several sites in the park. BRY C22403 (Yearsley 0008).

*CALOPLACA ULMORUM. Rare on bark at Elkhorn Campground in Fishlake National Forest. BRY C22526 (Yearsley 0009).

CANDELARIELLA DEFLEXA. Common on bark and lignum at several sites in the park as well as Elkhorn Campground in Fishlake National Forest. BRY C22416 (Yearsley 0010).

CANDELARIELLA VITELLINA. Rare on bark and lignum at Desert Overlook in Fishlake National Forest and along Old Wagon Trail in the park. BRY C22433 (Yearsley 0011).

CANDELARIELLA XANTHOSTIGMA. Rare on lignum at Desert Overlook in Fishlake National Forest. BRY C22434 (Yearsley 0012).

*CATAPYRENIUM ACAROSPOROIDES. Rare on lignum at several sites in the park. This species is typically saxicolous. BRY C22406 (Yearsley 0013).

*CATAPYRENIUM TUCKERMANII. Rare on bark and lignum at Bitter Creek Divide and along Old Wagon Trail in the park. Spore size varies somewhat from Thomson's (1987) description. Spore length for our material falls within the designated range; however, spore width is somewhat larger (6.5-9µm). BRY C22407 (Yearsley 0014).

CLADONIA CHLOROPHAEA. Rare on decomposing lignum at Desert Overlook in Fishlake National Forest. BRY C22435 (Yearsley 0015).

*LECANIA FUSCELLA. Rare on lignum at Cedar Mesa Campground in the park. BRY C22205 (Yearsley 0016).

LECANORA CARPINEA. Rare on bark scars at Elkhorn Campground in Fishlake National Forest. BRY C22387 (Yearsley 0017).

LECANORA HAGENI. Common on bark and lignum at several sites in the park and Fishlake National Forest. BRY C22408 (Yearsley 0018).

LECANORA PINIPERDA. Rare on lignum along Old Wagon Trail in the park. BRY C22247 (Yearsley 0019).

LECANORA PULICARIS. Rare on lignum at Elkhorn Campground in Fishlake National Forest. BRY C22386 (Yearsley 0021).

LECANORA SALIGNA. Rare on lignum and bark at Longleaf Flat in the park and at Elkhorn Campground in Fishlake National Forest. BRY C22383 (Yearsley 0020).

LECANORA VALESIACA. Rare on bark at Desert Overlook in Fishlake National Forest. This species usually occurs on calcareous rock. BRY C22436 (Yearsley 0022).

LECANORA VARIA. Common on lignum at Elkhorn Campground in Fishlake National Forest. BRY C22532 (Yearsley 0023).

LECIDELLA EUPHOREA. Rare on bark and lignum at Elkhorn Campground in Fishlake National Forest. Also collected at Longleaf Flat and along Old Wagon Trail in the park. BRY C22480 (Yearsley 0024).

MELANELIA ELEGANTULA. Common on bark at Burr Trail Picnic Area in the park and at Desert Overlook in Fishlake National Forest. BRY C22437 (Yearsley 0025).

MELANELIA SUBOLIVACEA. Common on bark at Desert Overlook in Fishlake National Forest. Also at Burr Trail Picnic Area in the park. BRY C22439 (Yearsley 0026).

*PERTUSARIA SAXIMONTANA. Rare on lignum along Old Wagon Trail in the park. BRY C22484 (Yearsley 0027).

PHAEOPHYSCIA ADIASTOLA. Rare on bark at Longleaf Flat in the park. BRY C22517 (Yearsley 0028).

*PHAEOPHYSCIA CERNOHORSKYI. Rare on bark along the Fremont River Gorge in the park. BRY C22424 (Yearsley 0029).

PHAEOPHYSCIA CILIATA. Rare on bark along Cassidy Arch Trail in the park and at Elkhorn Campground in Fishlake National Forest. BRY C22488 (Yearsley 0030).

PHAEOPHYSCIA NIGRICANS. Rare on bark along the Fremont River Gorge in the park. BRY C22425 (Yearsley 0031).

PHYSCIA ADSCENDENS. Rare on bark at Elkhorn Campground in Fishlake National Forest. BRY C22535 (Yearsley 0032).

PHYSCIA CAESIA. Rare on bark at Desert Overlook in Fishlake National Forest. This species is generally saxicolous. BRY C22441 (Yearsley 0033).

PHYSCIA DUBIA. Common on lignum or bark at several sites in the park and at Desert Overlook in Fishlake National Forest. BRY C22410 (Yearsley 0034).

PHYSCIA STELLARIS. Common on bark at Bitter Creek Divide and Longleaf Flat in the park. Also collected at Desert Overlook in Fishlake National Forest. BRY C22445 (Yearsley 0035).

*PHYSCIELLA MELANCHRA. Rare on bark along the Fremont River Gorge in the park. BRY C22426 (Yearsley 0036).

*PHYSCIELLA NEPALENSIS. Rare on bark along Cassidy Arch Trail, at Longleaf Flat, and along wash below Burr Trail in the park. BRY C22418 (Yearsley 0037).

RHIZOPLACA MELANOPHTHALMA. Rare on bark at Desert Overlook in Fishlake National Forest. This species is typically saxicolous. BRY C22440 (Yearsley 0038).

RINODINA CONSTRICTULA. Rare on lignum at Cedar Mesa Campground in the park. This species is typically saxicolous. BRY C21581 (Yearsley 0039).

RINODINA EXIGUA. Common on bark and lignum along wash below Burr Trail in the park. BRY C22419 (Yearsley 0040).

*STENOCYBE MAJOR. Rare on bark along Cassidy Arch Trail in the park. This species is a non-lichenized Ascomycete. BRY C22490 (Yearsley 0041).

XANTHOPARMELIA PLITTII. Rare on bark at Desert Overlook in Fishlake National Forest. This species is typically saxicolous. BRY C22447 (Yearsley 0042).

XANTHORIA CANDELARIA. Rare on bark along wash below Burr Trail in the park. BRY C22420 (Yearsley 0043).

XANTHORIA FALLAX. Abundant on bark at Burr Trail Picnic Area and along Old Wagon Trail in the park. Also collected at Elkhorn Campground and Desert Overlook in Fishlake National Forest. BRY C22411 (Yearsley 0044).

XANTHORIA POLYCARPA. Common on bark and lignum at Burr Trail Picnic Area and along Old Wagon Trail in the park. Also collected at Desert Overlook and Elkhorn Campground in Fishlake National Forest. BRY C22412 (Yearsley 0045).

XYLOGRAPHA sp. Common on lignum at several sites in the park. BRY C22414 (Yearsley 0046).

## DISCUSSION AND CONCLUSIONS

Corticolous lichens are often substrate specific (Barkman 1958). In arid climates, saxicolous lichens may switch to bark, or more frequently lignum substrates. For example, in our study, *Aspicilia cinerea*, *Catapyrenium acarosporoides*, *Lecanora valesiaca*, *Physcia caesia*, *Rhizoplaca melanophthalma*, *Rinodina constrictula*, and *Xanthoparmelia plittii*, all typically saxicolous species, were collected from various bark and lignum substrates. Substrate crossover is likely facilitated by the arid conditions characteristic of the Colorado Plateau as well as the abundance of hard, dry, persistent wood which in some respects simulates rock.

Most of the species we have identified are crustose (67% or 31/46 species) while the remaining species are foliose (33% or 15/46 species). No fruticose species were collected; however, *Usnea hirta*, a fruticose lichen, has been collected occasionally from the bark of pinyon pine from similar sites on the Colorado Plateau. The preponderance of drought-tolerant crustose species was not surprising in light of the xeric conditions characteristic of the park. Most foliose species, collected during this study, were quite small. Diversity and abundance of foliose species was greatest at the higher elevation more mesic sites in Fishlake National Forest.

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# LICHENS OF BADLANDS NATIONAL PARK, SOUTH DAKOTA, USA

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## Abstract

One hundred seventy-one species of lichens and lichenicolous fungi are reported from Badlands National Park, South Dakota, USA, from collections spanning several years. *Macentina dictyospora* Orange is a genus and species new to North America. Several species represent major range extensions. The lichen flora is moderately similar to two other well-collected areas in the region; 77% of the species reported here are shared with those areas. The three major lichen substrates available are calcareous rock, bark and wood, and prairie soil. Two uncommon habitats contribute disproportionately to park lichen diversity: deciduous and conifer tree groves near permanent surface water, and conifer-mixed grass "savanna" on high buttes.

## Introduction

Badlands National Park (BNP) is located in southwestern South Dakota, USA, 80-160 km (50-100 mi) east of the southern Black Hills (BH) and in their rain shadow. The park encompasses about 985.5 $km^2$ (244,000 acres), about equally divided into North and South Units (Figure 1) connected by a narrow neck of the park crossed by South Dakota Highway 44. Part of the South Unit, the Palmer Creek Area, is separated from the rest of the park. The park extends about 110 km (70 mi) east to west, and almost 50 km (30 mi) north to south in its western part in a broad, irregular arc. Elevation ranges from a low of 730 m in the lowest flats to almost 1000 m at several high pinnacles or buttes; average relief between high grassland or butte tops and low grassland is 100-250 m.

The climate of BNP is semiarid continental, with an average annual rainfall of 406 mm (16 in). Summers are hot, with an average of 13 days with highs over 38°C (100°F), though July and August nights average 17°C (62°F). Winters are cold, with an average of 18 days with highs below -18°C (0°F). Average growing season is 152 frost free days (Hauk 1969).

Permanent surface water is found at only a few places in the park. A few small permanent natural ponds and springs are widely scattered. Sage Creek flows continuously in most years from the northwestern part of the park. The permanent White River flows through about 3.5 km (2 mi) of the southern edge of the park. Other streams and ponds dry up seasonally, with water available under the surface for rooted plants.

The park includes the largest protected mixed grass prairie in the United States, interspersed with steep unvegetated butte slopes and spires and sparsely vegetated gentler slopes and erosion flats. Woody vegetation is uncommon in the park. With the exception of widespread sagebrush (*Artemisia* spp.) and other grassland shrubs, woody vegetation is found mostly in protected draws and in the vicinity of seasonal or permanent surface water. The most common and widespread tree is juniper or redcedar (hybrids between rocky mountain juniper, *Juniperus scopulorum* Sarg. and eastern redcedar *J. virginiana* L.), with the deciduous shrubs chokecherry (*Prunus virginiana* L.) and skunkbush sumac (*Rhus aromatica* Ait. var. *trilobata* (Nutt.) A. Gray) in protected draws. Ponderosa pine (*Pinus ponderosa* Laws.) occurs with juniper on a few high buttes. Cottonwood (*Populus deltoides* Marsh subsp. *monilifera* (Ait.) Eckenw.) is found in stream beds and pond areas, sometimes with green ash (*Fraxinus pennsylvanica* Marshall), elms (*Ulmus* sp.), and deciduous shrubs. Vascular plant names follow Great Plains Flora Association (1986). Woody vegetation occasionally forms small dense thickets, but these are never large enough to be called forests. In the past occasional fires swept the plains, limiting woody vegetation to protected areas. Fire suppression since the 1930's has allowed

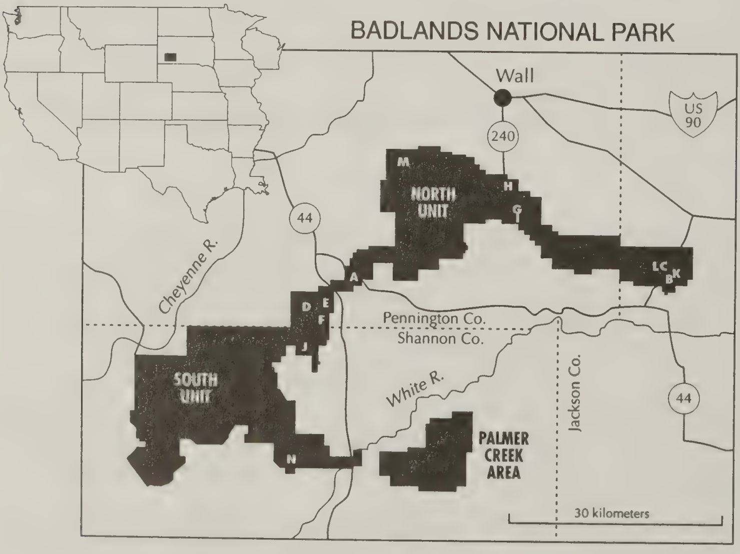

Figure 1. Badlands National Park and vicinity showing the general location of collecting areas, designated by letters (see text). B and K together comprise the Millard Ridge area, J marks Cedar Butte, and M marks the Sage Creek area.

expansion of woody growth. Fire is being reintroduced with prescribed burns for management of some park areas, with the expectation that woody growth will be reduced in those areas.

Available substrates for lichens in BNP include woody plants, rocks, and ground in sparse grassland. Woody plants (described above) grow slowly, so all but the smallest provide a long-lived surface for lichen colonization. Rocks are almost exclusively sedimentary. The Eocene age Chadron formation and Oligocene age Brule formation are mostly soft, easily erodable mudstones with clay-size particles. These rocks provide relatively short-duration mineral substrates for lichens. Both include layers of slightly harder sandstone with calcareous cement. Some of the sandstone deposits include pebble- to cobble-sized stones and have relatively hard cement; these channel sandstones erode more slowly and have more durable surfaces than other rocks. Moderately hard tufa layers (consolidated volcanic ash) are interspersed with other rocks. All of these rocks include calcium carbonate minerals which evolve $CO_2$ when treated with hydrochloric acid (HCl+ reaction). The Cretaceous age Pierre shales have different chemistry, but they also react weakly HCl+, indicating the availability of cations useful as mineral nutrients. Park soils are all derived from these formations and are neutral to alkaline in chemistry. The most common non-calcareous rock is chalcedony (a silicious solution deposit) which appears on the ground surface as thin, light fragments which are mobile and so provide mostly short-duration substrate for lichens. Waterworn silicate and granitic gravels originating from the Black Hills to the west include heavier and more stable cobbles. They accumulate on the surface in small, widely scattered "desert pavement" areas throughout the park.

Very little lichen collecting was done in the park before this study; only four lichens were officially recorded for the park as of 1988 (Bessken, personal communication.

## Methods

I spent several days each year collecting in BNP in 1988, 1990, and 1991, with two days in 1992. During this time I collected from thirteen different areas in the park (Figure 1), selected in collaboration with park personnel to represent a wide range of potential habitats and substrates for lichens. At each area I collected vouchers for all lichen species seen, from all substrates available. Particularly lichen-rich areas were revisited several times. I recorded substrate and habitat for each specimen collected, and noted abundance of species which could be recognized in the field. No formal sample design was adopted, nor was any attempt made to quantify abundance. In all, 822 collections were made; about 90% of them are represented in this publication. Location, elevation and description of collecting areas are listed by letter below with collection years; general locations are marked by letters on the map in Figure 1.

A: Lat.42°45'N,Long.102°30'W; T3S,R13E,E1/4Sec25; 840 m; Brule mudstone slopes and sparsely vegetated erosion slopes; 1988,1992.

B: Lat.43°45'N,Long.101°56'W; T3S,R18E,SW1/4Sec26; 800 m; Cliff Shelf Nature Trail area: juniper and deciduous wooded groves with a permanent pond, Brule mudstone; 1991.

C: Lat.43°46'N,Long.101°57'30"W; T3S,R18E,E1/4Sec22; 800 m; Brule mudstone slopes and sparsely vegetated erosion flats; 1988.

D: Lat.43°43'15"N,Long.102°34'45"W; T4S,R13E,NE1/4Sec8; 890 m; sparsely vegetated erosion flats, mixed grass prairie; 1988,1990.

E: Lat.43°43'20"N,Long.102°31'45"W; T4S,R13E,NW1/4Sec11; 860 m; Brule sandstone outcrops and sparsely vegetated erosion flats; 1988.

F: Lat.43°41'20"N,Long.102°34'5"W; T43N,R44W,NE1/4Sec21; 960 m; wooded draw off Sheep Mountain, N of county line; 1988.

G: Lat.43°50'40"N,Long.102°11'30"W; T2S,R16E,NW1/4Sec27; 820 m; weathered Pierre shale slopes with sandstone nodules; 1988.

H: Lat.43°52'10" N,Long.102°13'30"W; T2S,R16E,SE1/4Sec17; 940 m; juniper grove; 1988.

I: Lat.42°49'45"N,Long.102°11'45"W; T2S,R16E,NW1/4Sec34; 780 m; deciduous tree grove, bank of dry stream; 1988.

J: Lat.43°40'30"N,Long.102°35'W; T43N,R44W,Sec29; 980-990 m; top of Cedar Butte: mixed grass prairie and conifer groves; 1990, 1991.

K: Lat.43°46'N,Long.101°55'45"W; T3S,R18E,SW1/4Sec26; 750-850 m; Millard Ridge area: ridgetops and steep, narrow canyons with sparse vegetation in Brule mudstone and sandstone, sparsely vegetated erosion flats; 1990,1991.

L: Lat.43°46'N,Long.101°57'W; T3S,R18E,Sec21,22; 800-810 m; Medicine Root Trail area: mixed grass prairie, sparsely vegetated erosion flats, Brule mudstone slopes, and silicious gravel deposits; 1990,1991.

M: Lat.43°54'N,Long.102°25'W; T2S,R14E,Sec1,2; 780-830 m; Sage Creek valley: mixed conifer-deciduous wooded draws, mixed grass prairie, silicious gravel deposits, Chadron mudstone slopes, weathered Pierre shale slopes with nodules and rock outcrops, deciduous tree groves on banks of permanent stream; 1990,1991,1992.

N: Lat.43°31'15"N,Long.102°36'30"W; T41N,R44W,SW1/4Sec18,N1/2Sec19; 860-930 m; Fog Creek area: mixed conifer-deciduous wooded groves near small permanent stream, mixed grass prairie, sparsely vegetated erosion flats; 1991.

Identifications were made at the University of Wisconsin-Madison, with the exception of specimens sent to other lichenologists for identification or confirmation, as noted in the species list below. Chemical contents were checked when necessary with microcrystal tests for *Cladonia* (Thomson 1967; Hale 1979) and thin-layer chromatography with solvent A (White & James 1985) for other groups; results are noted in brief after listed species. A complete set of vouchers has been deposited in WIS, and an almost-complete set of duplicates has been deposited in the Herbarium of Badlands National Park.

## List of Species

A total of 167 lichen species and four species of lichenicolous fungi are reported for BNP, based mostly on my collections. In addition, one species of ascomycete fungus which strongly resembles a lichen is reported at the end of the list. Collection localities and substrates are reported for each species, and a representative specimen in WIS is cited as a Will-Wolf collection number, with its location letter (see Figure 1) when needed. Two species not also collected by me are included in brackets. In addition to these species, about 15 taxa remain unidentified, including two *Caloplaca* species (*fide* Wetmore) and two *Rinodina* species (*fide* Sheard). Names for lichens and lichenicolous fungi follow Esslinger and Egan (1995) except where noted. Species also reported from Theodore Roosevelt National Park (TRNP: Wetmore 1985) and the Black Hills (BH: Wetmore 1967, personal communication) are marked with subscripts (see notes at end of list). Nomenclatural synonomy reported in Esslinger and Egan (1995) was used to compare the species list below with those of Wetmore (1967, 1985).

| **Species Name** | **Areas** | **Substrate**[c] |
|---|---|---|
| *Acarospora arenacea* H. Magn., 2000 | A | si |
| [b]*Acarospora badiofusca* (Nyl.) Th. Fr., 2507 | N | si |
| *Acarospora nevadensis* H. Magn., 2807 | M | si |
| *Acarospora californica* Zahlbr., M:2806 | KMN | ca,si |
| [b]*Acarospora glaucocarpa* (Ach.) Körber, 2600. | B | ca |
| *Acarospora coloradiana* H. Magn., 2019. | C | ca |
| *Acarospora fuscescens* H. Magn., 2601. | B | ca |
| [ab]*Acarospora schleicheri* (Ach.) A. Massal., K:2158. | CK | ca |
| [b]*Acarospora strigata* (Nyl.) Jatta, C:2020. | CM | ca |
| *Acarospora veronensis* A. Massal., A:2002. | AN | ca |
| [ab]*Agrestia hispida* (Mereschk.) Hale & Culb., M:2329. | BM | g |
| [ab]*Amandinea punctata* (Hoffm.) Coppins & Scheid., B:2618. | BJN | ca,b(c) |
| [ab]*Arthonia lapidicola* (Taylor) Branth & Rostrup, C:2022. | CEL | ca |
| [b]*Aspicilia calcarea* (L.) Mudd, M:2353. | AGM | ca,si |

This species was distinguished from the following two using the characters listed below (based on species descriptions, assorted keys, and specimens in WIS):

| | A. calcarea | A. contorta | A. desertorum |
|---|---|---|---|
| Thallus morphology | Areoles always contiguous. | Areoles isolated to partly contiguous. | Contiguous areolate to radiate at margins. |
| | -- Areoles flat (partly concave) to -- -- centrally elevated, not bullate.-- | | Areoles convex to bullate. |
| Thallus color | --Thallus white to pale gray.-- | | Thallus tan to brown. |
| | Thallus epruinose. | Thallus pruinose. | Thallus epruinose. |
| Apothecia | -- Apothecia single in areoles, -- -- pruinose margin often prominent.-- | | Apothecia single to grouped in areoles. |

Wetmore (personal communication) thinks most North American A. calcarea specimens belong in A. contorta; the two taxa are kept separate here pending a published study because this group is notoriously difficult.

| | | |
|---|---|---|
| [a]*Aspicilia contorta* (Hoffm.) Kremp., 2369. | L | ca |
| *Aspicilia desertorum* (Kremp.) Mereschk., M:2671. | ALMN | ca,si |
| [b]*Aspicilia laevata* (Ach.) Arnold, 2232. | M | ca |

| | | |
|---|---|---|
| [ab]*Bacidia bagliettoana* (Massal. & deNot.) Jatta, D:2482. | DJM | o |
| [b]*Bacidia beckhausii* Körber, J:2417. | JN | b(c,d) |
| [b]*Bacidia herbarum* (Stizenb.) Arnold, 2463. | J | o |
| *Bacidia schweinitzii* (Fr. *ex* Michener) A. Schneider, 2631. | B | b(d) |
| [a]*Buellia elegans* Poelt, M:2805. | MD | g |
| *Buellia schaereri* DeNot., 2715. | J | b(c) |
| *Buellia turgescens* Tuck., B:2610. (Det. Sheard) | BJ | b(c) |
| *Buelliella minimula* (Tuck.) Fink, K:2161. Lichenicolous on *Caloplaca atroalba* and other crustose spp. | CDGK | p:ca |
| [b]*Caloplaca approximata* (Lynge) H. Magn., K:2162. | KLM | ca,si |
| [a]*Caloplaca atroalba* (Tuck.) Zahlbr., K:2167. (Det. Wetmore) One bark specimen, very unusual for this species. | ABCDGJKLMN | ca,si,b(d) |
| [ab]*Caloplaca cerina* (Hedwig) Th. Fr., M:2286. | BCMN | o,b(c,d) |
| *Caloplaca dakotensis* Wetmore, 2425. (Det. Wetmore) | J | b(c) |
| [ab]*Caloplaca decipiens* (Arnold) Blomb. & Forss., K:2790. Also reported by Wetmore (1967). | CKLM | ca |
| [b]*Caloplaca ferruginea* (Hudson) Th. Fr., I:2121. | IK | b(d) |
| [a]*Caloplaca flavorubescens* (Hudson) J.R. Laundon, I:2119 | IJ | b(c,d) |
| *Caloplaca fraudans* (Th. Fr.) H. Olivier, L:2373. | KLM | ca |
| [ab]*Caloplaca holocarpa* (Hoffm. *ex* Ach.) M. Wade, M:2287. | ABDIKMN | o,b(c,d) |
| *Caloplaca cf invadens* gp., not *castellana* (Räsänen) Poelt., 2026. (Det. Poelt). - Lichenicolous on *Caloplaca trachyphylla*. | C | p:ca |
| *Caloplaca lactea* (Massal.) Zahlbr., L:2695. | LM | ca |
| [ab]*Caloplaca microphyllina* (Tuck.) Hasse, J:2424. | BJMN | b(c,d) |
| [ab]*Caloplaca saxicola* (Hoffm.) Nordin, K:2144. (Det. Wetmore) All specimens have a subsquamulose growth form and tan upper surface (possibly pruina) unusual for this species; one specimen on bark. Similar to *Caloplaca lobulata* (Flörke) de Lesd. | CKM | ca,b(c) |
| [a]*Caloplaca trachyphylla* (Tuck.) Zahlbr., C:2028. | CKM | ca |
| [ab]*Caloplaca ulmorum* (Fink) Fink, 2075. | F | b(c) |
| [ab]*Candelaria concolor* (Dickson) Stein, F:2083. | FJMN | b(c,d) |
| [ab]*Candelariella aurella* (Hoffm.) Zahlbr., L:2374. | ABCEFHKL | ca,b(c) |
| [a]*Candelariella deflexa* (Nyl.) Zahlbr., M:2289. | BCDEFIJKMN | ca,b(c,d) |
| [a]*Candelariella efflorescens* R.C. Harris & W.R. Buck, 2428. | J | b(c) |
| [a]*Candelariella subdeflexa* (Nyl.) Lettau, F:2078. | BFKMN | b(c,d) |
| *Candelariella terrigena* Räsänen, 2394. | J | g |
| [ab]*Candelariella vitellina* (Hoffm.) Müll. Arg., 2095. | G | ca |
| *Catapyrenium compactum* (Massal.) R. Sant., 2792. | K | ca |
| [b]*Catapyrenium daedalum* (Krempelh.) Stein, 2702. | L | g |
| [ab]*Catapyrenium lachneum* (Ach.) R. Sant., A:2006. | ADIKLMN | g |
| [ab]*Catapyreneum plumbeum* (de Lesd.) J.W. Thomson, | CDM | ca,g |

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|---|---|---|
| C:2032. | | |
| *Catapyrenium schaereri* (Fr.) R. Sant., L:2375. | LM | ca |
| [b]*Catillaria chalybeia* (Borrer) A. Massal., 2376. | L | ca |
| [a]*Catillaria nigroclavata* (Nyl.) Schuler, J:2719. | FJM | b(c) |
| [ab]*Cladonia chlorophaea* (Flörke *ex* Sommerf.) Sprengel, 2397. fumarprotocetraric acid only, in GE | J | g |
| *Cladonia cryptochlorophaea* Asah., 2430. cryptochlorophaeic acid in GE | J | g,b(c) |
| [ab]*Cladonia fimbriata* (L.) Fr., 2058. | F | g |
| [ab]*Cladonia macilenta* var. *bacillaris* (Genth) Schaerer, 2429. | J | b(c) |
| *Cladonia merochlorophaea* Asah., merochlorophaeic acid + (J:2395) and - (F:2059) fumarprotocetraric acid in GE | DFJM | g |
| *Cladonia pocillum* (Ach.) Grognot, N:2496. fumarprotocetraric acid only, in GE | KN | g |
| *Cladonia polycarpoides* Nyl., 2781. | J | g |
| [ab]*Cladonia robbinsii* A. Evans (sterile), 2492. usnic + barbatic acids in GE | D | g |
| [ab]*Cladonia subulata* (L.) F. H. Wigg, 2784. | J | g |
| [b]*Cladonia sulphurina* (Michaux) Fr., 2785. | J | g |
| [ab]*Collema cf coccophorum* Tuck. (sterile), A:2007. | AHN | g |
| [ab]*Collema furfuraceum* (Arnold) Du Rietz, 2431. | J | b(c) |
| [b]*Collema subflaccidum* Degel., N:2530. | JN | b(c,d) |
| [ab]*Collema tenax* (Swartz) Ach., L:2359. | ABHIKL | g |
| [ab]*Cyphelium notarisii* (Tul.) Blomb. & Forss., J:2405. | JM | b(c) |
| *Dactylospora inquilina* (Tuck.) Hafellner, 2721. Lichenicolous on *Lecanora* sp. | J | p:b(c) |
| [ab]*Diploschistes scruposus* (Schreber) Norman, J:2466. | DIJLN | o,b(c) |
| *Diplotomma epipolium* (Ach.) Arnold, M:2341. | ACDGKMN | ca,si |
| [ab]*Endocarpon pusillum* Hedwig, L:2361. | BKL | g |
| [ab]*Flavopunctelia flaventior* (Stirton) Hale, J:2436. | HJMN | b(c) |
| [ab]*Flavopunctelia soredica* (Nyl.) Hale, J:2437. | FHJMN | b(c) |
| [ab]*Fulgensia bracteata* (Hoffm.) Räsänen, J:2467. | DHJKLN | g |
| [ab]*Fulgensia fulgens* (Swartz) Elenkin, K:2183. | DIJKLN | g |
| [ab]*Heppia lutosa* (Ach.) Nyl., L:2355. | JKLMN | g |
| [a]*Hyperphyscia adglutinata* (Flörke) Mayrh. & Poelt, M:2661. | FJKMN | b(c) |
| [b]*Lecania dubitans* (Nyl.) A.L. Sm., B:2643. | BN | b(d) |
| [ab]*Lecania erysibe* (Ach.) Mudd, A:2009. | ACN | ca |
| [a]*Lecania fuscella* (Schaerer) Körber, D:2045. | ADK | b(d) |
| [ab]*Lecanora chlarotera* Nyl., H:2110. | HJM | b(c) |
| *Lecanora circumborealis* Brodo & Vitik., J:2726. TLC: atranorin, roccellic acid. | JMN | b(c) |
| *Lecanora crenulata* Hook, A:2011. | ABDEGJKMN | ca,si |
| [ab]*Lecanora dispersa* (Pers.) Sommerf., N:2515. | JKN | ca,si |
| [ab]*Lecanora hagenii* (Ach.) Ach., N:2531. TLC, typical collections: unknown UVL white spots at RF5-6. | BDFHIJKMN | b(c,d) |

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|---|---|---|
| Four collections, *e.g.* J:2763, also have gangaleoidin. | | |
| [ab]*Lecanora impudens* Degel., J:2441. | JN | b(c,d) |
| [ab]*Lecanora muralis* (Schreber) Rabenh., 2514. | N | si |
| [ab]*Lecanora piniperda* Körber, N:2546. | BN | b(d) |
| *Lecanora meridionalis* H. Magn., 2409. | J | b(c) |
| TLC: atranorin, roccellic, gangaleoidin. | | |
| *Lecanora salicicola* H. Magn., 2730. | J | b(c) |
| [b]*Lecanora symmicta* (Ach.) Ach., J:2731. | JN | b(c,d) |
| [*Lecidella anomaloides* (Massal.) Hertel & R. Kilias] | --- | ----- |
| Wetmore 10125 in MIN, collected 1960. | | |
| [ab]*Lecidella euphorea* (Flörke) Hertel, J:2767. | FHJKMN | b(c,d) |
| [a]*Lecidella patavina* (Lynge) Hertel & Leuck., K:2141. | ACK | ca,si |
| [b]*Lempholemma cf. albonigrum* (sterile), J:2402. | DJ | g,o |
| *Lichinella minnesotensis* (Fink) Essl., E:2089. | EK | ca |
| [ab]*Lobothallia alphoplaca* (Wahlenb.) Hafellner, 2808. | M | si |
| *Macentina dictyospora* Orange, det. Coppins, M:2302 | MN | b(c,d) |
| Genus and species new to North America. *Macentina* Vezda (Verrucariaceae) has tiny, pale globose perithecia with no involucrellum, pale elongated cells in vertical x-section of the exciple, disappearing paraphyses, periphyses present, asci clavate with an ocular chamber, and 8 colorless, septate spores/ascus (Coppins & Vezda 1977). My four collections have finely granular-verrucose crustose thalli, 0.1-0.2 mm wide perithecia, submuriform spores 17-23 x 6-9 $\mu$m, and hymenial gelatin I+ red, K/I+ blue, consistent with *M. dictyospora* (Orange 1991). Specimens were found on the edges of bark plates of medium to large trees (willow, elm, juniper) in moist wooded draws. | | |
| [ab]*Megaspora verrucosa* (Ach.) Hafellner & V. Wirth, 2449. | J | b(c) |
| [b]*Melanelia elegantula* (Zahlbr.) Essl., 2734. | J | b(c,d) |
| *Melanelia infumata* (Nyl.) Essl., 2444. | J | b(c) |
| [ab]*Melanelia subargentifera* (Nyl.) Essl., J:2445. | BDJ | o,b(c) |
| [a]*Melanelia subolivacea* (Nyl.) Essl., 2770. | J | b(c) |
| *Melaspilea* sp., 2590 | N | p:w(c) |
| Lichenicolous on unidentified granular crustose lichens. This is probably a new species. In common with *M. tribuloides* (Tuck.) Müll. Arg. (see Fink 1935), my specimens have lirellate fruits, carbonaceous exciple and epithecium, pale hymenium, unevenly 2-celled spores 14-18 x 7-8 $\mu$m and 8/ascus, and asci with I- apical dome 5 $\mu$m thick and I+ red contents when young. The type of *M. tribuloides* (FH: Tuckerman, no #, Texas, as *Opegrapha tribuloides*) has an I-, K/I- (greenish yellow) hymenium, saccate asci, and spores darkening to brown in the ascus. In contrast, my #2590 has I+ blue hymenium, clavate asci, and spores remaining hyaline. | | |
| [b]*Micarea peliocarpa* (Anzi) Coppins & R. Sant., 2736. | J | b(c) |
| *Ochrolechia androgyna* (Hoffm.) Arnold (sterile), 2737. | J | b(c) |
| [ab]*Parmelia sulcata* Taylor, J:2446. | JN | b(c) |
| [b]*Peccania arizonica* (Tuck.) Herre, 2504. | N | g |
| [b]*Peccania texana* (Tuck.) Wetmore, N:2505. | LN | g |

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|---|---|---|
| [ab]*Peltigera canina* (L.) Willd., 2788. | J | g |
| [b]*Peltigera didactyla* (With.) J.R. Laundon, 2448. | J | g |
| [ab]*Peltigera rufescens* (Weiss) Humb., J:2470. | FJ | g |
| [ab]*Peltula patellata* (Bagl.) Swinscow & Krog, 2356. | L | g |
| [ab]*Pertusaria saximontana* Wetmore, 2447. | J | b(c) |
| [a]*Phaeophyscia cernohorskyi* (Nadv.) Essl., M:2300. | BFJKMN | b(c,d) |
| [b]*Phaeophyscia ciliata* (Hoffm.) Moberg, 2113. | H | b(c) |
| [ab]*Phaeophyscia nigricans* (Flörke) Moberg, I:2124. | IM | b(c,d) |
| [ab]*Phaeophyscia orbicularis* (Necker) Moberg, I:2125. | IK | b(c,d) |
| *Phaeophyscia pusilloides* (Zahlbr.) Essl., 2584. | N | b(c,d) |
| [ab]*Physcia adscendens* (Fr.) H. Olivier, F:2073. | FIJKMN | b(c,d) |
| [ab]*Physcia aipolia* (Ehrh. *ex* Humb.) Fürnr., F:2084. | FKM | b(c,d) |
| [b]*Physcia americana* G. Merr., 2114. | H | b(c) |
| [a]*Physcia bizania* (Massal.) Zahlbr., J:2452. | BJMN | o,b(c,d) |
| [ab]*Physcia dimidiata* (Arnold) Nyl., J:2453. | JN | b(c) |
| [a]*Physciella chloantha* (Ach.) Essl., K:2236. | FK | b(c,d) |
| [a]*Physciella melanchra* (Hue) Essl., M:2257. | FMN | b(c,d) |
| [b]*Physconia enteroxantha* (Nyl.) Poelt, J:2454. (Det. Esslinger) | JN | b(c) |
| *Physconia perisidosa* (Erichsen) Moberg, F:2081. (Det. Esslinger) | FJ | b(c) |
| [b]*Polychidium muscicola* (Sw.) S. Gray, 2456. | J | o,b(c) |
| [ab]*Polysporina simplex* (Davies) Vezda, A:2014. | ACEJKLMN | ca,si |
| [ab]*Psora decipiens* (Hedwig) Hoffm., A:2015. | ADIJKLN | g |
| [b]*Psorotichia schaereri* (Massal.) Arnold, M:2679. | JM | ca |
| *Pyrenopsis cf phaeococca* Tuck., 2211. | K | ca |
| *Rinodina castanomela* (Nyl.) Arnold, K:2173. (Det. Sheard) | ACKLM | ca,si |
| [ab]*Rinodina colobina* (Ach.) Th. Fr., 2588. (Det. Sheard) | N | b(c) |
| [a]*Rinodina mucronatula* H. Magn., 2196. (Det. Sheard) | K | g |
| [ab]*Rinodina pyrina* (Ach.) Arnold, F:2088. (Det. Sheard) | ABFIJKMN | b(c,d) |
| [a]*Rinodina riparia* Sheard, N:2536. (Sheard 1998; Det. Sheard) | FN | b(c,d) |
| [*Rinodina zwackhiana* (Kremp.) Körber] Reported by Anderson (1962). | --- | ---- |
| *Ropalospora chlorantha* (Tuck.) S. Ekman, 2418. | J | b(c) |
| *Sarcogyne novomexicana* H. Magn., M:2345. | LMN | ca,si |
| [ab]*Sarcogyne regularis* Körber, K:2154. | JKM | ca |
| [a]*Squamarina lentigera* (Weber) Poelt, D:2051. | DILN | g |
| [ab]*Staurothele drummondii* (Tuck.) Tuck., C:2041. Also Wetmore 10120 in MIN, collected 1960. | BCDGJK<br>LMN | ca,si |
| [ab]*Staurothele elenkinii* Oxner, C:2040. | CJKM | ca |
| [a]*Staurothele monicae* (Zahlbr.) Wetmore, C:2039. | CDGJKM | ca |
| [b]*Strangospora microhaema* (Norman) R. Anderson, 2117. | I | b(d) |
| [b]*Strangospora cf moriformis* (Ach.) Stein, 2665. | M | b(c) |
| *Strangospora ochrophora* (Nyl.) R. Anderson, 2647. | B | b(d) |
| *Thelidium olivaceum* (Fr.) Körber, 2518. | N | ca |

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|---|---|---|
| [ab]*Toninia sedifolia* (Scop.) Timdal, D:2052. | DJKL | g |
| [ab]*Trapeliopsis granulosa* (Hoffm.) Lumbsch., 2774. | J | b(c) |
| [ab]*Usnea hirta* (L.) F. H. Wigg., J:2457. | FJ | b(c) |
| *Verrucaria calkinsiana* Servít, 2476. | J | ca |
| [b]*Verrucaria fuscella* (Turner) Winch, M:2348. | CKLM | ca |
| [a]*Verrucaria muralis* Ach., K:2177. | KM | ca |
| *Verrucaria cf. muralis* Ach., M:2303 | MN | b(c,d) |
| The five collections on bark (3 tree species) are consistent with descriptions of *V. muralis* on rock. They are quite similar to one another, with moderately thick, pale gray-brown thallus, perithecia almost sessile and with conspicuous pale ostiole, and hymenium I+ red, K/I+ blue. | | |
| [b]*Verrucaria nigrescens* Pers., K:2157. | GKM | ca |
| [b]*Xanthoparmelia dierythra* (Hale) Hale, N:2520. | MN | si |
| TLC: usnic, norstictic and connorstictic acids. | | |
| [ab]*Xanthoparmelia plittii* (Gyelnik) Hale, J:2458. | DJ | b(c) |
| TLC: usnic, stictic and norstictic acids. Two full-sun specimens have dark rhizines and underside blackening in places, but they lack the additional substances typical for *X. conspersa*. | | |
| [b]*Xanthoparmelia subdecipiens* (Vainio) Hale, 2521. | N | si |
| TLC: usnic acid. | | |
| *Xanthoparmelia cumberlandia* (Gyelnik) Hale, 2814. | M | si,g |
| TLC: usnic, stictic and norstictic acids. Specimens vary from being loosely attached on pebbles to vagrant on soil, are profusely apotheciate and have lobe widths of 1-5mm. | | |
| [ab]*Xanthoria elegans* (Link) Th. Fr., A:2017. | ABMN | ca,si |
| [ab]*Xanthoria fallax* (Hepp) Arnold, H:2115. | BFHJKMN | b(c,d) |
| [ab]*Xanthora polycarpa* (Hoffm.) Rieber, I:2128. | BIKN | b(c,d) |

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|---|---|---|
| *Lecanidion atratum* (Hedw.) Rabenh., 2053. | D | b(c) |

(Det. Coppins) This ascomycete fungus strongly resembles a lichen, and has occasionally been described as a *Bacidia* species (Coppins, personal communication). It is neither lichenized nor lichenicolous.

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[a] Also reported from Theodore Roosevelt National Park (Wetmore 1985).
[b] Also reported from the Black Hills (Wetmore 1967, personal communication).
[c] ca=calcareous rocks, see text; si=non-calcareous rocks; o=non-woody organic substrates; g=soil; b=bark or wood (c=conifers, d=deciduous trees or shrubs); p=lichenicolous: host substrate given.

## Discussion

The 163 lichen species and three lichenicolous fungus species reported here probably represent most of the total lichen flora of BNP. The northwestern part of the South Unit of BNP (Fig. 1) remains undercollected, and the Palmer Creek Area was not visited.

**Species.** The genus *Macentina* is first reported from North America as *M. dictyospora* Orange. The four collections were all accidental, with the specimen distinguished only under a dissecting scope. The species may actually be fairly common here. Only a few collections have been reported so far from Europe (Coppins, personal communication).

*Acarospora arenacea* is reported well north of its normal southwestern USA range. It is moderately abundant at a single site in BNP, immediately adjacent to a highway and very close to where the road surface formerly switched from asphalt to gravel. Since the species has not been found at other similar sites, nor away from disturbed areas, the possibility that *A. arenacea* is a human introduction to BNP should be considered.

The lichenicolous fungus *Melaspilea* sp. is probably a new species, and is reported far north of the southeastern USA coastal plain range of its close relative *M. tribuloides*.

*Lecanora circumborealis* and *L. meridionalis* are found in more arid climates than is usual for these species.

*Xanthoparmelia plittii*, usually a species of acid rock, was found only on juniper wood at BNP. *X. cumberlandia* has an unusual vagrant growth form. None of the typical vagrant *Xanthoparmelia* species was found.

*Rinodina castanomela* shares an unusual (for the genus) subsquamulous growth form with a variant of *Caloplaca saxicola* found in BNP; both are moderately common there.

**Floras.** Comparison of the BNP lichen flora with those of both the nearby Black Hills (BH) and Theodore Roosevelt National Park (TRNP) about 320 km (200 mi) to the north shows much overlap, but also significant differences. Some differences in taxonomic interpretation were considered when floras were compared. Wetmore's (1967, 1985) *Cladonia chlorophaea* included all chemical species in the group (Wetmore, personal communication), so I did not count *C. cryptochlorophaea* and *C. merochlorophaea* for comparisons. Wetmore's (1967) *Physcia grisea* and *Physconia detersa* (1985) may have included *Physconia perisidiosa*. In each case, those species were counted as one group for comparison of floras. Thus 159 BNP lichen species were used for comparison with the lichen floras of TRNP and BH.

Sixty-nine (43%) of BNP lichen species are shared with both BH and TRNP. BH and TRNP have each been more thoroughly collected than BNP. Common arid land ground taxa, taxa common on bark and wood in general and on conifers, and taxa common on calcareous rock comprised most of the shared species.

An additional 33 species are shared only between BNP and BH; a moderately large proportion (30%) of these are taxa found on both conifer and deciduous substrates. BH, more than ten times the size of BNP, and with much greater topographic and habitat diversity, has over 400 lichen species (Wetmore 1967). A total of 102 (64%) of BNP species are shared with BH.

Another 24 species are shared only between BNP and TRNP; a large proportion (38%) of these are taxa of deciduous tree bark and wood. TRNP, about one third the size of BNP, has similar plains habitat and erosion features, but has more area of moist habitat, woodland, and stable non-calcareous rock substrate than does BNP. TRNP has 204 lichen species (Wetmore 1985). A total of 90 (57%) of BNP species are shared with TRNP.

Thirty-four (21%) of the compared species found at BNP are not reported from either BH or TRNP; taxa on calcareous rock (47%) and on conifers (28%) predominate in this group. Most of the species found only in BNP are uncommon and have erratic distributions in the park. Three of these species, however, *Diplotomma epipolium*, *Lecanora crenulata*, and *Verrucaria calkinsiana*, are common and widespread in BNP as well as elsewhere in arid western North America.

The lichen flora of BNP is primarily a microlichen flora; only 33% of the species can be classed as macrolichens (foliose, fruticose and at least medium-sized squamulose growth forms), and over half of these are small macrolichens (*e.g.* the genus *Physcia*). This contrasts with the lichen flora of TRNP (Wetmore 1985), which has 54% macrolichen species, more than half of them large macrolichens (*e.g.* the genus *Parmelia*). While both BNP and TRNP are in the semi-arid plains region, BNP has a much lower proportion and much less variety of moisture-rich habitat within its boundaries.

**Communities and Habitats.** Three groups of lichen species based on substrate preference are distinct and well represented in BNP: those on calcareous rock, on bark and wood, and on soil. There is relatively little overlap between groups. Bark and wood lichens form the largest group, with 73 species. The most common of these, found at seven or more sites and on both conifers and deciduous species, are the microlichens *Caloplaca cerina*, *C. holocarpa*, *Candelariella deflexa*, and *Rinodina pyrina*, plus *Xanthoria fallax*, the only common macrolichen species. A total of 30 species have been found on both conifers and deciduous species. *Candelariella aurella* is common both on conifer bark and on calcareous rock, one of the few species equally common on two different substrate groups. An additional 37 species have been found only on conifers, and six species only on deciduous taxa.

Forty-seven species occur on calcareous rock. The most common are *Caloplaca atroalba*, *Diplotomma epipolium*, *Lecanora crenulata*, *Polysporina simplex*, and *Staurothele drummondii*. Most of these also grow on the scarce silicious rocks; in addition there are six species found only on silicious rocks. Several of the relatively common calcareous rock lichens are occasionally found on woody plants, especially where calcareous dust has lodged in the bark. Only one of the 31 species growing on soil is relatively common: *Catapyrenium lachneum*.

Three widely spaced (> 55 km distant), large (4-10 ha) areas with varied habitats were each visited repeatedly. The Millard Ridge area (B and K, Figure 1) is at the northern and eastern end of the park, in Oligocene Brule rock deposits. The Sage Creek site (M, Figure 1) is at the northwestern corner of the park, with Cretaceous Pierre Shale and Eocene Chadron deposits. Both of these areas have calcareous rock outcrops of varying hardness, some silicious rocks, sparsely vegetated prairie soils, and mixed conifer and deciduous tree groves near permanent free water. Sixty-four and 67 species, respecively, were found at the sites, with just over half the species in common. Six species at Millard Ridge and five species at Sage Creek have been collected nowhere else.

The Millard Ridge and Sage Creek areas include habitats widespread in BNP, and they also both include conifer and deciduous tree groves adjacent to free water, a relatively rare habitat in the park. Twenty-one lichen species appear to be restricted to these moist habitats, being found in one or more of the three examples visited (B,M,N, Figure 1) and nowhere else. Eight macrolichen species on bark, wood or rock are included among the twenty.

The third area, Cedar Butte (J, Figure 1), is in the northeastern part of the South Unit, with Oligocene Brule rock deposits. It is one of the few high buttes having ponderosa pine, and has extensive groves of pine and juniper interspersed with mixed grass prairie. It has relatively fewer rock deposits on top, and has no permanent water, though being high, it is cooler and therefore less dry than most of BNP. Eighty lichen species have been found here, almost half the total flora. Only 34% of the species are shared with either of the other two large areas, and 38% of the species were collected only at this locality. The Cedar Butte site is the only example I visited of high, cool, conifer-mixed grass "savanna," a rare habitat in the park. It illustrates well how important this habitat is to increasing the lichen species diversity in BNP.

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I learned lichenology from Dr. John Thomson starting almost 30 years ago when I came to UW-Madison as an ecology graduate student. I was quite surprised when he told me that he has never taught a course in lichenology. John has been a kind, patient, and extremely supportive teacher to me and to several other lichenologists who came here to learn from him over the years; we are the lucky few.

I have greatly enjoyed and benefited from his consultation and encouragement as I moved from student to independent researcher over the years. John has built up and maintained (with minimal financial resources) an outstanding lichen herbarium, reference library and reprint collection which I have been fortunate to be able to use regularly.

John and his wife Olive have remained active and engaged long after retirement age. John comes in regularly to work on his manuscript "Lichens of Wisconsin," when he's not helping Olive with their extensive garden or on trips to garden club or lichenolgy conferences. Plus he still finds time and energy to identify boxes and boxes of lichen specimens from colleagues and students across the continent. And keep up with myriad changes in the profession! My goal for myself as I age is to be as active, engaged, and open to advances in lichenology and life in general as is Dr. John Thomson.

---Susan Will-Wolf

*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
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# SEARCHING FOR CALICIALES IN THE ADIRONDACKS OF NEW YORK

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Abstract: Twenty-one Caliciales species in 9 genera are reported for three previously investigated northern hardwoods stands in the Adirondacks of New York. Given the fact that no Caliciales were listed among the 63 lichen taxa recorded in the original study, and that most of the species recorded in the reinvestigation were associated with microhabitats that were not included in the original sampling procedure, it is suggested that it is not so much the small size of these species that eludes detection as it is the fact that we are not looking for them in the right places.

## INTRODUCTION

Since remarking in 1845 that "it is not every eye that can see a *Calicium*; nor are they easily to be found. . .", Edward Tuckerman's "most puzzling group of lichens", the Caliciales, are, today, as elusive as ever (Tuckerman 1845). How is it that these species--perhaps our most sensitive biomonitors, either escape detection completely, or are represented in our floras by only the commonest and most obvious forms? Are they really that small, or have we been looking for them in the wrong places? Twenty years' experience teaching a field course in lichenology and searching for Caliciales species in the Northeast suggest the latter and becomes the working hypothesis for the current investigation.

Since the summer of 1986, I have been engaged in a research project in which lichens are being used to assess the continuity of forest ecosystems in northern New England and Maritime Canada. Patterned after a study by Francis Rose (1974, 1976) in Britain, the continuity of 33 northern hardwood and spruce-fir stands in Maine, New Hampshire, Vermont, and New Brunswick have been assessed using indices of ecological continuity that are based upon the percentage occurrence of ancient forest indicator lichen species found at each site (Selva 1994, 1996). The data show that not only do epiphytic lichen floras become richer over time--with older stands harboring more rare species, but that the total number and presence of particular Caliciales species collected at a site is, itself, an indicator of continuity.

According to Tibell (1980), the Caliciales are "very sensitive to changes in forest climate, and most species indeed seem to depend on the occurrence of mature forests containing trees of different ages and a varied light and humidity regime." Like Tibell, who noted that, because of clearcutting, the majority of Caliciales species "have already been exterminated over vast areas of Scandinavia and are now found only in forest reserves and national parks", I, too, have recorded similar declines in northern New England where many of the rarer Caliciales are restricted to old-growth and ancient forest sites (e.g., Selva 1988, 1994, 1996). Interestingly, of the 20 lichen index species selected by Tibell (1992) for an Indicator Species Index of Forest Continuity designed for the boreal forests from southern Sweden to Lapland, 10 belong to the Caliciales.

During the summer of 1994, I decided to expand my study area westward into the Adirondacks of northern New York. The lichens at Adirondack Mountain Reserve, Ampersand Mountain, and Forked Lake Forest Preserve, two old-forest and one young forest stand, respectively, had previously been studied by Schmitt and Slack (1990) as part of a comparison of epiphytic lichens and bryophytes between the Adirondack Mountains and the Southern Blue Ridge Mountains of North Carolina. They compared host specificity for *Acer saccharum*, *A. rubrum*, *Betula alleghaniensis*, *Fagus grandifolia*, and *Tsuga canadensis* both between the Adirondacks and Blue Ridge Mountains, as well as with other studies for which epiphyte data was available. On the basis of lichen species lists provided by me, for example, they determined that 61% of the species they recorded on *Acer saccharum*, 59% of the species they recorded on *Betula alleghaniensis*, and 57% of the species they recorded on *Fagus grandifolia* in the Adirondacks can also be found in northern Maine (Schmitt and Slack 1990).

When I began looking at the actual species represented in these percentages, I found it curious that there were no Caliciales species recorded among the 63 lichen taxa reported by them for the Adirondacks. I decided to conduct my own investigation of these sites and, in order to test my hypothesis, would concentrate my collecting effort on microhabitats not included in the original sampling procedure. Specifically, this meant that I would include "the full range of southern exposures", "the lower half meter of trunks", lignicolous substrates, and trees at various stages of decomposition (Schmitt and Slack 1990).

## METHODS

The mixed northern hardwoods sites at Adirondack Mountain Reserve, Ampersand Mountain, and Forked Lake Forest Preserve in the Adirondack State Park in northern New York--previously investigated by Schmitt and Slack (1990) and described by them in detail--were visited over the course of three days by me and a field assistant.

Caliciales specimens were collected from all corticolous and lignicolous substrates, with no bias as to their condition, in a conscious effort to collect specimens from the diversity of substrate types present. Epiphytes from standing as well as fallen trees, whether intact or at some stage of decompositon, were collected in systematic traverses of the terrain. Specimens on standing trees were collected from breast height downward to soil level, and from accessible branches. All surfaces and edges of substrate fragments were examined in the lab, where specimens were identified using standard techniques and following nomenclature according to Esslinger and Egan (1995). Specimens are currently housed in the herbarium at the University of Maine at Fort Kent.

## RESULTS AND DISCUSSION

Because the aging old-growth forest is a dynamic place offering a wide variety of ever-changing microhabitats, a reliable typological concept of Caliciales communities is not easily developed. It includes, in large part, the so-called Calicion alliance discussed by Barkman (1958), James, Hawksworth and Rose (1977), and Rose and Wolseley (1984) and described by them as a species diverse association, rich in the Caliciaceae, found on dry sides of ancient trees and on decorticated wood in humid situations with plenty of diffuse light but without direct sunlight.

In my investigations of the alliance, to date, in Maine, New Brunswick, New Hampshire and Vermont, recognizable patterns of distribution have become apparent. Because of the even supply of wood in various stages of decay that characterize natural forests in late successional stages, the species diversity of Caliciales on decorticated surfaces increases with stand age and decomposition of the substrate. A 60 year old hardwood stand, for example, may have only 2-3 species–represented almost invariably by *Mycocalicium subtile* and other “weedy” Mycocaliciaceae, while an old-growth stand may have 5-10 lignicolous Caliciales. Specific microhabitats include standing, decorticated hulks, stumps, and fallen logs and branches and exposed heartwood of living trees. Substrates are typically dry, the surface intact and smooth vs powdery or crumbly.

Certain species typically found on lignum (e.g., *Calicium salicinum, Mycocalicium subtile,* and *Chaenotheca trichialis*) are more frequently also found on bark in aging forests. This may be due in large part to the acidification of bark that occurs during stand succession (Barkman 1958). Also borne out in my earlier investigations is the contention by Hyvarinen et al. (1992) that the tolerance of many of the Caliciaceae to acidity "may be a decisive factor in competition with macrolichens for space". This would help explain the near exclusion of all but the Caliciales on the trunks of many of the oldest trees at many of these old-growth sites. I have found up to four or five Caliciales species on the bark of trees passed over by others for lack of a macrolichen flora.

While preliminary results show that the Calicion may be found on all sides of older trees–from near the base to approximately 2 meters high, you will not find many species growing among the rest of the lichen epiphytes on the trunk. You will find them instead on the side of the tree where they are not competing with the other lichens and bryophytes for space and where they are out of direct sunlight. Some of the exceptions are *Sphinctrina*, which typically grows parasymbiotically with *Pertusaria* or *Lecanora* species and *Phaeocalicium polyporaeum*, which grows associated with polypores. Also, except for *Sphinctrina*, neither the upper trunk nor the canopy branches of hardwoods or conifers support much of a Caliciales flora.

Some of the least investigated of the Caliciales microhabitats include that of smooth bark--specifically that of saplings and seedlings, but sometimes also including the branches of older trees. Several *Stenocybe* and *Phaeocalicium* species are restricted to the smooth bark of *Alnus, Betula, Quercus*, or *Rhus,* for example. Other microhabitats are the roots of upturned trees, cave-like "grottos" formed at the base of trees, the surface of polypores, and resin--including that formed around broken branch collars. Species may also be restricted to the more porous inner bark of certain species, found down in the cracks of deeply fissured bark, and on the lower surface of bark chips and flakes.

Twenty-one Caliciales species in 9 genera (Table 1) were collected on eleven different tree species at the three Adirondack State Park sites under investigation (Table 2). Eighteen of these species were collected on *Acer saccharum, Acer rubrum, Betula alleghaniensis, Fagus grandifolia*, and *Tsuga canadensis*, the host trees studied by Schmitt and Slack (1990), while 3 species *Calicium trabinellum, Sphinctrina anglica,* and *Stenocybe major* were collected exclusively on other tree species.

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Table 1. The following Caliciales species were recorded at the three Adirondack sites under investigation.

1. *Calicium parvum*
2. *Calicium salicinum*
3. *Calicium trabinellum*
4. *Chaenotheca chrysocephala*
5. *Chaenotheca ferruginea*
6. *Chaenotheca furfuracea*
7. *Chaenotheca stemonea*
8. *Chaenotheca trichialis*
9. *Chaenothecopsis brevipes*
10. *Chaenothecopsis debilis*
11. *Chaenothecopsis pusilla*
12. *Chaenothecopsis pusiola*
13. *Chaenothecopsis rubescens*
14. *Chaenothecopsis savonica*
15. *Cyphelium lucidum*
16. *Microcalicium disseminatum*
17. *Mycocalicium subtile*
18. *Phaeocalicium polyporaeum*
19. *Sphinctrina anglica*
20. *Sphinctrina turbinata*
21. *Stenocybe major*

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All species were found associated with one or more of the microhabitats discussed in the introduction to this section, which would seem to confirm the hypothesis that we have heretofore been looking for Caliciales species in the wrong places.

Most of the species reported here and much of the information on substrate ecology corresponds with data reported by me for northern Maine (Selva 1988). Among the more interesting species recorded here is *Chaenothecopsis brevipes*, which was found growing on *Betula alleghaniensis* at Forked Lake Forest Preserve. This is only the second published report of this species in North America, although the species reported by Harris (1977) as *Chaenothecopsis* sp. #2 was later annotated by Leif Tibell as *C. brevipes* (Harris, personal communication). As in Maine, where it was first reported (Selva 1988), it was found growing with *Chaenothecopsis rubescens* over *Arthonia byssacea*. The only Adirondack species that I have yet to find in Maine is *Sphinctrina anglica*. According to Lofgren and Tibell (1979) this species has, for reasons that are not yet understood, been experiencing a pronounced decline in Europe and is considered by them to be extremely rare. Unlike *Sphinctrina turbinata*, which, like other northeastern *Sphinctrina* species, is found growing on *Pertusaria, Sphinctrina anglica* is associated with an otherwise sterile crust identified by some as a *Lecanora*.

Finally, inasmuch as Schmitt and Slack (1990) do not list their species by site, but for the Adirondacks as a whole, it is impossible to assess the continuity of these stands using the index of ecological continuity developed by Selva (1994, 1996) for northern hardwoods. The Caliciales data alone, however, confirms the old-growth status of the stands at Adirondack Mountain Reserve and Ampersand Mountain and suggest that the stand at Forked Lake is as well. In fact, with 16 Caliciales species, including *Chaenothecopsis brevipes* and *Sphinctrina anglica*, the Forked Lake stand may well be an ancient one.

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As one of the reviewers of my first lichenological manuscript, "The Caliciales of Northern Maine", John Thomson's flattering comments not only made my day, but actually helped convince me that this was the field of research I belonged in. His continued support over the years has encouraged me to pursue the high standards that he set during his career as a researcher and teacher.

John Thomson is a great natural teacher. I first met him on the 1971 ABLS foray in Alberta and British Columbia. He had guided the bus driver to the nearest tree and was instructing him in the identification of corticolous lichens!

Later I visited my son, a graduate student at the University of Wisconsin, and stopped in to see Dr. Thomson. As a shy beginner in lichenology I did not risk bringing any of my many problems with me. What a mistake! He greeted me, "What, you didn't bring anything for me to look at?" Needless to say, on future visits I brought my puzzles along. And I became bold enough to mail even more specimens. He was always gracious and helpful.

Thanks, Dr. Thomson.

--- Claire Schmitt

Table 2. Caliciales found as corticolous (C) or lignicolous (L) epiphytes at Adirondack Mountain Reserve, Ampersand Mountain, and Forked Lake Forest Preserve. Host trees studied are *Acer saccharum* (As), *Acer rubrum* (Ar), *Betula alleghaniensis* (Ba), *Fagus grandifolia* (Fg), *Fraxinus americana* (Fa), *Prunus serotina* (Pse), *Tsuga canadensis* (Tc), *Thuja occidentalis* (To), *Picea rubens* (Pr), *Pinus strobus* (Pst), *Abies balsamea* (Ab), and unidentifiable lignicolous substrates (US). The lichen species are indicated by the numbers from Table 1.

| | Adirondack Mountain Reserve | | | | | | | Ampersand Mountain | | | | | Forked Lake Forest Preserve | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | As | Ba | Fa | To | Fg | Tc | Pr | As | Tc | Ba | Fg | US | As | Ar | Ba | US | Ab | To | Pse | Pst | Tc | Pr |
| 1 | | | | | | C | | | | | | | | | | | | | | | | |
| 2 | | | | | | | | | | | | | | L | | L | | | | | | |
| 3 | | | | | | | | | | | | | | | | L | | L | | | | |
| 4 | | C | | | | C | | | C | | | | | | C | | | | C | | | |
| 5 | | | | | | | | | C | C | | L | | | C | | | L | C | | C | |
| 6 | C | | | | C | | | C | | | | | | | C | | | | | | | |
| 7 | C | | | | | | | | | | | | | | | | | | | | | |
| 8 | C<br>L | C | | | L | | | | L | | | | | | C<br>L | L | L | | C | | | |
| 9 | | | | | | | | | | | | | | | $C^1$ | | | | | | | |

| | As | Ba | Fa | To | Fg | Tc | Pr | As | Tc | Ba | Fg | US | As | Ar | Ba | US | Ab | To | Pse | Pst | Tc | Pr |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10 | | | | | C<br>L | | | | | | | | L | L | L | L | | | | | | |
| 11 | | L | | | | C | C | | C | | | | | | | | | | | | C | C |
| 12 | L | | | | L | | | | | | | | | | L | L | L | | | | | |
| 13 | C[1] | C[1] | C[1] | C[1] | | | | C[1] | | | | | | | C[1] | | | | | | | |
| 14 | | C | | | | | | C | | | | | | | | | | | | | | |
| 15 | | | | | | | | | | | | | | | C | | | | | | | |
| 16 | | C | | | | | | | | | | | | | | | | | | | | |
| 17 | | | | | L | L | C<br>L | C | L | | | | | L | C | L | L | | L | | C | |
| 18 | | C[2] | | | | | | | | | C[2] | | | | | | | | | | | |
| 19 | | | | | | | | | | | | | | | | | | C[4] | | C[4] | | |
| 20 | | C[3] | | | | | | | | | | | | C[3] | | | | | | | | |
| 21 | | | | | | | | | | | | | | | | | C | | | | | |

[1] Growing over *Arthonia byssacea*

[2] Growing on polypore *Hirschioporus pergamenus*

[3] Growing over *Pertusaria macounii*

[4] Growing over *Lecanora* sp.

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# AN ANNOTATED CHECKLIST OF MAINE MACROLICHENS

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**ABSTRACT:** An annotated checklist of fruticose, foliose, squamulose, and filamentous lichens of Maine has been compiled from published and unpublished sources. It contains 349 species, of which 47 have not been previously published for Maine. One species, *Parmeliopsis capitata* R. C. Harris, has been legitimized with a Latin diagnosis. For each species, information has been provided on relative abundance in Maine, general distribution in Maine, first published report, latest monograph report, county distribution (for species with less than 10 known sites in Maine), and a specimen citation (for newly reported species and for species with less than 5 known sites). A list of excluded species is also provided. The relative richness of the Maine macrolichen flora as well as its biogeographical affinities are discussed.

## INTRODUCTION

Just over 100 years ago two important papers on Maine lichens appeared. F. L. Harvey (1894) published a list of 115 taxa known from Maine, most collected by Joseph Blake in the 1850's and identified by Edward Tuckerman, but also including species recorded by Tuckerman (1882,1888) and ones collected by Harvey and probably identified by Clara E. Cummings. In the same year Eckfeldt (1894) published a chapter on lichens in Rand and Redfield's book on the flora of Mt. Desert Island listing 273 lichen taxa, based on collections by himself, M. L. Wilson, E. L. Rand , and J. H. Redfield during the previous six years; these specimens were identified by Eckfeldt, Wilson, and Cummings. Most of Blake's specimens are now at the University of Maine Herbarium (MAINE), and many of those in Eckfeldt's list are in the New England Botanical Club's Herbarium (NEBC) at Harvard University. Since neither of these herbaria has been well studied previously by lichenologists, the present authors have made a special effort to search these herbaria to verify Harvey's and Eckfeldt's reported species.

During the subsequent 100 years numerous collectors and authors have contributed to the knowledge of Maine's lichens, only a few of which can be mentioned here (for a complete bibliography of floristic studies on Maine lichens, see Selva 1996). The well-known lichenologist G. K. Merrill collected intensively in Maine, especially in Knox County, from just after the turn of the century until just before his death in 1927. Merrill kept a county list of Maine lichens (Merrill ca. 1926) that was more comprehensive than any previously (or subsequently) published, containing approximately 650 taxa. Unfortunately, this list was never published, but it is available from Harvard's Farlow Library. J. C. Parlin also collected intensively, in his case from southern Oxford County in southwestern Maine, and published a comprehensive list of his collecting efforts in 1939. His list is notable for its excellent coverage of *Cladonia*s, identified by Alexander Evans. Also in 1939, a European lichenologist, G. Degelius, visited the State for two weeks and published his results the following year (Degelius 1940); his taxonomy was more modern than that of Parlin and Merrill. For the next 40 years little floristic lichen work in Maine was done. In the 1980's two important studies were carried out: Sullivan and Wetmore on the lichens of Acadia National Park (Wetmore 1984; Sullivan 1996), and Selva on the lichen epiphytes of northern Maine (Selva 1986, 1988, 1989).

Maine (Figure 1) is the northeasternmost state, abutting New Hampshire on the West, Quebec, Canada on the Northwest, New Brunswick, Canada on the Northeast, and the Atlantic Ocean on the Southeast. It is 86,027 sq. km (33,215 sq. miles) in extent and occupies almost exactly one-half of New England (Lautzenheiser 1972); it extends north 4½ degrees of latitude from around 43° N, and west 4° from about the 67th meridian. In elevation it ranges from sea level to 1605 meters (Mt. Katahdin). Its bedrock geology consists mostly of Paleozoic metamorphic rock (Cambrian to Devonian), but extensive areas of intrusive granite also occur. Limestone-loving lichens are most common in Knox and Aroostook Counties, but some also occur scattered throughout most of the State. The entire State was covered by glaciers during the Pleistocene.

Maine's climate has been summarized by Lautzenheiser (1972). Temperature extremes range form -44° C (-48° F) to 41° C (105° F). Mean maximum temperature in July ranges from around 21° C (70° F) in extreme eastern Maine to 29° C (84° F) in southwestern parts; mean minimum temperatures range from -10° C (14° F) in southernmost Maine (and in the mid-coast islands of Deer Isle, Isle au Haut, and Mt. Desert Island) to less than -18° C (0° F) in northernmost Maine. The mid-coast islands mentioned above have been found to have some species at the northernmost extent of their range (e.g. *Parmelinopsis horrescens* and *Cladonia mateocyatha*) as well as other species at their southernmost extent (e.g. *Alectoria ochroleuca* and *Psoroma hypnorum*). This paradoxical result presumably arises because these islands are both mild in the winter and cool in the summer because of the influence of the ocean. Maine's precipitation is relatively even throughout the year, with serious droughts uncommon; it ranges from 91 cm (36") in northern Maine to 122 cm (48") in eastern Maine. Fog is common along the immediate coast, especially in northeastern parts, and also at high elevations in the mountains; these areas of frequent fog also correspond with areas where lichens grow the most luxuriantly in Maine.

The natural vegetation zones of Maine follow the climate and vary from temperate through boreal to alpine. The dotted line in Figure 1 shows the division between two such zones in Maine, that between a region dominated by spruce, fir, and northern hardwoods in northern and eastern Maine and that dominated by transitional hardwoods, white pine, and hemlock in southern and central Maine. This map was generated from maps of McMahon (1990) and Westveld et al. (1956). The northern region can be considered boreal (hemiboreal in Ahti's (1964) scheme), while the southern region can be considered temperate. As mentioned above, the mid-coast islands are considered to have elements of both northern and southern regions (the dividing line in Figure 1 splits to accommodate these islands). In addition to temperate and boreal regions, Maine has one true alpine region (Mt. Katahdin in Piscataquis Co.) and several mountains whose tops have some alpine zone characteristics (e.g. Bigelow Mt. in Somerset Co., Saddleback Mt. in Franklin Co. and Old Speck in Oxford Co.).

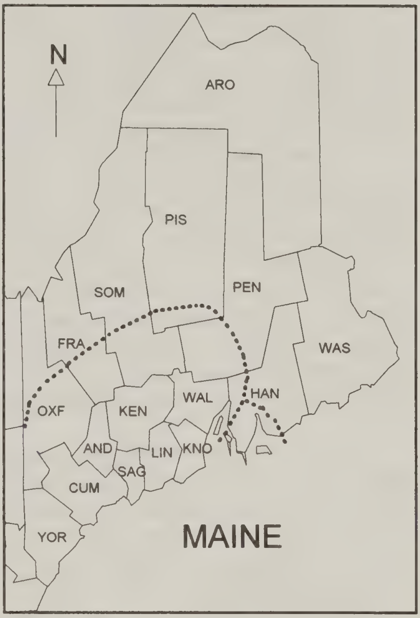

**FIGURE 1**

## EXPLANATION OF CONVENTIONS USED IN THE CHECKLIST

This checklist includes only squamulose, foliose, fruticose, and filamentous forms of lichens (macrolichens); crustose, granular, and subsquamulose forms have been excluded. Species names follow the Sixth Checklist (Esslinger & Egan 1995), with the following exceptions: (1) subspecies and varieties are not included; (2) *Parmeliopsis capitata* R. C. Harris is included; (3) *Catapyrenium squamulosum* (Ach.) Breuss becomes *Placidium squamulosum* (Ach.) Breuss (Breuss 1996); (4) *Leptogium hirsutum* Sierk is considered a variety of *L. burnetiae* C. W. Dodge (Goward et al. 1994); (5) *Thamnolia subuliformis* (Ehrh.) Culb. is considered conspecific with *T. vermicularis* (Sw.) Ach. *ex* Schaerer (Kärnefelt & Thell 1995); (6) *Usnea variolosa* Mot. is considered conspecific with *Usnea hirta* (L.) F. H. Wigg. (Clerc 1997).

An asterisk (*) before a species name indicates that that species has not previously been reported for Maine. Most reports of limited circulation (e.g.

Selva 1986, 1988, 1989; Wetmore 1984; Sullivan 1996) have been considered valid reports, but Merrill's unpublished list (ca. 1926) has not. If an author has reported a species that later has been split (e.g. *Cladonia coccifera* (L.) Willd.), and the specimen has not later been re-identified, it is not considered a valid report. An exclamation point (!) immediately preceding the species name indicates that one or both of the present authors has examined a specimen of that species from Maine. An indication of how common the species is in Maine immediately follows the species name: rare (1-4 known sites), uncommon (5-9 sites), fairly common (10-19 sites), common (20-39 sites), and abundant (40 or more sites). A site is generally considered different if it is more than 1.6 km (1 mile) from another site; the area above tree line on Mt. Katahdin, however, is considered one site. A species' distribution in Maine is indicated by a letter abbreviation following the indication of its abundance: S, all known sites are from the southern area in Figure 1 (including the mid-coast islands); N, all known sites are from the northern area of Figure 1 (including the mid-coast islands); W, widespread, from both northern and southern areas; C, only known from coastal areas (within 16 km [10 miles] of the ocean).

On the line below the species name, up to three kinds of information are presented sequentially: (1) in square brackets [ ]: first accepted published report (Merrill ca. 1926 shown in parentheses as "Merrill's list") and, if present, the latest monograph reporting the species in Maine; (2) in parentheses ( ): county distribution in Maine (only displayed when a species is rare or uncommon in Maine); (3) in curved brackets { }: specimen citation (for newly reported and rare species). In order to be cited as the first published report, the author had to name the species correctly, either the current name or one that can be shown to be equivalent to a current name by valid synonyms. Harvey (1894, 1896) and Eckfeldt (1894) were only cited if one of the present authors verified the cited specimen. If a species was later split, e.g. *Parmelia saxatilis* (L.) Ach., the author's report was accepted only if one of the present authors re-identified a specimen cited by the original author. In selecting the specimen to cite, preference was given to ones seen by one or both of the present authors, to those of the collector who first found it, and to specimens found in the major herbaria. Secondary sources, such as Fink 1935 and Hale 1979, were not relied on for inclusion of a species in the checklist. Herbaria abbreviations follow Holmgren et al. (1990), except for private herbaria. If a species has been found in two counties and two specimens are cited, the order of the specimen cited is the same as the order of the counties. When only one site is known, the town or other location is also given, with the following abbreviations: MDI, Mt. Desert Island; Mt. K, Mt. Katahdin; S.P., State Park.

Following the Checklist is a list of excluded species, divided into four categories: (1) unverified reports: old reports of species that may well occur in Maine but which have not later been verified; (2) probable misidentifications: reported species that the present authors (or other authors) believe likely to be based on misidentifications; (3) borderline species considered crustose; (4) species names not validly published

# CHECKLIST

! **Ahtiana aurescens** (Tuck.) Thell & Randlane - fairly common (W)
[(Merrill's list); Degelius 1940]

! **Alectoria ochroleuca** (Hoffm.) A. Massal. - 1 site (C)
[Eckfeldt 1894] (HAN) {MDI, 1888, Eckfeldt 3, NEBC!}

! **Alectoria sarmentosa** (Ach.) Ach. - uncommon (N)
[Howe 1911a; Brodo & Hawksworth 1977] (HAN, KNO, PIS, WAS)

! **Allocetraria oakesiana** (Tuck.) Randlane & Thell - abundant (W)
[Eckfeldt 1894; Hale 1956]

! **Anaptychia palmulata** (Michaux) Vainio - fairly common (W)
[(Merrill's list); Degelius 1940]

* ! **Anaptychia setifera** Räsänen - 1 site (N)
(ARO) {T15 R9 WELS, 1984, Selva 1111, SELVA!}

! **Anzia colpodes** (Ach.) Stizenb. - uncommon (W)
[Harvey/Eckfeldt 1894; Hale 1955a] (AND, ARO, CUM, HAN, KNO, PEN, PIS)

! **Arctoparmelia centrifuga** (L.) Hale - common (W)
[Tuckerman 1882]

! **Arctoparmelia incurva** (Pers.) Hale - fairly common (W)
[Tuckerman 1882]

**Baeomyces carneus** Flörke - 1 site (N)
[Thomson 1967] (PIS) {Mt. K, Wiley 16, WIS}

! **Baeomyces rufus** (Hudson) Rebent. - fairly common (W)
[Eckfeldt 1894; Thomson 1967]

! **Biatora anthracophila** (Nyl.) Hafellner - uncommon (N)
[Sullivan 1996] (ARO, HAN)

**Bryocaulon divergens** (Ach.) Kärnefelt - 1 site (N)
[Degelius 1940: SW slope of Mt. Katahdin at 1400 m]

! **Bryoria capillaris** (Ach.) Brodo & D. Hawksw. - fairly common (N)
[Brodo & Hawksworth 1977]

**Bryoria friabilis** Brodo & D. Hawksw. - 1 site (C)
[Brodo & Hawksworth 1977] (SAG) {Reid S.P., Taylor 487, MSC}

! **Bryoria furcellata** (Fr.) Brodo & D. Hawksw. - abundant (W)
[Harvey/Eckfeldt 1894; Brodo & Hawksworth 1977]

! **Bryoria fuscescens** (Gyelnik) Brodo & D. Hawksw. - fairly common (W)
[Brodo & Hawksworth 1977]

! **Bryoria implexa** (Hoffm.) Brodo & D. Hawksw. - 1 site (C)
[(Merrill's list); Brodo & Hawksworth 1977] (KNO) {Camden, 1904, Merrill s.n., FH!}

**Bryoria lanestris** (Ach.) Brodo & D. Hawksw. - 1 site (N)
[Brodo & Hawksworth 1977] (PEN) {Bangor, 1896, E. D. Merrill s.n., US}

! **Bryoria nadvornikiana** (Gyelnik) Brodo & D. Hawksw. - common (W)
[Degelius 1940; Brodo & Hawksworth 1977]

! **Bryoria salazinica** Brodo & D. Hawksw. - 2 sites (C)
[Brodo & Hawksworth 1977] (WAS) {Farlow s.n., FH!}

! **Bryoria trichodes** (Michaux) Brodo & D. Hawksw. - abundant (W)
[Brodo & Hawksworth 1977]

! **Candelaria concolor** (Dickson) Stein - common (W)
[Parlin 1923]

! **Candelaria fibrosa** (Fr.) Müll. Arg. - uncommon (W)
[Parlin 1939] (ARO, CUM, PEN)
! **Cetraria aculeata** (Schreber) Fr. - fairly common (W)
[Eckfeldt 1894; Kärnefelt 1986]
! **Cetraria arenaria** Kärnefelt - fairly common (W)
[Kärnefelt 1979]
! **Cetraria islandica** (L.) Ach. - 2 sites (N)
[Harvey 1894] (PIS) {1856, Blake s.n., MAINE!; Richards, MAINE!}
! **Cetraria laevigata** Rass. - uncommon (N)
[Kärnefelt 1979] (FRA, HAN, OXF, PIS, SOM)
! **Cetraria muricata** (Ach.) Eckfeldt - 4 sites (C)
[Kärnefelt 1986] (SAG, WAS) {WAS, 1996, Hinds 3622, HINDS!}
! **Cetrariella delisei** (Bory *ex* Schaerer) Kärnefelt & Thell - 2 sites (N)
[Eckfeldt 1894; Kärnefelt 1979] (HAN, PIS) {PIS, 1939, Degelius s.n., US}
! **Cetrelia chicitae** (Culb.) Culb. & C. Culb. - common (W)
[Culberson 1965]
! **Cetrelia olivetorum** (Nyl.) Culb. & C. Culb. - common (W)
[Culberson 1962; Culberson & Culberson 1968]
! **Cladina arbuscula** (Wallr.) Hale & Culb. - abundant (W)
[Parlin 1935; Ahti 1961]
! **Cladina mitis** (Sandst.) Hustich - abundant (W)
[Parlin 1935, Ahti 1961]
! **Cladina rangiferina** (L.) Nyl. - abundant (W)
[Harvey/Eckfeldt 1894; Ahti 1961]
! **Cladina stellaris** (Opiz) Brodo - abundant (W)
[Harvey/Eckfeldt 1894; Ahti 1961]
! **Cladina stygia** (Fr.) Ahti - uncommon (N)
[Torrey 1938] (ARO, FRA, HAN, PIS)
* ! **Cladina submitis** (A. Evans) Hale & Culb. - 1 site (S)
[(Ahti 1961:?)] (YOR) {Ferry Beach S.P., 1995, Hinds 3312, HINDS!}
! **Cladina subtenuis** (Abbayes) Hale & Culb. - uncommon (S)
[Degelius 1940; Ahti 1961] (CUM, OXF, SAG, WAL)
! **Cladina terrae-novae** (Ahti) Hale & Culb. - fairly common (W)
[(Ahti 1961: "most likely"); Wetmore 1984]
! **Cladonia acuminata** (Ach.) Norrlin - uncommon (W)
[Parlin 1935; Thomson 1968] (AND, ARO, CUM, PEN, WAL)
! **Cladonia amaurocraea** (Flörke) Schaerer - uncommon (N)
[Harvey 1894] (ARO, FRA, PIS, SOM)
! **Cladonia apodocarpa** Robbins - 3 sites (S)
[Parlin 1935] (OXF, SOM) {SOM, 1993, Hinds 2944a, HINDS!}
! **Cladonia atlantica** A. Evans - fairly common (C)
[Wetmore 1984]
* ! **Cladonia borealis** S. Stenroos - 1 site (N)
(HAN) {MDI, 1888, Eckfeldt s.n., NEBC!}
! **Cladonia boryi** Tuck. - common (W)
[Harvey/Eckfeldt 1894; Ahti 1973]
! **Cladonia botrytes** (K. Hagen) Willd. - 4 sites (W)
[Degelius 1940] (ARO, CUM, PIS) {ARO, 1972, Hurst 202, HURST!}
! **Cladonia brevis** (Sandst.) Sandst. - 2 sites (S)
[Evans 1932; Thomson 1968] (HAN, KEN) {HAN, 1983, Sullivan 1223, MIN}

! **Cladonia caespiticia** (Pers.) Flörke - fairly common (W)
[Eckfeldt 1894]

! **Cladonia cariosa** (Ach.) Sprengel - fairly common (W)
[Fink 1906]

! **Cladonia carneola** (Fr.) Fr. - 2 sites (S)
[Parlin 1939; Thomson 1968] (OXF, SAG) {OXF, 1936, Parlin 12736, US!}

! **Cladonia caroliniana** Tuck. - fairly common (C)
[Ahti 1973]

! **Cladonia cenotea** (Ach.) Schaerer - abundant (W)
[Eckfeldt 1894]

! **Cladonia cervicornis** (Ach.) Flotow - common (W)
[Fink 1904]

! **Cladonia chlorophaea** (Flörke *ex* Sommerf.) Sprengel - common (W)
[Bowler 1972]

* ! **Cladonia coccifera** (L.) Willd. - 2 sites (N)
(ARO, PIS) {ARO, 1992, Hinds 2806, HINDS!}

! **Cladonia coniocraea** (Flörke) Sprengel - abundant (W)
[Eckfeldt 1894]

! **Cladonia conista** A. Evans - uncommon (W)
[Parlin 1935] (ARO, FRA, HAN, LIN, OXF, PIS)

! **Cladonia cornuta** (L.) Hoffm. - common (W)
[Parlin 1939]

! **Cladonia crispata** (Ach.) Flotow - abundant (W)
[Riddle 1909; Thomson 1968; includes *C. subsubulata* Nyl.]

! **Cladonia cristatella** Tuck. - abundant (W)
[Harvey/Eckfeldt 1894]

! **Cladonia cryptochlorophaea** Asah. - uncommon (W)
[Bowler 1972] (CUM, FRA, HAN, PEN, SOM)

! **Cladonia cylindrica** (A. Evans) A. Evans - uncommon (S)
[Pitman 1932] (FRA, HAN, OXF, YOR)

! **Cladonia decorticata** (Flörke) Sprengel - uncommon (W)
[Parlin 1935] (ARO, CUM, KNO, HAN, OXF, PEN, PIS, SOM)

! **Cladonia deformis** (L.) Hoffm. - common (W)
[Eckfeldt 1894]

! **Cladonia digitata** (L.) Hoffm. - common (W)
[Eckfeldt 1894]

! **Cladonia dimorphoclada** Robbins - 1 site (S)
[Ahti 1973] (KNO) {1924, Merrill, FH! (Sandstede Clad. Exs. 1471)}

! **Cladonia ecmocyna** Leighton - 3 sites (N)
[Evans 1952; Thomson 1968] (HAN, PIS, WAS) {HAN, 1894, Rand s.n., FH!}

! **Cladonia farinacea** (Vainio) A. Evans - uncommon (W)
[Wetmore 1984] (ARO, HAN, KEN, PEN, PIS)

! **Cladonia fimbriata** (L.) Fr. - common (W)
[Eckfeldt 1894]

! **Cladonia floerkeana** (Fr.) Flörke - common (W)
[Torrey 1934]

! **Cladonia furcata** (Hudson) Schrader - abundant (W)
[Merrill 1909a; Riddle 1909]

! **Cladonia gracilis** (L.) Willd. - abundant (W)
[Harvey/Eckfeldt 1894; Ahti 1980]

! **Cladonia grayi** G. Merr. *ex* Sandst. - abundant (W)
[Parlin 1935]

! **Cladonia incrassata** Flörke - fairly common (W)
[Merrill 1924]

! **Cladonia macilenta** Hoffm. - abundant (W)
[Riddle 1909]

* ! **Cladonia macrophylla** (Schaerer) Stenh. - 1 site (N)
(PIS) {Mt. K, 1992, Hinds 2608, HINDS!}

! **Cladonia mateocyatha** Robbins - uncommon (S)
[Pitman 1932] (HAN, OXF)

! **Cladonia maxima** (Asah.) Ahti - abundant (W)
[Ahti 1980]

! **Cladonia merochlorophaea** Asah. - fairly common (N)
[Bowler 1972]

! **Cladonia metacorallifera** Asah. - 1 site (N)
[Selva 1988] (ARO) {T14 R13 WELS, 1987, Selva 1363, SELVA!}

! **Cladonia multiformis** G. Merr. - common (W)
[Merrill 1909a]

! **Cladonia ochrochlora** Flörke - uncommon (W)
[Torrey 1934] (AND, ARO, KEN, OXF, PIS, SAG)

! **Cladonia parasitica** (Hoffm.) Hoffm. - uncommon (S)
[Riddle 1909, Thomson 1968] (CUM, HAN, OXF, PEN)

! **Cladonia peziziformis** (With.) J. R. Laundon - 1 site (S)
[(Merrill's list); Thomson 1968] (KNO) {Rockport, 1914, Merrill s.n., FH!}

! **Cladonia phyllophora** Hoffm. - uncommon (W)
[(Merrill's list); Torrey 1934] (ARO, HAN, KNO, OXF)

! **Cladonia pleurota** (Flörke) Schaerer - common (W)
[Pitman 1932; Stenroos 1989]

* ! **Cladonia pocillum** (Ach.) Grognot - 2 sites (S)
[(Merrill's list)] (KNO) {1907, Merrill s.n., FH!}

! **Cladonia polycarpoides** Nyl. - uncommon (S)
[Merrill 1909b] (CUM, KNO, HAN, OXF, PEN)

! **Cladonia pyxidata** (L.) Hoffm. - common (W)
[Cummings & Seymour 1894]

! **Cladonia ramulosa** (With.) J. R. Laundon - fairly common (W)
[Riddle 1909]

* ! **Cladonia rappii** A. Evans - 2 sites (C)
(OXF, WAS) {1936, Parlin, MAINE!; 1970, Malcolm s.n., MAINE!}

! **Cladonia rei** Schaerer - fairly common (W)
[Pitman 1932]

! **Cladonia scabriuscula** (Delise) Nyl. - common (W)
[Riddle 1909]

! **Cladonia sobolescens** Nyl. *ex* Vainio - uncommon (W)
[Parlin 1935] (CUM, OXF, PEN)

! **Cladonia squamosa** Hoffm. - abundant (W)
[Harvey/Eckfeldt 1894]

! **Cladonia strepsilis** (Ach.) Grognot - common (W)
[Torrey 1934; Thomson 1968]

! **Cladonia subulata** (L.) F. H. Wigg. - uncommon (W)
[Parlin 1935] (ARO, HAN, OXF, PEN)

! **Cladonia sulphurina** (Michaux) Fr. - uncommon (W)
[Wetmore 1984] (ARO, CUM, FRA, HAN, KNO, SOM)

! **Cladonia turgida** Hoffm. - abundant (W)
[Harvey/Eckfeldt 1894]

! **Cladonia uncialis** (L.) F. H. Wigg. - abundant (W)
[Harvey/Eckfeldt 1894]

**Coccocarpia palmicola** (Sprengel) Arv. & D. J. Galloway - 1 site
[Arvidsson 1982]

* ! **Collema bachmanianum** (Fink) Degel. - 1 site (S)
[(Merrill's list)] (KNO) {Rockland, 1997, Hinds 3834, HINDS!}

! **Collema flaccidum** (Ach.) Ach. - 3 sites (W)
[Merrill 1912; Degelius 1954, 1974] (ARO, KNO, PEN) {KNO, 1909, Merrill, FH!}

! **Collema furfuraceum** (Arnold) Du Rietz - 3 sites (W)
[Degelius 1954] (HAN, PEN) {HAN, 1990, Hinds 2491b, HINDS!}

* ! **Collema fuscovirens** (With.) J. R. Laundon - 4 sites (S)
[(Merrill's list)] (KEN, KNO, SOM) {SOM, 1984, Hinds 647, HINDS!}

! **Collema leptaleum** Tuck. - uncommon (W)
[Eckfeldt 1894; Degelius 1974] (ARO, CUM, HAN, PEN, PIS)

* ! **Collema limosum** (Ach.) Ach. - 2 sites (W)
[(Merrill's list)] (ARO, KNO) {ARO, 1988, Hinds 2217, HINDS!}

! **Collema nigrescens** (Hudson) DC. - fairly common (W)
[Harvey 1894; Degelius 1954]

* ! **Collema occultatum** Bagl. - 1 site (N)
(PEN) {Lee, 1993, Hinds 2981, HINDS!}

* ! **Collema polycarpon** Hoffm. - 1 site (S)
(KNO) {Rockland, 1997, Hinds 3853, HINDS!}

**Collema pulcellum** Ach. - 1 site (N)
[Degelius 1940, 1974: Togue Ponds, 1939] (PIS)

! **Collema subflaccidum** Degel. - common (W)
[Degelius 1954, 1974]

! **Collema tenax** (Sw.) Ach. - uncommon (W)
[Parlin 1939] (ARO, KEN, KNO, LIN)

* ! **Collema undulatum** Laurer *ex* Flotow - 1 site (S)
(KNO) {Rockland, 1997, Hinds 3844, HINDS!}

**Degelia plumbea** (Lightf.) P. M. Jørg. & P. James - 1 site (C)
[Tuckerman 1882; Jørgensen 1978: MDI; also 2 reports in Eckfeldt 1894] (HAN)

! **Dendriscocaulon umhausense** (Auersw.) Degel. - 4 sites (W)
[Selva 1986] (ARO, KNO, PIS) {ARO, 1985, Selva 1664, SELVA!}

! **Dermatocarpon luridum** (With.) J. R. Laundon - fairly common (W)
[Merrill 1911b]

! **Dermatocarpon miniatum** (L.) W. Mann - fairly common (W)
[Eckfeldt 1894]

* ! **Dermatocarpon moulinsii** (Mont.) Zahlbr. - 3 sites (N)
(ARO, PIS) {ARO, 1984, Selva 1116, SELVA!}

! **Dibaeis baeomyces** (L.f.) Rambold & Hertel - abundant (W)
[Harvey/Eckfeldt 1894; Thomson 1967]

**Dirinaria frostii** (Tuck.) Hale & Culb. - 1 site
[Tuckerman 1858]

* **Endocarpon pusillum** Hedwig - 1 site (S)
[(Merrill's list)] (KNO)

! **Ephebe lanata** (L.) Vainio - uncommon (W)
[Sullivan 1996] (ARO, HAN, KNO, PIS, SOM, WAS)
! **Evernia mesomorpha** Nyl. - abundant (W)
[Howe 1911b]
! **Everniastrum catawbiense** (Degel.) Hale *ex* Sipman - fairly common (N)
[Sullivan 1996] (HAN, WAS) {HAN, 1991, Hinds 2568, HINDS!}
! **Flavocetraria cucullata** (Bellardi) Kärnefelt & Thell - 4 sites (N)
[Harvey 1894] (FRA, OXF, PIS, SOM) {PIS, 1856, Blake s.n., MAINE!}
! **Flavocetraria nivalis** (L.) Kärnefelt & Thell - 3 sites (N)
[Harvey 1894] (FRA, PIS) {PIS, 1856, Blake s.n., MAINE!}
* ! **Flavoparmelia baltimorensis** (Gyelnik & Fóriss) Hale - 4 sites (S)
(CUM, HAN, OXF, PEN) {OXF, 1925, Parlin 7884, US!}
! **Flavoparmelia caperata** (L.) Hale - abundant (W)
[Harvey 1894; Hale 1976a]
* ! **Flavopunctelia flaventior** (Stirton) Hale - 2 sites (C)
(WAS) {1973, Lepore 133, MAINE!; 1996, Maxfield s.n., MAINE!}
* ! **Flavopunctelia soredica** (Nyl.) Hale - 1 site (N)
(ARO) {Presque Isle, 1972, Hurst 220, HURST!}
! **Fuscopannaria ahlneri** (P. M. Jørg.) P. M. Jørg. - 3 sites (N)
[Jørgensen 1978] (ARO, PIS) {ARO, 1991, Hinds 2525, HINDS!}
! **Fuscopannaria leucophaea** (Vahl) P. M. Jørg. - uncommon (W)
[Merrill 1912] (ARO, CUM, KEN, KNO, PEN, PIS, SOM, WAL)
! **Fuscopannaria leucosticta** (Tuck.) P. M. Jørg. - 2 sites (W)
[(Merrill list); Degelius 1940] (KNO, PIS) {PIS, 1939, Degelius, FH!}
! **Heterodermia galactophylla** (Tuck.) Culb. - 1 site
[Tuckerman 1860; Kurokawa 1962] {1849, Tuckerman s.n., FH!}
! **Heterodermia hypoleuca** (Muhl.) Trevisan - uncommon (W)
[Harvey 1896; Kurokawa 1962] (ARO, KEN, KNO, PEN, SOM, WAL)
! **Heterodermia obscurata** (Nyl.) Trevisan - uncommon (N)
[Degelius 1940] (HAN, KNO, PIS)
! **Heterodermia speciosa** (Wulfen) Trevisan - common (W)
[Harvey/Eckfeldt 1894]
! **Heterodermia squamulosa** (Degel.) Culb. - 4 sites (W)
[Wetmore 1984] (HAN, PEN, SOM) {SOM, 1976, Hinds 216, HINDS!)
! **Hydrothyria venosa** J. L. Russell - 1 site (N)
[Norton 1926] (OXF) {Andover, 1987, Hinds 1048, HINDS!}
! **Hypocenomyce friesii** (Ach.) P. James & Gotth. Schneider - uncommon (W)
[Sullivan 1996] (ARO, HAN, YOR)
! **Hypocenomyce scalaris** (Ach.) Choisy - fairly common (W)
[Tuckerman 1888; Dirig 1990]
* ! **Hypogymnia austerodes** (Nyl.) Räsänen - 1 site (C)
(KNO) {Rockport, 1910, Merrill s.n., US!}
! **Hypogymnia bitteri** (Lynge) Ahti - 2 sites (N)
[Selva 1986] (ARO, PIS) {ARO, 1984, Selva 1437, SELVA!}
! **Hypogymnia farinacea** Zopf - 1 site (C)
[Merrill 1914] (KNO) {Rockland, 1910, Merrill s.n., FH!}
! **Hypogymnia krogiae** Ohlsson - abundant (W)
[Ohlsson 1973]
! **Hypogymnia physodes** (L.) Nyl. - abundant (W)
[Harvey/Eckfeldt 1894]

! **Hypogymnia tubulosa** (Schaerer) Hav. - abundant (W)
[(Merrill's list); Degelius 1940]

! **Hypogymnia vittata** (Ach.) Parrique - uncommon (N)
[(Merrill's list); Degelius 1940] (ARO, PIS)

! **Hypotrachyna revoluta** (Flörke) Hale - 3 sites (C)
[Degelius 1940] (CUM, WAS) {WAS, 1971, Hale 37606, US!}

! **Imshaugia aleurites** (Ach.) S. F. Meyer - abundant (W)
[Eckfeldt 1894]

! **Imshaugia placorodia** (Ach.) S. F. Meyer - uncommon (S)
[Plitt 1924; Culberson 1956] (HAN, KNO, SAG, YOR)

! **Lasallia papulosa** (Ach.) Llano - abundant (W)
[Eckfeldt 1894; Llano 1950]

! **Lasallia pensylvanica** (Hoffm.) Llano - common (W)
[Merrill 1910b; Llano 1950]

! **Leptogium burnetiae** C. W. Dodge - uncommon (N)
[Sierk 1964; includes *L. hirsutum* Sierk] (ARO, PEN, PIS, SOM, WAS)

! **Leptogium chloromelum** (Sw. *ex* Ach.) Nyl. - 1 site (S)
[Harvey 1894] (CUM) {Harrison, 1857, Blake s.n., MAINE!}

! **Leptogium corticola** (Taylor) Tuck. - uncommon (W)
[Eckfeldt 1894; Sierk 1964] (HAN, KNO, OXF, PIS)

! **Leptogium cyanescens** (Rabenh.) Körber - abundant (W)
[Harvey/Eckfeldt 1894; Sierk 1964]

! **Leptogium laceroides** (de Lesd.) P. M. Jørg. - 4 sites (W)
[Degelius 1940; Sierk 1964] (ARO, PEN, PIS) {PIS, 1984, Hinds 1254, HINDS!}

! **Leptogium lichenoides** (L.) Zahlbr. - 4 sites (W)
[(Merrill's list); Sierk 1964] (ARO, KNO, PIS) {KNO, 1984, Hinds 1255, HINDS!}

! **Leptogium milligranum** Sierk - uncommon (W)
[Sierk 1964] (ARO, KEN, KNO, PEN, PIS)

! **Leptogium saturninum** (Dickson) Nyl. - fairly common (W)
[Merrill 1910c; Sierk 1964]

! **Leptogium tenuissimum** (Dickson) Körber - uncommon (W)
[Cummings & Seymour 1894; Sierk 1964] (ARO, HAN, KNO. SAG)

! **Leptogium teretiusculum** (Wallr.) Arnold - 2 sites (W)
[Degelius 1940; Sierk 1964] (KNO, PIS) {PIS, 1939, Degelius s.n., FH!}

! **Lobaria pulmonaria** (L.) Hoffm. - abundant (W)
[Harvey/Eckfeldt 1894; Jordan 1973]

! **Lobaria quercizans** Michaux - abundant (W)
[Degelius 1940; Jordan 1973]

! **Lobaria scrobiculata** (Scop.) DC. - common (W)
[Eckfeldt 1894; Jordan 1973]

! **Melanelia disjuncta** (Erichsen) Essl. - fairly common (W)
[Esslinger 1977b]

! **Melanelia exasperata** (De Not.) Essl. - uncommon (W)
[(Merrill's list); Parlin 1939; Esslinger 1977b] (ARO, KNO, OXF, PIS, WAL)

! **Melanelia exasperatula** (Nyl.) Essl. - 3 sites (N)
[Sullivan 1996] (HAN, WAS) {WAS, 1996, Biazrov A1/6. MAINE!}

! **Melanelia fuliginosa** (Fr. *ex* Duby) Essl. - common (W)
[Esslinger 1977b]

! **Melanelia halei** (Ahti) Essl. - common (W)
[Ahti 1966; Esslinger 1977b]

! **Melanelia hepatizon** (Ach.) Thell - fairly common (W)
[Howe 1913b]

* ! **Melanelia infumata** (Nyl.) Essl. - 1 site (N)
(PIS) {Kineo Mt., 1992, Hinds 2720, HINDS!}

! **Melanelia olivacea** (L.) Essl. - uncommon (W)
[Esslinger 1977b] (ARO, HAN, KNO, WAS)

! **Melanelia panniformis** (Nyl.) Essl. - fairly common (W)
[(Merrill's list); Esslinger 1977b]

! **Melanelia septentrionalis** (Lynge) Essl. - fairly common (W)
[Ahti 1966; Esslinger 1977b]

! **Melanelia sorediata** (Ach.) Goward & Ahti - common (W)
[Merrill 1912; Esslinger 1977b]

! **Melanelia stygia** (L.) Essl. - common (W)
[Harvey/Eckfeldt 1894; Esslinger 1977b]

! **Melanelia subargentifera** (Nyl.) Essl. - 3 sites (W)
[Parlin 1923; Esslinger 1977b: ?] {PIS, 1992, Hinds 2733, HINDS!}

! **Melanelia subaurifera** (Nyl.) Essl. - abundant (W)
[Merrill 1920a; Esslinger 1977b]

! **Menegazzia terebrata** (Hoffm.) A. Massal. - fairly common (W)
[Eckfeldt 1894; Hale 1955a]

! **Myelochroa aurulenta** (Tuck.) Elix & Hale - fairly common (W)
[(Merrill's list); Degelius 1940; Hale 1976b]

! **Myelochroa galbina** (Ach.) Elix & Hale - common (W)
[(Merrill's list); Parlin 1929; Hale 1976b]

! **Nephroma arcticum** (L.) Torss. - 3 sites (N)
[Eckfeldt 1894; Wetmore 1960] (ARO, HAN, SOM) {HAN, 1888, Eckfeldt, FH!}

! **Nephroma bellum** (Sprengel) Tuck. - fairly common (W)
[Wetmore 1960]

! **Nephroma helveticum** Ach. - fairly common (W)
[Harvey/Eckfeldt 1894; Wetmore 1960]

! **Nephroma laevigatum** Ach. - uncommon (C)
[Merrill 1911a; Wetmore 1960] (HAN, KNO)

! **Nephroma parile** (Ach.) Ach. - common (W)
[Eckfeldt 1894; Wetmore 1960]

! **Nephroma resupinatum** (L.) Ach. - uncommon (W)
[Harvey 1894; Wetmore 1960] (ARO, CUM, KNO, PIS)

! **Normandina pulchella** (Borrer) Nyl. - uncommon (N)
[Degelius 1940] (ARO, PIS, SOM, WAS)

* ! **Omphalina hudsoniana** (H. S. Jenn.) H. E. Bigelow - 1 site (N)
(PIS) {Mt. K, 1902, Blakesly s.n., FH!}

! **Pannaria conoplea** (Ach.) Bory - 2 sites (N)
[Selva 1989] (ARO) {1988, Hinds 2220, HINDS!}

! **Pannaria lurida** (Mont.) Nyl. - 1 site (C)
[Merrill 1910a] (KNO) {S. Thomaston, 1926, Merrill Lich. Exs. 113, FH!}

! **Pannaria pezizoides** (Weber) Trevisan - fairly common (W)
[Eckfeldt 1894]

! **Pannaria rubiginosa** (Ach.) Bory - uncommon (W)
[(Merrill's list); Degelius 1940] (ARO, HAN, KNO, PIS, SOM)

* ! **Parmelia fertilis** Müll. Arg. - 1 site (N)
(HAN) {Lead Mt., 1996, Biazrov W5/9, MAINE!}

! **Parmelia neodiscordans** Hale - 2 sites (C)
[Hale 1987] (HAN) {holotype: Hale 37496, US; 1990, Hinds 2492, HINDS!}
! **Parmelia omphalodes** (L.) Ach. - fairly common (N)
[Wetmore 1984; Hale 1987]
! **Parmelia saxatilis** (L.) Ach. - abundant (W)
[Eckfeldt 1894; Hale 1987]
! **Parmelia squarrosa** Hale - abundant (W)
[Hale 1971, 1987]
! **Parmelia sulcata** Taylor - abundant (W)
[Merrill 1909c; Hale 1987]
! **Parmeliella triptophylla** (Ach.) Müll. Arg. - fairly common (W)
[(Merrill's list); Degelius 1940]
! **Parmelinopsis horrescens** (Taylor) Elix & Hale - 1 site (C)
[Sullivan 1996] (KNO) {Isle au Haut, 1983, Sullivan 1706, MIN!}
* ! **Parmeliopsis ambigua** (Wulfen) Nyl. - 1 site (N)
(SOM) {Bigelow Mt., 1997, Hinds 3858, HINDS!}
! **Parmeliopsis capitata** R. C. Harris[1] - abundant (W)
[Harris et al. 1988, as *Foraminella capitata* ined.]
! **Parmeliopsis hyperopta** (Ach.) Arnold - common (W)
[Cummings & Seymour 1894]
! **Parmotrema arnoldii** (Du Rietz) Hale - 3 sites (N)
[Degelius 1940; Hale 1965] (HAN, PIS, WAS) {1939, Degelius s.n., US!}
! **Parmotrema chinense** (Osbeck) Hale & Ahti - fairly common (S)
[Eckfeldt 1894]
! **Parmotrema crinitum** (Ach.) Choisy - abundant (S)
[Eckfeldt 1894; Hale 1965]
! **Peltigera aphthosa** (L.) Willd. - common (W)
[Harvey/Eckfeldt 1894; Thomson 1950]
! **Peltigera canina** (L.) Willd. - common (W)
[Eckfeldt 1894; Thomson 1950]
! **Peltigera degenii** Gyelnik - uncommon (N)
[Thomson 1950] (ARO, PEN, PIS, WAS)
! **Peltigera didactyla** (With.) J. R. Laundon - fairly common (W)
[Cummings & Seymour 1894; Thomson 1950]
! **Peltigera elisabethae** Gyelnik - 3 sites (N)
[Selva 1989] (ARO) {1984, Selva 1413, SELVA!}
! **Peltigera evansiana** Gyelnik - fairly common (W)
[Parlin 1939; Thomson 1950]

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[1] ***Parmeliopsis capitata*** R. C. Harris, sp. nov.

Similis *P. ambiguae* (Wulfen) Nyl. sed soraliis capitatis, plerumque ad extremum loborum brevum adscendentum, interdum ad laminas; sorediis farinosis; lobis divergentibus, minus applanatis, colore non valde flavidis, frequenter olivascentibus vel cinerascentibus, subtus pallidioribus, albidis ad fulvum vel interdum badiis; habitatione frequenter in ramulis coniferarum; distributione plus meridionale. Typus: West Virginia, top of Spruce Knob, Pendleton Co., Aug. 1956, on twigs of *Picea rubens* in mountains, *Hale, Lich. Amer. exs. 68* (holotypus, NY; isotypus, MICH).

This species will be described and discussed in detail in a future contribution to the *Lichen Flora of Eastern North America*. Another widely distributed collection which may be used as a reference (although occasionally mixed with *P. hyperopta* (Ach.) Arnold) is *Cummings & Seymour, Decades of N. Amer. Lich. 108* (as *Parmelia ambigua*).

! **Peltigera horizontalis** (Hudson) Baumg. - fairly common (W)
[Eckfeldt 1894; Thomson 1950]

* ! **Peltigera lepidophora** (Vainio) Bitter - 4 sites (W)
(ARO, KNO, PEN) {KNO, 1984, Hinds 718, HINDS!}

! **Peltigera leucophlebia** (Nyl.) Gyelnik - common (W)
[Thomson 1950]

* ! **Peltigera malacea** (Ach.) Funck - 3 sites (N)
(ARO, PIS) {1953, Richards 229, MAINE!}

! **Peltigera membranacea** (Ach.) Nyl. - uncommon (W)
[(Merrill's list); Thomson 1950] (ARO, FRA, HAN, KNO, PIS, WAS)

* ! **Peltigera neckeri** Hepp *ex* Müll. Arg. - 2 sites (W)
(KEN, PEN) {1993, Hinds 2927, HINDS!; 1984, Hinds 723, HINDS!}

* ! **Peltigera neopolydactyla** (Gyelnik) Gyelnik - 1 site (N)
(ARO) {T15 R9 WELS, 1989, Hinds 2354, HINDS!}

! **Peltigera polydactylon** (Necker) Hoffm. - abundant (W)
[Harvey/Eckfeldt 1894; Thomson 1950]

! **Peltigera praetextata** (Flörke *ex* Sommerf.) Zopf. - fairly common (W)
[Thomson 1950]

! **Peltigera rufescens** (Weiss) Humb. - common (W)
[Eckfeldt 1894; Thomson 1950]

* ! **Peltigera scabrosa** Th. Fr. - 1 site (N)
(ARO) {T15 R9 WELS, 1989, Hinds 2361, HINDS!}

**Peltigera venosa** (L.) Hoffm. - 1 site (S)
[Parlin 1939: Turner, 1928; also unverified report by Eckfeldt 1894] (AND)

! **Phaeophyscia adiastola** (Essl.) Essl. - uncommon (W)
[Esslinger 1977a] (ARO, KEN, KNO, PEN, PIS)

! **Phaeophyscia ciliata** (Hoffm.) Moberg - fairly common (W)
[Eckfeldt 1894; Esslinger 1978a]

! **Phaeophyscia decolor** (Kashiw.) Essl. - 2 sites (W)
[(Merrill's list); Thomson 1963] (ARO, OXF) {ARO, 1988, Hinds 2147, HINDS!}

**Phaeophyscia erythrocardia** (Tuck.) Essl. - 3 sites (S)
[Thomson 1963] (AND, KNO) {KNO, 1909. Merrill, YU}

! **Phaeophyscia hirtella** Essl. - 1 site (N)
[Selva 1988] (ARO) {T4 R7 WELS, 1987, Selva 3185, SELVA!}

! **Phaeophyscia hispidula** (Ach.) Essl. - 1 site (S)
[Merrill 1910a; Esslinger 1978a] (KNO) {Warren, 1909, Merrill s.n., FH!}

* ! **Phaeophyscia kairamoi** (Vainio) Moberg - 4 sites (W)
(FRA, PEN, SOM, WAS) {FRA, 1991, Hinds 2595b, HINDS!}

* ! **Phaeophyscia orbicularis** (Necker) Moberg - uncommon (W)
(CUM, HAN, KEN, KNO, OXF, PEN) {PEN, 1993, Hinds 2870, HINDS!}

! **Phaeophyscia pusilloides** (Zahlbr.) Essl. - common (W)
[Esslinger 1978a]

! **Phaeophyscia rubropulchra** (Degel.) Essl. - abundant (W)
[Parlin 1939; Esslinger 1978a]

! **Phaeophyscia sciastra** (Ach.) Moberg - uncommon (W)
[Merrill 1914; Thomson 1963] (ARO, CUM, FRA, KNO, YOR)

! **Phylliscum demangeonii** (Moug. & Mont.) Nyl. - 4 sites (N)
[Eckfeldt 1894] (ARO, HAN) {HAN, no date, Wilson s.n., NEBC!}

! **Physcia adscendens** (Fr.) H. Olivier - common (W)
[Degelius 1940; Thomson 1963]

! **Physcia aipolia** (Ehrh. *ex* Humb.) Fürnr. - common (W)
[Degelius 1940; Thomson 1963]

* **Physcia americana** G. Merr. - 2 sites (S)
[(on Merrill's list & Parlin 1939, both as *P. astroidea* (Clem.) Nyl.)] (HAN, OXF)

! **Physcia caesia** (Hoffm.) Fürnr. - fairly common (W)
[Eckfeldt 1894; Thomson 1963]

! **Physcia dubia** (Hoffm.) Lettau - fairly common (W)
[Degelius 1940; Thomson 1963]

**Physcia leptalea** (Ach.) DC. - 3 sites (S)
[(Merrill's list); Thomson 1963] (HAN, KNO, OXF) {OXF, 1927, Parlin, BPI}

! **Physcia millegrana** Degel. - common (W)
[Degelius 1940; Thomson 1963]

! **Physcia phaea** (Tuck.) J. W. Thomson - 4 sites (S)
[Thomson 1963] (KNO, OXF, PEN) {KNO, 1909, Plitt, FH!}

! **Physcia stellaris** (L.) Nyl. - abundant (W)
[Harvey 1894; Thomson 1963]

! **Physcia subtilis** Degel. - uncommon (W)
[Thomson 1963] (OXF, HAN, KNO, PIS)

! **Physcia tenella** (Scop.) DC. - uncommon (C)
[Thomson 1963] (HAN, KNO, OXF, WAS)

! **Physciella chloantha** (Ach.) Essl. - fairly common (W)
[(Merrill's list); Parlin 1939; Esslinger 1978b]

* ! **Physciella melanchra** (Hue) Essl. - uncommon (W)
(YOR, HAN, PEN, SOM) {SOM, 1993, Hinds 3002, HINDS!}

! **Physconia detersa** (Nyl.) Poelt - abundant (W)
[(Merrill's list); Thomson 1984/Wetmore 1984]

* ! **Physconia enteroxantha** (Nyl.) Poelt - 1 site (N)
(ARO) {Ft. Kent, 1988, Hinds 2087, HINDS!}

* ! **Physconia leucoleiptes** (Tuck.) Essl. - 4 sites (W)
(ARO, FRA, KEN, PEN) {FRA, 1991, Hinds 2589, HINDS!}

**Pilophorus fibula** (Tuck.) Th. Fr. - 1 site (C)
[Yoshimura & Sharp 1968; Jahns 1981: MDI, US; also Eckfeldt 1894] (HAN)

* ! **Placidium squamulosum** (Ach.) Breuss - 1 site (S)
(KNO) {Rockland, 1997, Hinds 3854, HINDS!

* ! **Placynthium asperellum** (Ach.) Trevisan - 2 sites (W)
(ARO, KNO) {1988, Hinds 2146, HINDS!; 1984, Hinds 770, HINDS!}

! **Placynthium flabellosum** (Tuck.) Zahlbr. - 1 site (S)
[Henssen 1963] (KNO) {Camden, 1912, Merrill 221, FH!}

! **Placynthium nigrum** (Hudson) Gray - 4 sites (W)
[Henssen 1963] (ARO, KNO) {1911, Merrill, FH!}

! **Platismatia glauca** (L.) Culb. & C. Culb. - abundant (W)
[Eckfeldt 1894; Culberson and Culberson 1968]

! **Platismatia tuckermanii** (Oakes) Culb. & C. Culb. - abundant (W)
[Howe 1913b; Culberson & Culberson 1968]

! **Pseudevernia cladonia** (Tuck.) Hale & Culb. - fairly common (W)
[Eckfeldt 1894; Hale 1955a]

! **Pseudevernia consocians** (Vainio) Hale & Culb. - fairly common (W)
[Hale 1968]

! **Pseudocyphellaria crocata** (L.) Vainio - fairly common (W)
[Harvey/Eckfeldt 1894; Magnusson 1940-1941]

* ! **Psora pseudorussellii** Timdal - 2 sites (S)
[(Merrill's list, as *Psora russellii*)] (KNO) {1911, Merrill, FH!; 1997, Hinds 3836!}

! **Psoroma hypnorum** (Vahl) Gray - 1 site (C)
[Eckfeldt 1894] (HAN) {MDI, 1888, Eckfeldt 19, NEBC!}

! **Punctelia rudecta** (Ach.) Krog - abundant (W)
[Howe 1913b; Culberson & Culberson 1956]

! **Punctelia subrudecta** (Nyl.) Krog - uncommon (W)
[(Merrill's list); Wetmore 1984] (HAN, KNO, WAL, WAS)

! **Pycnothelia papillaria** Dufour - common (W)
[Eckfeldt 1894]

! **Pyxine sorediata** (Ach.) Mont. - abundant (W)
[Harvey 1896; Imshaug 1957]

! **Ramalina americana** Hale - abundant (W)
[Hale 1978]

! **Ramalina dilacerata** (Hoffm.) Hoffm. - common (W)
[Tuckerman 1882]

! **Ramalina farinacea** (L.) Ach. - common (W)
[Eckfeldt 1894; Bowler & Rundel 1978]

! **Ramalina intermedia** (Delise *ex* Nyl.) Nyl. - fairly common (W)
[Merrill 1910b; Bowler & Rundel 1974]

! **Ramalina pollinaria** (Westr.) Ach. - uncommon (W)
[Parlin 1939] (ARO, OXF, PIS)

! **Ramalina roesleri** (Hochst. *ex* Schaerer) Hue - common (W)
[Howe 1914]

! **Ramalina thraustra** (Ach.) Nyl. - uncommon (N)
[Selva 1986] (ARO, HAN, PIS, WAS)

* ! **Rimelia reticulata** (Taylor) Hale & Fletcher - 1 site (S)
[(Merrill 1911a, as *Parmelia cetrata*)] (KNO) {Rockport, 1909, Merrill s.n., FH!}

! **Solorina saccata** (L.) Ach. - 3 sites (W)
[Thomson 1984] (ARO, FRA, KNO) {ARO, 1995, Hinds 3335, HINDS!}

! **Sphaerophorus fragilis** (L.) Pers. - 1 site (N)
[Harvey 1894] (PIS) {Mt. K, 1924, Norton s.n., FH!}

! **Sphaerophorus globosus** (Hudson) Vainio - 3 sites (C)
[Eckfeldt 1894] (HAN, WAS) {1888, Eckfeldt s.n., NEBC!}

* ! **Stereocaulon alpinum** Laurer *ex* Funck - 1 site (N)
[(Thomson 1984?)] (PIS) {Mt. K, 1991, Hinds 2618, HINDS!}

! **Stereocaulon condensatum** Hoffm. - uncommon (W)
[(Merrill's list); Parlin 1939] (HAN, KNO, PEN, WAS)

! **Stereocaulon dactylophyllum** Flörke - common (W)
[Eckfeldt 1894; Lamb 1977]

! **Stereocaulon glaucescens** Tuck. - uncommon (W)
[Lamb 1977] (ARO, FRA, PEN, PIS)

! **Stereocaulon grande** (H. Magn.) H. Magn. - 1 site (N)
[Lamb 1977] (HAN) {MDI, 1894, unknown collector s.n., FH!}

* ! **Stereocaulon intermedium** (Savicz) H. Magn. - 1 site (N)
(WAS) {Steuben, 1988, Hinds 1183, HINDS!}

* ! **Stereocaulon nanodes** Tuck. - 1 site (N)
(ARO) {Hersey, 1974, Lepore 155, MAINE!}

! **Stereocaulon paschale** (L.) Hoffm. - common (W)
[Harvey 1894; Lamb 1977]

! **Stereocaulon pileatum** Ach. - fairly common (W)
[Riddle 1910; Lamb 1977]
! **Stereocaulon saxatile** H. Magn. - abundant (W)
[Lamb 1977]
! **Stereocaulon subcoralloides** (Nyl.) Nyl. - 3 sites (N)
[Lamb 1977] (ARO, WAS) {ARO, 1988, Hinds 2094, HINDS!}
! **Stereocaulon tomentosum** Fr. - common (W)
[Harvey/Eckfeldt 1894; Lamb 1977]
* ! **Sticta beauvoisii** Delise - 1 site (C)
(HAN) {MDI, no date, Wilson s.n., US!}
! **Sticta fuliginosa** (Hoffm.) Ach. - 1 site (C)
[Eckfeldt 1894] (HAN) {MDI, no date, White s.n., NEBC!}
* ! **Teloschistes chrysophthalmus** (L.) Th. Fr. - 1 site (S)
[(Eckfeldt 1894 - unverified)] (YOR) {Kittery, 1885, Thaxter 405, FH!}
! **Thamnolia vermicularis** (Sw.) Ach. *ex* Schaerer - 1 site (N)
[E. D. Merrill 1900] (PIS) {Mt. K, 1898, E. D. Merrill, MAINE!)
! **Tuckermannopsis americana** (Sprengel) Hale - abundant (W)
[Culberson & Culberson 1967]
! **Tuckermannopsis ciliaris** (Ach.) Gyelnik - uncommon (W)
[Culberson & Culberson 1967] (ARO, OXF, PEN, WAL, YOR)
! **Tuckermannopsis fendleri** (Nyl.) Hale - uncommon (S)
[Merrill 1920b] (KNO, SAG, YOR)
! **Tuckermannopsis orbata** (Nyl.) M. J. Lai - abundant (W)
[Culberson & Culberson 1967]
! **Tuckermannopsis sepincola** (Ehrh.) Hale - fairly common (W)
[Greenwood 1927]
! **Umbilicaria americana** Poelt & T. Nash - common (W)
[Poelt & Nash 1993]
! **Umbilicaria cylindrica** (L.) Delise *ex* Duby - 1 site (N)
[Eckfeldt 1894] (HAN) {MDI, 1880, Eckfeldt 20, NEBC!}
! **Umbilicaria deusta** (L.) Baumg. - abundant (W)
[Tuckerman 1882; Llano 1950]
* ! **Umbilicaria hirsuta** (Sw. *ex* Westr.) Hoffm. - 4 sites (W)
(KNO, PEN, PIS) {PIS, 1951, Dolley s.n., MAINE!}
! **Umbilicaria hyperborea** (Ach.) Hoffm. - uncommon (W)
[Harvey 1894; Llano 1950] (FRA, OXF, PIS, SOM, WAS)
**Umbilicaria krascheninnikovii** (Savicz) Zahlbr. - 1 site (N)
[Thomson 1984: Mt. Katahdin] (PIS)
! **Umbilicaria mammulata** (Ach.) Tuck. - abundant (W)
[Harvey/Eckfeldt 1894; Llano 1950]
! **Umbilicaria muehlenbergii** (Ach.) Tuck. - abundant (W)
[Harvey/Eckfeldt 1894; Llano 1950]
! **Umbilicaria polyphylla** (L.) Baumg. - uncommon (N)
[Tuckerman 1882] (FRA, HAN, KNO)
! **Umbilicaria proboscidea** (L.) Schrader - 2 sites (N)
[Harvey 1894] (PIS, SOM) {1898, E. D. Merrill s.n., FH!; 1988, HINDS!}
! **Umbilicaria torrefacta** (Lightf.) Schrader - uncommon (N)
[Harvey 1894; Llano 1950] (HAN, KNO, PIS)
! **Umbilicaria vellea** (L.) Hoffm. - 1 site (N)
[Poelt & Nash 1993] (PIS) {Mt. K, 1935, S. K. Harris 1957, NEBC!}

! **Usnea cavernosa** Tuck. - uncommon (W)
[Howe 1910] (ARO, CUM, HAN, LIN, PIS)

! **Usnea ceratina** Ach. - uncommon (C)
[Eckfeldt 1894] (CUM, HAN, WAS)

**Usnea dasaea** Stirton - 1 site (S)
[Clerc & Herrera-Campos 1997] (KEN) {Manchester, Sargent s.n., US}

! **Usnea filipendula** Stirton - abundant (W)
[Howe 1909]

* ! **Usnea fulvoreagens** (Räsänen) Räsänen - common (W)
{PIS, 1984, Hinds 426, HINDS!}

! **Usnea hesperina** Mot. - 1 site (C)
[Motyka 1936-1938] (KNO) {Matinicus Isl., 1915, FH!}

! **Usnea hirta** (L.) F. H. Wigg. - common (W)
[Harvey 1894]

! **Usnea longissima** Ach. - common (W)
[Harvey 1894]

! **Usnea merrillii** Mot. - common (C)
[Motyka 1936-1938]

! **Usnea mutabilis** Stirton - fairly common (S)
[Davis 1964] (HAN, KEN, PEN, SAG, YOR)

! **Usnea pachyclada** Mot. - 1 site (N)
[Motyka 1936-1938] (WAS) {Head Harbor Isl., Norton, holotype, FH!}

! **Usnea rubicunda** Stirton - 3 sites (W)
[Motyka 1936-1938] (CUM, KNO, WAS) {KNO, 1921, Merrill, FH!}

! **Usnea strigosa** (Ach.) Eaton - common (W)
[Howe 1909; Hale 1962]

! **Usnea subfloridana** Stirton - abundant (W)
[Motyka 1936-1938]

* ! **Usnea subscabrosa** Mot. - 3 sites (C)
(HAN, WAS) {HAN, 1985, Hinds 844, HINDS!}

! **Usnea trichodea** Ach. - abundant (W)
[Howe 1909]

! **Vulpicida pinastri** (Scop.) J.-E. Mattsson & M. J. Lai - abundant (W)
[Eckfeldt 1894; Mattsson 1993]

! **Vulpicida viridis** (Schwein.) J.-E. Mattsson & M. J. Lai - 1 site (S)
[Merrill 1920b] (YOR) {Alfred, 1997, Hinds 3864, HINDS!}

* ! **Xanthoparmelia angustiphylla** (Gyelnik) Hale - uncommon (W)
(HAN, KNO, WAS) {HAN, 1932, Plitt s.n., US!}

! **Xanthoparmelia conspersa** (Ehrh. *ex* Ach.) Hale - abundant (W)
[Harvey/Eckfeldt 1894; Hale 1964]

! **Xanthoparmelia cumberlandia** (Gyelnik) Hale - fairly common (W)
[Hale 1967, 1990]

! **Xanthoparmelia plittii** (Gyelnik) Hale - uncommon (W)
[Wetmore 1984] (ARO, HAN, KEN)

! **Xanthoparmelia somloënsis** (Gyelnik) Hale - common (W)
[Hale 1955b]

! **Xanthoparmelia tasmanica** (Hook f. & Taylor) Hale - 3 sites (N)
[Sullivan 1996] (ARO, HAN, WAS) {WAS, 1971, Hale 37501, US!}

! **Xanthoria elegans** (Link) Th. Fr. - abundant (W)
[Harvey/Eckfeldt 1894; Lindblom 1997]

! **Xanthoria fallax** (Hepp) Arnold - 3 sites (W)
[Hinds & Hinds 1994; Lindblom 1997] (FRA, OXF, PEN) {FRA,1993, Hinds 2967, HINDS!}
! **Xanthoria fulva** (Hoffm.) Poelt & Petutschnig - uncommon (S)
[Lindblom 1997] (FRA, HAN, KNO, PEN, WAL)
! **Xanthoria hasseana** Räsänen - fairly common (W)
[Lindblom 1997]
! **Xanthoria parietina** (L.) Th. Fr. - abundant (W)
[Harvey/Eckfeldt 1894; Lindblom 1997]
! **Xanthoria polycarpa** (Hoffm.) Rieber - fairly common (C)
[Eckfeldt 1894; Lindblom 1997]
! **Xanthoria sorediata** (Vainio) Poelt - 3 sites (N)
[Hinds & Hinds 1993] (ARO, PIS, WAS) {ARO, 1989, Hinds 2397, HINDS!}
! **Xanthoria ulophyllodes** Räsänen - common (W)
[Hinds & Hinds 1994; Lindblom 1997]

## EXCLUDED SPECIES

Unverified Reports

**Brodoa oroarctica** (Krog) Goward (Eckfeldt 1894, as *Parmelia encausta* (Sm.) Nyl., on rocks, MDI)

**Collema fragrans** (Sm.) Ach. (on Hale's 1979 map for Maine)

**Evernia prunastri** (L.) Ach. (Merrill ca. 1926 listed this species in addition to numerous records of *E. thamnodes* (Flot.) Arn. (= *E. mesomorpha* Nyl.)

**Heppia lutosa** (Ach.) Nyl. (Eckfeldt 1894, as *Heppia Despreauxii* (Mont.) Tuck., MDI)

**Hyperphyscia adglutinata** (Flörke) H. Mayrh. & Poelt (Parlin 1939, as *Physcia adglutinata* (Flk.) Nyl., Androscoggin Co.)

**Lasallia pustulata** (L.) Mérat (Merrill ca. 1926 listed this species for Knox Co. in addition to numerous records of *L. pustulata* (L.) Hoffm. v. *papulosa* (Ach.) Tuck. (= *L. papulosa* (Ach.) Llano)

**Peltigera collina** (Ach.) Schrader (several reports, including Parlin 1939, as *Peltigera scutata* (Dicks.) Duby, Oxford Co.)

**Parmotrema perforatum** (Jacq.) A. Massal. (Eckfeldt 1894, as *Parmelia perforata* (Jacq.) Ach., on tree trunks, MDI)

**Parmotrema stuppeum** (Taylor) Hale (on Hale's 1979 map for Maine)

**Physconia muscigena** (Ach.) Poelt (on Hale's 1979 map for Maine)

**Pseudephebe pubescens** (L.) Choisy (Eckfeldt 1894, as *Parmelia lanata* (L.) Wallr., on rocks, MDI)

**Psora decipiens** (Hedwig) Hoffm. (on Hale's 1979 map for Maine)

**Psorula rufonigra** (Tuck.) Gotth. (Eckfeldt 1894, as *Biatora rufo-nigra* Tuck., on rocks, MDI)

**Punctelia appalachensis** (Culb.) Krog (Eagle Hill Wildlife Research Station list)

**Rimelia cetrata** (Ach.) Hale & Fletcher (Parlin 1939, as *Parmelia cetrata* Ach., Oxford Co.)

**Stereocaulon botryosum** Ach. (Fink 1935, as *Stereocaulon alpinum* Laurer var. *botyrosum* (Ach.) Laurer)

**Stereocaulon vesuvianum** Pers. (Parlin 1939, as *S. denudatum* Floerke)

Presumed misidentifications

**Alectoria lata** (Taylor) Lindsay (Eckfeldt 1894, as *A. ochroleuca osteina* Nyl.)

**Alectoria nigricans** (Ach.) Nyl. (Eckfeldt 1894, as *A. ochroleuca nigrescens* Ach.): specimen seen was misidentification of a mixture of *Alectoria sarmentosa* (Ach.) Ach. and *Bryoria* sp.)

**Anaptychia runcinata** (With.) J. R. Laundon (several reports, as *A. aquila* (Ach.) Mass. or (Ach.) Nyl.): misidentifications of *A. palmulata* (Michaux) Vainio (Esslinger & Egan 1995)

**Bryoria bicolor** (Ehrh.) Brodo & D. Hawksw. (Howe 1911a & Fink 1935, as *Alectoria bicolor* (Ehrh.) Nyl.): specimen seen was misidentification of *Bryoria nadvornikiana* (Gyelnik) Brodo & D. Hawksw.

**Bryoria chalybeiformis** (L.) Brodo & D. Hawksw. (Sullivan 1996): specimens seen appeared to be *B. fuscescens* (Gyelnik) Brodo & Hawksw. (var. *positiva* (Gyelnik) Brodo & Hawksw.)

**Cetraria ericetorum** Opiz (Thomson 1984): most are probably *C. arenaria* Kärnefelt, not separately mapped by Thomson 1984; (Degelius 1940, as *C. crispa* (Ach.) Nyl., coast and Mt. Katahdin): probably *C. arenaria* Kärnefelt and *C. laevigata* Rass., respectively

**Cetrelia cetrarioides** (Duby) Culb. & C. Culb. (Degelius 1940, as *Parmelia cetrariodes* Del.): probably *Cetrelia chicitae* (Culb.) Culb. & C. Culb.

**Cladina ciliata** (Stirton) Trass (Parlin 1939, as *Cladonia tenuis* (Floerke) Harm.): probably *Cladina subtenuis* (Abbayes) Hale & Culb.

**Cladina portentosa** (Dufour) Follmann (Parlin 1939, as *Cladonia impexa* Harm. f. *laxiuscula* (Del.) Sandst.): probably *Cladina terrae-novae* (Ahti) Hale & Culb.

**Cladonia bellidiflora** (Ach.) Schaerer (Harvey 1894): misidentification of *C. cristatella* (Riddle 1909)

**Cladonia didyma** (Fée) Vainio (Eckfeldt 1894, as *C. pulchella* Schwein; Fink 1935): misidentification (Riddle 1909)

**Cladonia foliacea** (Huds.) Willd. (Eckfeldt 1894, as *C. alcicornis* (Leight.) Floerke): misidentifications for North America (Esslinger & Egan 1995)

**Cladonia glauca** Flörke (Pitman 1932; Merrill ca. 1926): specimens seen of Merrill were misidentifications

**Cladonia humilis** (With.) J. R. Laundon (Sullivan 1996): probably *C. conista* A. Evans (personal communication, R. C. Harris)

**Collema ryssoleum** (Tuck.) A. Schneider (Merrill ca. 1926, as *C. ryssoleum* Tuck.; Fink 1935, as *Synechoblastus ryssoleus* (Tuck.) Fink): specimen seen was misidentified

**Hypogymnia enteromorpha** (Ach.) Nyl. (Degelius 1940, as *Parmelia enteromorpha* Ach.): in eastern North America now considered *H. krogiae* Ohlsson

**Leptogium burgessii** (L.) Mont. (several reports): misidentifications for North America (Hale & Culberson 1970)

**Letharia vulpina** (L.) Hue (Eckfeldt 1894, as *Evernia vulpina* (L.) Ach.)

**Lobaria amplissima** (Scop.) Forssell (several reports, as *Sticta amplissima* (Scop.) Mass. or (Scop.) Rabh.): now considered *Lobaria quercizans* Michaux

**Melanelia commixta** (Nyl.) Thell (several reports, as *Cetraria fahulensis* (L.) Schneider): specimens seen were *Melanelia hepatizon* (Ach.) Thell

**Parmelina quercina** (Willd.) Hale (several reports, as *Parmelia quercina* (Willd.) Vainio and *Parmelia tiliacea* (Hoffm.) Floerke or (Hoffm.) Ach.): probably misidentifications of *Myelochroa galbina* (Ach.) Elix & Hale

**Peltigera ponojensis** Gyelnik (Sullivan 1996): specimen seen appeared to be *P. rufescens* (Weiss) Humb.

**Physcia clementei** (Sm.) Lynge (several reports, as *P. astroidea* (Clem.) Nyl.): probably misidentifications of *Physcia americana* G. Merr.

**Physcia tribacia** (Ach.) Nyl. (several reports): probably *P. millegrana* Degel.

**Physconia distorta** (With.) J. R. Laundon (Parlin 1939, as *Parmelia pulverulenta* (Tayl.) Nyl.): misidentifications for North America (Esslinger & Egan 1995)

**Physconia grisea** (Lam.) Poelt (Merrill ca. 1926, as *Physcia pityrea* (Ach.) Lamy): misidentifications for North America (Esslinger & Egan 1995)

**Placynthium pannariellum** (Nyl.) H. Magn. (Merrill 1914): misidentification of *P. flabellosum* (Tuck.) Zahlbr. (Henssen 1963)

**Platismatia lacunosa** (Ach.) Culb. & C. Culb. (several reports, as *Cetraria lacunosa* Ach.): specimens seen were misidentifications of *P. tuckermanii* (Oakes) Culb & C. Culb.

**Pseudevernia furfuracea** (L.) Zopf (several reports): misidentifications for North America (Esslinger & Egan 1995)

**Pseudocyphellaria aurata** (Ach.) Vainio (Fink 1935, as *Sticta aurata* Ach.)

**Pseudocyphellaria anthrapsis** (Ach.) H. Magn. (Fink 1935, as *Sticta anthrapsis* Ach.)

**Psora russellii** (Tuck.) A. Schneider (Merrill ca. 1926, as *Biatora Russellii* Tuck.): now considered *P. pseudorussellii* Timdal

**Punctelia borreri** (Sm.) Krog (Eckfeldt 1894 & Parlin 1939, as *Parmelia borreri* Turn.): probably *Punctelia subrudecta* (Nyl.) Krog

**Ramalina calicaris** (L.) Fr. (several reports, including Selva 1986): specimens seen appeared to be *R. americana* Hale

**Ramalina fastigiata** (Pers.) Ach. (several reports): specimens seen were misidentifications of *R. americana* Hale

**Ramalina fraxinea** (L.) Ach. (several reports): specimens seen were misidentifications of *R. americana* Hale

**Ramalina polymorpha** (Lilj.) Ach. (Eckfeldt 1894; Merrill ca. 1926; Parlin 1939): eastern North American specimens are misidentifications (Howe 1913a)

**Solorina crocea** (L.) Ach. (on Hale's 1979 map for Maine)

**Sticta herbacea** (Hudson) Ach. (Harvey 1894; Fink 1935): misidentifications for North America (Esslinger & Egan 1995)

**Sticta sylvatica** (Hudson) Ach. (Fink 1935)

**Usnea barbata** (L.) F. H. Wigg. (several reports): misidentifications (Hale & Culberson 1970)

**Usnea florida** (L.) F. H. Wigg. (several reports, including Motyka 1936-1938): now considered *U. strigosa* (Ach.) Eaton (Fiscus 1972)

**Usnea lapponica** Vainio (several reports): ones seen were all *Usnea fulvoreagens* (Räsänen) Räsänen (Clerc 1992)

**Usnea plicata** (L.) Weber (Parlin 1939, as *U. plicata* (L.) Wigg.): misidentifications for North America (Esslinger & Egan 1995)

**Usnea subfusca** Stirton (Motyka 1936-1938): misidentification (Brodo 1968)

**Vulpicida juniperinus** (L.) J.-E. Mattsson & M. J. Lai (several reports, as *Cetraria juniperina* (L.) Ach.): misidentifications of *V. pinastri* (Scop.) J.-E. Mattsson & M. J. Lai or *V. viridis* (Schwein.) J.-E. Mattsson & M. J. Lai

Considered Crustose

**Euopsis granatina** (Sommerf.) Nyl. (Tuckerman 1882; Harvey/Eckfeldt 1894, as *Pannaria granatina* (Sommerf.) Tuck.)

**Icmadophila ericetorum** (L.) Zahlbr. (Eckfeldt 1894, as *Baeomyces aeroginosus* (Scop.) DC.)

**Leproloma membranaceum** (Dickson) Vainio (Eckfeldt 1894, as *Pannaria lanuginosa* (Ach.) Koerber; and Parlin 1939, as *Amphiloma lanuginosum* (Hoffm.) Nyl.)

**Ochrolechia frigida** (Sw.) Lynge (Degelius 1940): excluded because the genus *Ochrolechia* is considered crustose

**Rhizoplaca chrysoleuca** (Sm.) Zopf (Parlin 1939, as *Lecanora rubina* (Vill.) Ach.)

Species Names Not Validly Published

**Parmelia onsetensis** G. Merr. (Parlin 1939)

**Physcia mollis** G. Merr. (Parlin 1939)

## DISCUSSION

Verification of Species on List

To ensure that species included on the checklist were correctly identified, the authors examined specimens of as many species as possible (333 indicated by "!" on the checklist). Of the 16 species not examined, 10 were cited by monographers, 2 by the authors of the species (*Dirinaria frostii* and *Physcia americana*), 1 by Thomson 1984 (*Umbilicaria krascheninnikovii*, cited specifically in the text), and 1 (*Bryocaulon divergens*) by Degelius (1940), who undoubtedly was familiar with the species in Europe. That leaves only two species: *Peltigera venosa*, reported by both Parlin (1939) and Eckfeldt (1894) and *Endocarpon pusillum,* on Merrill's ca. 1926 list; both are distinctive species that would be difficult to mistake for any other.

There are 47 species reported from Maine for the first time in this paper. Any identifications that the authors thought were questionable were verified by Richard Harris or Theodore Esslinger.

Number of Species

The number of Maine macrolichen species listed in the checklist is 349, approximately equally divided among the abundance categories (Table 1):

**TABLE 1. Maine Macrolichen Species Numbers**

| Frequency | Number | Percentage |
|---|---|---|
| One site | 61 | 17.5% |
| Rare (2-4 sites) | 61 | 17.5% |
| Uncommon (5-9 sites) | 64 | 18.3% |
| Fairly common (10-19 sites) | 53 | 15.2% |
| Common (20-39 sites) | 52 | 14.9% |
| Abundant (40+ sites) | 58 | 16.6% |
| TOTAL | 349 | 100.0% |

One approach to answering the question of whether 349 species constitutes a high number for the size of the State is to compare the actual number found in Maine with the expected number based on the species-area equation $S=CA^z$ , where S is the expected number of species, C is a constant, A is the area of Maine, and z is a parameter that ranges among floras and faunas from 0.15 to 0.35 (Wilson 1992). To determine the approximate value of C and z, data from 14 lichen studies (including the present study) were compiled, and a best-fit regression equation determined using log-transformed values for number of species and area. The resulting regression equation had an adjusted coefficient of determination ($R^2$) of 85.6% and corresponded to the species-area equation $S= 12.1\ A^{0.289}$. Table 2 provides information on the studies used and the results obtained; areas of all but Southern Ontario are from Merriam-Webster, Inc. 1988.

**TABLE 2. Actual and Expected Number of Macrolichen Species**

| LOCATION | REFERENCE | AREA (SQ. MI) | MACRO-LICHEN SPECIES | EXPECTED NUMBER OF OF SPECIES | RATIO |
|---|---|---|---|---|---|
| U.S. & Canada | Esslinger & Egan '95 | 7460882 | 1215 | 1169 | 104% |
| British Columbia | Goward et al. '94 | 366255 | 480 | 489 | 98% |
| Sweden & Norway | Santesson '93 | 298714 | 554 | 461 | 120% |
| British Isles | Purvis et al. '92 | 120198 | 428 | 354 | 121% |
| Missouri | Ladd '96 | 69686 | 218 | 303 | 72% |
| Florida | Harris '95; Moore '68 | 58560 | 194 | 288 | 67% |
| New York | Harris '97 | 49576 | 334 | 274 | 122% |
| Newfoundland (Isl.) | Ahti '83 | 43359 | 250 | 264 | 95% |
| Tennessee | Skorepa '72 | 42244 | 280 | 262 | 107% |
| Ohio | Taylor'67; Flen.& '90 | 41222 | 215 | 260 | 83% |
| Southern Ontario | Wong & Brodo '92 | 40334 | 209 | 258 | 80% |
| Maine | [present study] | 33215 | 348 | 244 | 143% |
| Worcester Co.(MA) | Ahmadjian '58 | 1513 | 81 | 100 | 81% |
| Long Island, NY | Brodo '68 | 1401 | 136 | 98 | 139% |

Table 2 shows that the number of macrolichen species reported from Maine in the present study is more than 40% higher than the expected number and is the highest ratio in the Table, so it can be concluded that Maine has a very rich macrolichen flora. Some of the reasons for the high number of species in Maine might be the following: (1) significant areas within its borders of two major biogeographical regions, the boreal and temperate zones, as well as a small area of a third major biogeographical region, the arctic-alpine zone; (2) its plentiful and seasonally even precipitation and its proximity to the ocean; (3) intensive collecting since the nineteenth century; (4) relatively low levels of air pollution.

Eleven species have not been found since the 19th century. These are either generally rare species (*Degelia plumbea*, *Heterodermia galactophylla*) or they are at the edge of their range, either at the southern edge (*Alectoria ochroleuca, Bryoria lanestris, Psoroma hypnorum, Umbilicaria cylindrica*) or at the northern edge (*Dirinaria frostii, Leptogium chloromelum, Sticta beauvoisii, Sticta fuliginosa, Teloschistes chrysophthalmus*). The authors believe that only in the case of *Teloschistes chrysophthalmus* is it likely that air pollution is the reason for the absence of the species in the twentieth century (Hinds and Hinds 1996).

## Biogeographical Affinities

In an effort to determine the biogeographical affinities of the macrolichen species of Maine, the known overall distribution in eastern North America of all species in the checklist was compiled, based on monographs and certain key floristic works such as Flenniken & Showman 1990, Harris 1995, Moore 1968, Mozingo 1948, and Thomson 1984). Four broad biogeographical zones were used: arctic-alpine (A), boreal (B), temperate (T), and subtropical (S), based in part on a map (Fig. 8.3) in Hunt 1974. The subtropical zone is considered to be the southeast coastal plain from North Carolina to Louisiana and including all of Florida. The temperate zone coincides with regions north of the subtropical zone dominated by hardwoods as their natural vegetation, while the boreal zone is dominated by softwoods, especially spruce and fir. All species were coded as to whether they occurred in one or more of these four broad zones. If a species was found in a given zone (unless clearly exceptional), that region was included, even if the species was most characteristic of another zone. Table 3 shows the result of the compilation.

**TABLE 3**

| ZONES | # | % |
|---|---|---|
| A | 12 | 3.4% |
| AB | 57 | 16.3% |
| ABT | 53 | 15.2% |
| ABTS | 4 | 1.2% |
| B | 35 | 10.0% |
| BT | 110 | 31.5% |
| BTS | 26 | 7.5% |
| T | 22 | 6.3% |
| TS | 30 | 8.6% |
|  | 349 | 100.0% |
|  |  |  |
| A's | 126 | 17.6% |
| B's | 285 | 39.8% |
| T's | 245 | 34.2% |
| S's | 60 | 8.4% |
|  | 716 | 100.0% |

Clearly the most common biogeographical distribution type for macrolichen species in Maine is the boreal-temperate type, either broadly distributed throughout the boreal and temperate zone, or commonly showing a Great Lakes-Appalachian distribution (Brodo 1968). This result is consistent with the fact that the border between boreal and temperate regions splits Maine (see Figure 1). Since Maine has some arctic-alpine habitat but no subtropical habitat within its borders, it is perhaps also not surprising that its lichen flora is weighted somewhat more heavily towards the boreal and arctic than towards the temperate and subtropical.

A number of species reach their southern, northern, or eastern limits in eastern North America (eNA) in Maine. The following tables present the ones believed to reach their limits in Maine, although further work or unpublished studies may show some of these entries to be incorrect. Only species with relatively well characterized distributions have been included.

## TABLE 4. Species Farthest South in eNA in Maine

| | | |
|---|---|---|
| *Alectoria ochroleuca* | HAN (Mt. Desert Island) | Eckfeldt 1894 |
| *Alectoria sarmentosa* | KNO (Isle au Haut) | Sullivan 1996 |
| *Bryocaulon divergens* | PIS (Mt. Katahdin) | Degelius 1940 |
| *Bryoria friabilis* | SAG (Reid State Park) | Brodo & Hawksworth 1977 |
| *Bryoria lanestris* | PEN (Bangor) | Brodo & Hawksworth 1977 |
| *Cladonia botrytes* | CUM (Prince's Point) | Degelius 1940 |
| *Degelia plumbea* | HAN (Mt. Desert Island) | Jørgensen 1978 |
| *Hypogymnia austerodes* | KNO (Rockport) | [present study] |
| *Melanelia disjuncta* | KNO | Esslinger 1977b |
| *Melanelia panniformis* | SAG (Phippsburg) | Harris et al. 1988 |
| *Parmelia fertilis* | WAS (Lead Mountain) | [present study] |
| *Placynthium asperellum* | KNO (Rockport) | [present study] |
| *Psoroma hypnorum* | HAN (Mt. Desert Island) | Eckfeldt 1894 |
| *Ramalina pollinaria* | OXF (Hartford) | Parlin 1939 |
| *Ramalina roesleri* | CUM (Cundy's Harbor) | Degelius 1940 |
| *Ramalina thraustra* | HAN (Mt. Desert Island) | [present study] |
| *Stereocaulon grande* | HAN (Mt. Desert Island) | Lamb 1977 |
| *Umbilicaria krascheninnikovii* | PIS (Mt. Katahdin) | Thomson 1984 |

## TABLE 5. Species Farthest North in eNA in Maine

| | | |
|---|---|---|
| *Anzia colpodes* | ARO (T15 R6 WELS) | Selva 1989 |
| *Cladonia submitis* | YOR (Ferry Beach S. P.) | [present study] |
| *Cladonia subtenuis* | WAL (Unity) | [present study] |
| *Cladonia atlantica* | HAN (Mt. Desert Island) | Sullivan 1996 |
| *Cladonia caroliniana* | HAN (Mt. Desert Island) | Sullivan 1996 |
| *Cladonia dimorphoclada* | KNO | Ahti 1973 |
| *Cladonia mateocyatha* | HAN (Mt. Desert Island) | Sullivan 1996 |
| *Cladonia polycarpoides* | PEN (Orono) | [present study] |
| *Cladonia strepsilis* | WAS (Cherryfield) | Hinds & Hinds, unpublished |
| *Heterodermia obscurata* | PIS (Togue Pond) | Degelius 1940 |
| *Leptogium milligranum* | ARO (Crystal) | [present study] |
| *Menegazzia terebrata* | ARO (T13 R10 WELS) | Selva 1988 |
| *Normandina pulchella* | ARO (T14 R13 WELS) | Selva 1988 |
| *Pannaria lurida* | KNO (South Thomaston) | Merrill 1910a |
| *Parmelia neodiscordans* | HAN (Mt. Desert Island) | Hale 1987 |
| *Parmelinopsis horrescens* | KNO (Isle au Haut) | Sullivan 1996 |
| *Pseudevernia cladonia* | PIS (Big Reed Pond) | Selva 1986 |
| *Rimelia reticulata* | KNO (Rockport) | Merrill 1911 |
| *Usnea dasaea* | KEN (Manchester) | Clerc & H.-Campos 1997 |
| *Usnea mutabilis* | PEN (Orono) | Hinds and Harris 1997 |
| *Usnea subscabrosa* | WAS (Great Wass Island) | [present study] |
| *Usnea trichodea* | ARO (T13 R10 WELS) | Selva 1988 |
| *Vulpicida viridis* | YOR (Alfred) | Merrill 1920b |

## TABLE 6. Species Significantly Farther East Than Previously Reported

| SPECIES | LOCATION | SUBSTRATE |
|---|---|---|
| Dermatocarpon moulinsii | ARO (T11 R8 WELS) | Calcareous rock |
| Flavopunctelia soredica | ARO (Presque Isle) | Tree trunk in town |
| Melanelia infumata | PIS (Kineo Mt,) | Rock at base of cliff |
| Phaeophyscia orbicularis | HAN (Aurora) | Marble gravestone |
| Physciella melanchra | HAN (Waltham) | Marble gravestone |

Of the species reaching their southern limit in Maine, two are arctic-alpine species reaching Maine only on Mt. Katahdin (*Bryocaulon divergens*, *Umbilicaria kraschenninnikovii*), while all the others are boreal or arctic-boreal species. All but three of these boreal or arctic-boreal species reach their southernmost extent along the coast, where boreal habitat, especially on islands, extends as far south as Sagadahoc and northern Cumberland Counties ($43^0$ 45' N). The temperate species reaching their northernmost extent in Maine are not as concentrated along the coast as the boreal species reaching their southernmost extent, but even so about half are coastal. A majority of temperate species reach their easternmost extent in Maine, since there is little temperate habitat in the Canadian Maritimes. Most of these have not been included in Table 6, which is limited to species reported from Maine for the first time in the present study that represent a significant range extension from what was known previously.

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# ECOLOGY AND CONSERVATION OF *PSEUDOCYPHELLARIA RAINIERENSIS*, A PACIFIC NORTHWEST ENDEMIC LICHEN

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## ABSTRACT

*Pseudocyphellaria rainierensis* is an epiphytic cyanolichen endemic to humid forests extending from southeastern Alaska to Oregon in the Pacific Northwest of North America. It is extremely rare in both British Columbia and southeastern Alaska, where it is restricted to the understory and lower canopy of coastal old-growth forests. In Oregon and Washington, *P. rainierensis* occurs sporadically in mature forests as young as 140 years, but it can be abundant in humid old-growth forest canopies as long as branches are not overwhelmingly dominated by bryophytes. Its patchy distribution within forest stands may be attributed to dispersal limitations or, in some forests, to localized nutrient enrichment in the drip zone of certain tree species (e.g., *Chamaecyparis nootkatensis*). In the Oregon Cascades, transplant experiments demonstrated that a broad range of forest age classes can provide suitable habitat for *P. rainierensis*. Its absence from young forests could therefore be attributed to slow rates of dispersal and/or environmental instability associated with rapid canopy height growth. Edge effects are a potential threat to old-growth associated lichens, but *P. rainierensis* can acclimate to some forest edge environments and even flourish on large trees adjacent to clearings. Since logging has eliminated most *P. rainierensis* populations globally, short-term conservation of this species must rely on the establishment of old-growth forest reserves. Silvicultural procedures such as reduced size of cutting units, live tree retention, maintenance of understory *Taxus* and deciduous trees, uneven thinnings, and extended rotation ages have potential to promote *P. rainierensis* in managed forests in at least some portions of its range.

## INTRODUCTION

Lichen conservation has become an important consideration in the ongoing reassessment of forest management in the Pacific Northwest (Swanson and Franklin 1992, Rosentreter 1995). Nitrogen-fixing lichens (cyanolichens) are an ecologically significant component of many forests in this region. In humid old-growth forests, biomass of epiphytic cyanolichens may exceed several tons per hectare (Denison 1979, Rhoades 1981, McCune 1993, Neitlich 1993). The nitrogen fixed by these lichens represents a major nutrient input to the ecosystem and provides a base for complex food webs in the forest canopy (Carroll 1979). Approximately thirty cyanolichen species are associated with late successional and old-growth forests in the Pacific Northwest (Rosentreter 1995, Goward 1994). Several of these species rarely occur outside of old-growth forests (Sillett and Neitlich 1996).

Our purpose in this paper is to summarize current knowledge on the distribution and ecology of one cyanolichen, *Pseudocyphellaria rainierensis* Imsh. (Lobariaceae). This summary is based on results of recent studies as well as hypotheses guiding new research. Finally, we briefly discuss potential implications of current research for conservation of *P. rainierensis* in managed forests. Additional information on this species may be found in Goward (1996) and Sillett (1997). An excellent color photograph was published by McCune and Geiser (1997).

## GENERAL DESCRIPTION

*Pseudocyphellaria rainierensis* is a large, loosely attached foliose lichen with lobes 5-12 (-20) cm long and 0.5-3 cm wide. The thallus is thin, stiff, and brittle when dry. Characteristically this species grows draped over tree branches. It is pale bluish green when dry (turning creamy brown in the herbarium) and bears scattered white pseudocyphellae over the lower surface. The lower surface is also densely tomentose. This the only species of *Pseudocyphellaria* in the Northern Hemisphere species that contains both a green alga and a cyanobacterium. The green algal photobiont forms a more or less continuous layer, while the cyanobacterial photobiont is confined to internal cephalodia sometimes visible from above as small swellings or eruptive warts. The lobe margins are lobulate to lacerate or occasionally densely isidiate. Elongate or coralloid isidia are also often present over the upper surface, especially along stress cracks. Specialized isidia-bearing platforms (called "isidalia" by Goward 1996) are sometimes present. These peculiar structures arise where the cortex gathers upward in tiny circular pedestals.

Apothecia are seldom found in this species, though specimens from two Oregon populations possessed orangish red apothecia 1-2 mm across over the upper surface (Sillett 1997, unpubl.). The ascospores were hyaline, fusiform (30-60 µm x 5-7 µm), and 1- to 3-septate. Ascospore size, shape, number per ascus were highly variable, and ascus density was low (0-5 per apothecium). Asexual spores are also produced in tiny black pycnidia.

The chemistry of *P. rainierensis* is poorly known. The thallus yields the following spot tests: cortex K+ yellow, C-, KC-, PD-, I-, UV-; medulla K-, C-, KC-, PD-, I+ blue, UV+ white to blue or UV-.

## GEOGRAPHIC DISTRIBUTION

*Pseudocyphellaria rainierensis* is endemic to western North America and appears to be phylogenetically unrelated to other members of its genus in the Northern Hemisphere (Goward 1996). It was described by Imshaug (1950) based on collections made from Mount Rainier National Park, Washington. Since that time it has been collected from 47 sites ranging from 43°N to 58°N latitude (Figure 1).

Thirty-seven of these sites are located in Washington and Oregon. In western Washington, *P. rainierensis* has been found at sixteen sites: three on the Olympic Peninsula, three in the northern Cascades, two in the Alpine Lakes Wilderness, five in Mount Rainier National Park, and three in the southern Cascades (Neitlich et al. 1994, R. Lesher pers. comm.). In Oregon, it is known from twenty-one sites. Only one of these sites is located in the Oregon Coast Range. The rest, including the only known fertile populations, are located in the Cascade Mountains (Sillett 1997). Throughout this portion of its range, *P. rainierensis* is associated with humid old-growth forests in the *Abies amabilis*, *Picea sitchensis* or *Tsuga heterophylla* Zones (Franklin and

Figure 1. Global distribution of *Pseudocyphellaria rainierensis.* Large, shaded circles represent known populations. Small, unshaded circles represent cities.

Dyrness 1973). Here it colonizes a wide variety of conifers (e.g., *Abies amabilis, Pseudotsuga menziesii, Taxus brevifolia, Thuja plicata,* and *Tsuga heterophylla*), hardwoods (e.g., *Alnus rubra* and *Castanopsis chysophylla*), and shrubs (e.g., *Rhododendron macrophyllum*). One anomalous population has been reported from a 150-year-old *Abies lasiocarpa* stand on a lava flow on Mt. Baker (Rhoades 1981), but *P. rainierensis* has disappeared from this locality following defoliation associated with an outbreak of the Balsam Woolly Aphid, *Adelges piceae* (Rhoades pers. comm.). Another population was probably destroyed by the eruption of Mount Saint Helens in May 1980.

*Pseudocyphellaria rainierensis* is much rarer in British Columbia and southeastern Alaska, where it is known from only seven and three localities, respectively (Goward 1996, Geiser et al. 1994), all in the Coastal Western Hemlock Zone (Meidinger and Pojar 1991). We emphasize that its rarity in this portion of its range is not merely an artifact of undercollecting. One recent survey of 145 old forests in British Columbia, for example, turned up only a single specimen (Goward 1996), whereas in southeastern Alaska it was found to occur at only three of the 257 sites surveyed by Geiser et al. (1994). At least one of the British Columbia localities, moreover, appears to have been destroyed by logging (Goward 1996).

Throughout its range, *P. rainierensis* is restricted to the immediate coast, valley bottoms in the mountains, or lower slopes. In Oregon, it occurs to about 1200 m, though an altitudinal range of between roughly 500 and 1000 m is more typical (Sillett 1997). Farther north, in British Columbia, most localities are at or near sea level (Goward 1996). Thus, *P. rainierensis* has an essentially coastal distribution in the northern portion of its range but is more common in inland sites farther south (Figure 1). The near absence of *P. rainierensis* from the Oregon Coast Range may be attributed to the almost complete destruction of low elevation old-growth forests in Oregon (Harris 1984). Careful lichenological surveys of mid-elevation old-growth forests on public lands in southwestern Oregon may discover additional populations.

## VERTICAL DISTRIBUTION WITHIN THE CANOPY

Vertical distribution of epiphytes in humid forests of the Pacific Northwest changes dramatically during the canopy development that accompanies forest succession. Many lichens possessing only a green algal photobiont rapidly colonize young forests. As tree height increases, many of these chlorolichens remain abundant only in the upper and outer crown, perhaps because of unsuitable microclimates and/or competition from other epiphytes in the lower and inner crowns of large trees (Sillett 1995). Eventually, cyanolichens followed by bryophytes dominate branches in the lower canopy, gradually migrating upwards in response to increasing moisture availability or other factors (McCune 1993). Epiphytic mosses form thick mats on branches in humid old-growth forests. Canopy soil accumulates beneath moss mats, and this soil is exploited by a variety of organisms. Ultimately, large branches in the oldest, wettest forests support plant communities dominated by terrestrial species, including mosses, ferns, shrubs, and even trees (Sillett and Neitlich 1996, Sillett unpubl.).

Rates of change in vertical distributions of epiphytes appear to be highly variable, depending on factors such as rainfall, topography, and elevation (McCune 1993, Goward 1995, Sillett and Neitlich 1996). Relatively dry, upland old-growth forests typically support only chlorolichens; cyanolichens and bryophytes are scarce or absent except on the forest floor or near streams (Sillett and Neitlich 1996). Epiphytic cyanolichens dominate canopies of old-growth forests with intermediate moisture regimes, such as those surveyed at the H. J. Andrews Experimental Forest in Oregon (Pike et al. 1975, McCune 1993, Sillett and McCune in press), but they are relatively sparse in very wet, bryophyte-dominated forest canopies. For example, *P. rainierensis* is present in the canopy of very wet old-growth forests along the Carbon River (Mount Rainier National Park, WA) and the South Santiam River (Willamette National Forest, OR; Figure 2E), but its abundance is strikingly low compared to somewhat drier old-growth forests at similar elevations (Figure 2). Epiphytic bryophytes, including terrestrial mosses, dominate the canopies at both sites (Sillett unpubl.). Intense competition from bryophytes and/or unsuitable microclimates (e.g., too consistently wet) may limit the distribution of *P. rainierensis* and other epiphytic cyanolichens in very wet old-growth forest canopies.

Vertical shifts in epiphyte distributions within the canopy are likely to vary in amplitude as well as in rate. Field observations in British Columbia, for example, suggest that the upper limit of *Nephroma occultum*, an epiphytic cyanolichen, varies markedly from region to region, presumably in response to differences in macroclimate (Goward 1995). This observation led Goward to propose three “range classes” within the total geographic distribution of epiphytic macrolichens inhabiting forest canopies. In its “primary range,” a species extends into the upper canopy and is clearly well adapted to regional macroclimate. In its “secondary range,” the same species is less adapted and, therefore, absent from the upper canopy, perhaps reflecting an intolerance of summer droughts and/or winter freezes. Finally, in its “tertiary range,” the species may require particular microclimatic conditions found only in the understory and lower canopy of old-growth forests, which are relatively sheltered from macroclimatic extremes compared to upper and middle canopies (Geiger 1965).

The few existing surveys of *P. rainierensis* are insufficient to fully evaluate the dynamics of its vertical distribution, but a few tentative conclusions are warranted for some regions. British Columbia and southeast Alaska are within the tertiary range of *P. rainierensis* because of its restriction to the understory and lower canopy of old-growth forests (Goward 1996, L. Geiser, pers. comm.). In the Oregon Cascades, *P. rainierensis* attains its highest known vertical distribution (i.e., 50 m in the crown of a 70 m tall tree, Figure 2) and has been found in forests as young as 140 years. In this region, *P. rainierensis* is most abundant in the lower canopy and understory. Since *P. rainierensis* is rarely found in the upper canopy, it may lack a primary range at this time, and the Oregon Cascades may be part of its secondary range. Alternatively, its absence from the upper canopy in Oregon may indicate an inability to keep pace with vertical canopy growth because of poor dispersal. Vertical shifts in epiphyte distribution, however, are a stand-level phenomenon; epiphyte colonization does not necessarily proceed from the bottom up in all trees. For example, *P. rainierensis* occurred in the mid-crown of a 140-year-old Douglas-fir tree but was absent from the understory beneath this tree (Figure 2A).

## PATCHY DISTRIBUTION WITHIN FOREST STANDS

When it is present in a forest, *P. rainierensis* typically occurs in small, isolated “pockets” (e.g., understory trees and shrubs in well illuminated habitats, Pike et al. 1975) but is absent from intervening areas. Recent canopy-level surveys in the Oregon Cascades found it on fewer than twenty percent of the large trees climbed (Sillett unpubl.). In a ground-level study of a mixed-age stand, *P. rainierensis* was found in only three of 231 two-meter-radius litterfall plots systematically distributed over a two hectare area (Sillett and Goslin in prep.). We offer two hypotheses to explain this patchiness: 1) *P. rainierensis* accumulates slowly in forests because of poor dispersal abilities and/or 2) its occurrence is favored by nutrient enrichment and thus reflects the localized nature of nutrient loading in forests.

According to the first hypothesis, slow dispersal prevents *P. rainierensis* from extending over its full ecological range (i.e., occupying all or most of the suitable habitat) within a forest stand. The fact that the highest abundance of *P. rainierensis* ever recorded occurs in the oldest forest ever surveyed in Oregon, a 700-year-old mid-elevation forest near the bottom of the Middle Santiam River valley, is consistent with this hypothesis. In this forest, *P. rainierensis* was the sixth most abundance lichen species, it covered up to fifty percent of branch surfaces in the lower canopy, it was found in seventeen of twenty litterfall plots, and it occurred in each of the seven large trees climbed (Sillett 1995). Thus, several centuries may be required for *P. rainierensis* to become abundant in a forest stand even under optimal conditions (Figure 2).

Recent observations in British Columbia (Goward in prep.) support the nutrient enrichment hypothesis. In a low elevation old-growth forest on nutrient-rich soils, *P. rainierensis* was only found within the drip zone of old *Chamaecyparis nootkatensis* trees, where it grew intermingled with twenty-five other cyanolichen species on understory *Abies amabilis* trees. This "drip zone effect" was not observed in similar forests on nutrient-poor soils, suggesting that foliage of overstory *C. nootkatensis* trees leaches surplus nutrients, providing enriched throughfall to understory epiphytes. Nutrient concentrations, especially calcium, beneath *C. nootkatensis* trees are indeed higher than those beneath other conifers (Kiilsgaard et al. 1987). Limited support for this hypothesis also comes from the lichenological literature. Small-scale variation in the availability of soil calcium was partially responsible for major differences in epiphyte communities inhabiting different *Quercus* trees within a Norwegian forest; trees growing on calcium-enriched soils supported epiphyte communities with more cyanolichens (Gauslaa 1985). Similar correlations were found in study of epiphytes on *Quercus* and *Fraxinus* trees in Scotland, although a causal link between soil nutrients and epiphyte community structure can only be established with manipulative experiments (Bates 1992). Clearly, additional research is required to evaluate the merit of this hypothesis for *P. rainierensis*.

## ASSOCIATION WITH OLD GROWTH

We are using manipulative experiments to determine potential causes for strong positive associations between some epiphytic lichens and old growth in the Pacific Northwest. Three experiments were designed to test the following alternative but not mutually exclusive hypotheses: 1) particular conditions found only in old growth are necessary for lichen survival and growth, 2) slow dispersal limits lichen colonization of young forests, and 3) environmental instability associated with rapid height growth makes young forests unsuitable habitat for lichens. This research, which is summarized briefly below, could be used to develop conservation strategies for *P. rainierensis* and other endemic lichens in managed forests.

In the first experiment, mature thalli of *P. rainierensis* and *Lobaria oregana* were transplanted into forests of different ages in the Oregon Cascades to determine if either species required particular conditions found only in old forests (Sillett and McCune 1997). After one year, *P. rainierensis* thalli transplanted into young forests performed at

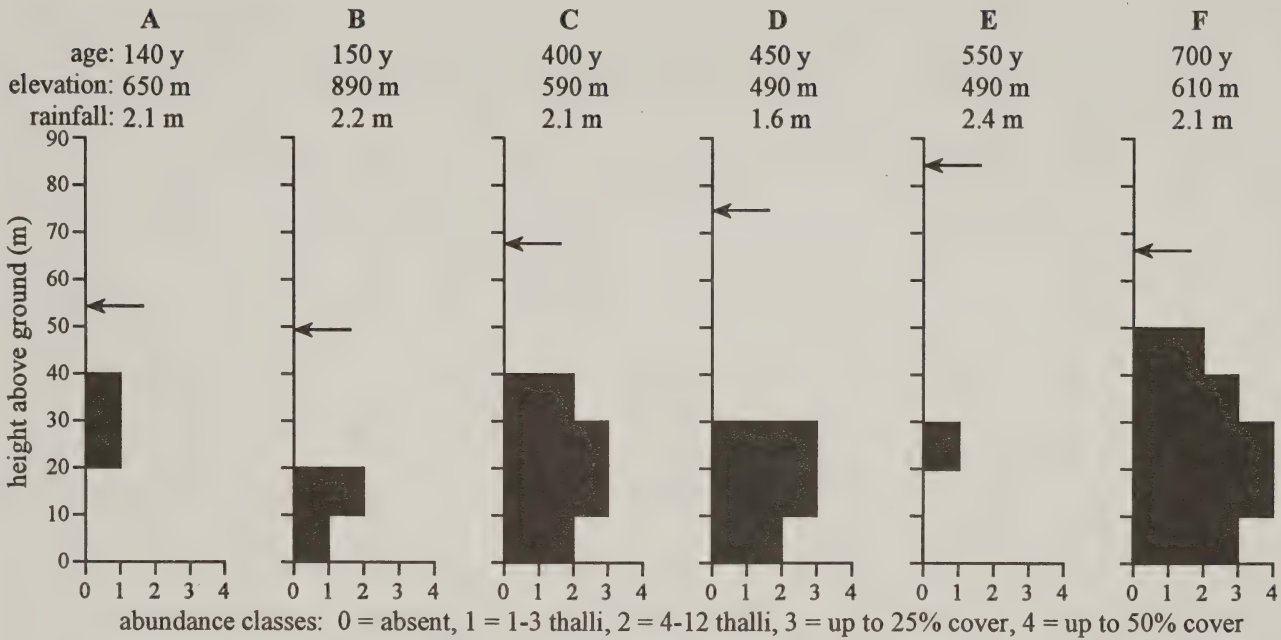

Figure 2. Vertical distribution of resident *Pseudocyphellaria rainierensis* populations along vertical transects in six forests from the Oregon Cascades. Approximate age, elevation, and annual rainfall are indicated for each forest. Each transect extended to the top of an individual *Pseudotsuga* tree, whose height is indicated by the horizontal arrow. Abundance was estimated visually at ten meter height intervals along the transect. Note that abundance is measured along a logarithmic scale.

least as well as those transplanted into old growth. Thalli in young forests actually remained more vigorous than thalli in old growth. They grew quite rapidly in each forest (Figure 3), and rates of mortality were uniformly low. These results indicate that in the Oregon Cascades, a broad range of forest age classes could provide suitable canopy habitats for *P. rainierensis*. Its failure to colonize young forests under natural conditions suggests that factors other than microclimate (e.g., dispersal) may be limiting in this portion of its geographic range.

Although it is possible to nondestructively collect propagules from lichen thalli for transplantation (Scheidegger 1995), the large quantities of propagules needed in the second experiment precluded the use of a rare species like *P. rainierensis.* In the first experiment, however, *L. oregana* also grew at least as well in young forests as it did in old growth. And like *P. rainierensis,* this large, old-growth associated foliose lichen has both a green alga and a cyanobacterium as photobionts. It also produces symbiotic propagules (lobules) as its primary means of dispersal (Rhoades 1983). Moreover, *L. oregana* was abundant enough to provide sufficient material for the second experiment without compromising existing populations.

In the second experiment, branches in forests of different ages were inoculated with *L. oregana* lobules to determine if dispersal limits epiphyte colonization of forest canopies. Branches were removed from trees, stripped of resident epiphytes, surface-sterilized, and lashed to tree crowns in young forests and in old growth (Sillett et al. in prep.). Half of these branches were manually covered with lobules each season for one year. Rates of establishment on all branches will be measured two years later. A significant inoculation effect would implicate dispersal as a limiting factor. The extent to which these results could apply to *P. rainierensis* and other lichens can be evaluated with a long-term experiment that required much less living material.

Rapid height growth quickly alters canopy microclimates in young forests; well-illuminated branches soon become shaded by expanding crowns. If dispersal of epiphytic cyanolichens can not keep pace with changing conditions, they may be unable to persist in young forests after successful colonization. More stable environmental conditions associated with older forests, which have only moderate height growth, would thus tend to promote the accumulation of slowly dispersing species. In the third experiment, thalli and symbiotic propagules of *P. rainierensis* were transplanted from old growth into young tree crowns to determine if they can persist within rapidly growing forests. The fate of introduced populations will be monitored over the coming decades to evaluate the long-term potential of these forests as habitats for epiphytic cyanolichens.

## EDGE EFFECTS

Much of the old growth remaining in the Pacific Northwest is impacted by edge effects (Norse 1990). Edges of old-growth forests bordering clearings are warmer, brighter, windier, and less humid than the forest interior (Chen et al. 1995), and epiphytic lichens on forest edges dry out much faster after rain than those in the forest interior (Renhorn et al. 1997). Intriguingly, *P. rainierensis* is able to persist on trees growing at the edges of clearings in some areas. In the Oregon Cascades, for example, luxuriant populations of this species have been found growing on a 55 m *Pseudotsuga* tree adjacent to a 20-year-old clearing, as well as on a 25 m *Tsuga* tree adjacent to a 40-year-old clearing. Immediately after logging, populations of *P. rainierensis* on edge trees probably suffer as exposed thalli sicken and die. Dieback, however, is apparently incomplete, and some thalli survive, ultimately acclimating to microclimatic conditions

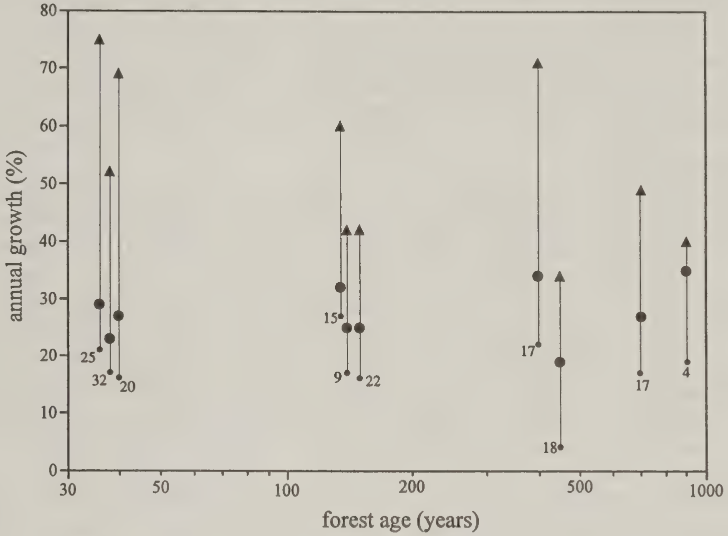

**Figure 3.** Annual growth rates for transplanted thalli of *Pseudocyphellaria rainierensis* in ten forests of different ages in the Oregon Cascades. Forty thalli were weighed and transplanted into tree crowns in each forest. After one year they were collected and reweighed. Data from the same forests are connected by thin, vertical lines. Three estimates of annual growth are presented for each forest. Average growth of all living, unfragmented thalli (small, shaded circles), average growth of healthy, unfragmented thalli (large, shaded circles), and maximum growth of a single thallus (shaded triangles). Many thalli died, disappeared, and/or fragmented during the experiment. The number of unfragmented, living thalli recovered from each forest is indicated at the base each vertical line.

near the forest edge. For example, *P. rainierensis* has persisted for more than a century on large *Pseudotsuga* trees that were isolated from each other by fire and subsequently surrounded by dense, regenerating forest (Sillett and Goslin in prep.). Likewise, reciprocal transplants of *P. rainierensis* among tree crowns in a 700-year-old forest revealed that thalli transplanted from the forest interior to the edge grew poorly, whereas thalli transplanted from the edge back to the edge grew quite well (Sillett 1994).

Several factors probably contribute to the apparent resilience of *P. rainierensis* to edge effects. Acclimation may occur most rapidly in humid forests supporting thick moss mats on branches. By retaining water, these mats may help desiccation-sensitive species grow by prolonging hydration periods (see Sillett 1995). Indeed, *P. rainierensis* thalli do grow slightly but significantly better on moss mats than on bare bark (Sillett and McCune in press). The cephalodiate nature of *P. rainierensis* may also contribute to its resilience. The capacity of its green algal photobiont to photosynthesize in humid air allows *P. rainierensis* to grow during conditions when many other cyanolichens, which have a single cyanobacterial photobiont, are dormant. Unlike green algal photobionts, cyanobacterial photobionts require liquid water for photosynthesis (Lange et al. 1988, 1993). The ability to photosynthesize in humid air could compensate growth losses attributable to shorter hydration periods following rain at forest edges. Finally, thalli from exposed habitats exhibit morphological changes (e.g., a thicker tomentum) that increase water storage capacity and decrease drying rates (Snelgar and Green 1981).

## CONSERVATION

*Pseudocyphellaria rainierensis* is rare throughout most or all of its range. Its patchy distribution, endemic status, strong association with old growth, and potential vulnerability to human disturbance led Goward (1996) to recommend it for endangered status in Canada and led Sillett (1997) to recommend it for threatened status in the United States. While this species is more abundant in Oregon and Washington than in Canada, even here it is essentially restricted to old growth. There can be little doubt that industrial logging has already led to its disappearance at many localities and could contribute to further declines. For this reason, we believe that *P. rainierensis* should be considered a threatened species throughout its range. At the present time, however, it is designated as “vulnerable” in Canada, and it receives no official endangerment status in the United States.

The simplest and certainly most effective strategy for conservation of *P. rainierensis* involves the protection of its remaining old-growth forest habitat. Unfortunately, only one of the six extant Canadian localities is currently situated within a protected area; all of the others are open to logging. In the United States, the situation may be less urgent, at least in the short term, because of the protection *P. rainierensis* is supposed to receive under the FEMAT plan (Rosentreter 1995). According to this plan, all sites with known populations will be protected and surveys will be conducted prior to ground-disturbing activities in potential habitat. Furthermore, many of the known populations in the United States are located within protected areas on public lands (i.e., National Parks, State Parks, Wilderness Areas, or Research Natural Areas).

In addition to protecting existing populations, long-term conservation of *P. rainierensis* will require creation of suitable habitats in managed forests. It may be possible to promote this species and other epiphytic lichens in managed forests by using certain silvicultural procedures. Reducing the size of cutting units, for example, may facilitate propagule dispersal into the regenerating forest from populations remaining in adjacent, older forests. Similarly, retaining large, live trees over the duration of stand rotation may permit inoculation of the regenerating forest canopy from populations persisting in the crowns of retained trees. Maintaining deciduous trees in the understory may speed recovery of *P. rainierensis* in regenerating forests because epiphytic cyanolichens tend to accumulate on deciduous trees more quickly than on conifers (Sillett and Neitlich 1996, Neitlich and McCune 1997). Retaining old *Taxus* trees in the understory will also help because their crowns often provide suitable *P. rainierensis* habitat for *P. rainierensis* in old growth (Sillett 1997). Uneven thinning of dense, regenerating forests should also promote *P. rainierensis* colonization because epiphytic cyanolichens frequently occupy well-illuminated substrates in canopy gaps (Pike et al. 1975, Neitlich and McCune 1997). Finally, extending rotation ages to over 200 years is likely to considerably improve chances of successful dispersal and establishment of *P. rainierensis;* some forests can accumulate considerable cyanolichen biomass in only 150 years (Rhoades 1981, Neitlich 1993, Sillett & McCune 1996). Such silvicultural procedures are more likely to prove successful in this species' secondary range (i.e., Oregon Cascades) than in its tertiary range (i.e., British Columbia and Alaska), where its level of old-growth dependency is presumably much greater.

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*LICHENOGRAPHIA THOMSONIANA*: NORTH AMERICAN LICHENOLOGY
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# PRODUCTION OF ASCOCARPS BY HIGH ARCTIC LICHENS IN RELATION TO ALTITUDE

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## Abstract

The percentage surface of the thallus occupied by apothecia was assessed in two crustose lichen species, *Rhizocarpon superficiale* (Schaerer) Vainio subsp. *boreale* Runem. and *Lecidea tesselata* Flörke s. lato, and within-species comparisions were made between sites at different elevations in granitic mountains at 79°N in Central Ellesmere Island, Canada. At the lowest altitudes apothecia covered approximately 24% of the surface area of *R. superficiale* and 14% of *L. tesselata*, but there were significant site-to-site differences in each of the species. In both taxa apothecial production was significantly lower at high elevations where conditions were more growth-limiting.

## Introduction

Lichens dominate in high arctic regions (Thomson 1972), yet in the most extremely cold and dry polar environments the lichen flora is impoverished (e.g., Maycock & Fahselt 1992, Inoue 1995). Under the most growth-limiting conditions, the majority of species are crustose microlichens (Thomson 1984, Maycock & Fahselt 1992). In terms of reproductive structures, lichens in the most severe polar environments tend to be species that produce apothecia rather than vegetative propagules (Fahselt et al. 1989, Sancho & Valladares 1993).

While it is widely appreciated that the abundance of apothecia varies within lichen species, there has been little attempt to relate ascocarp production within a single taxon to position along a natural environmental gradient. The objectives of this paper were to quantify reproductive effort

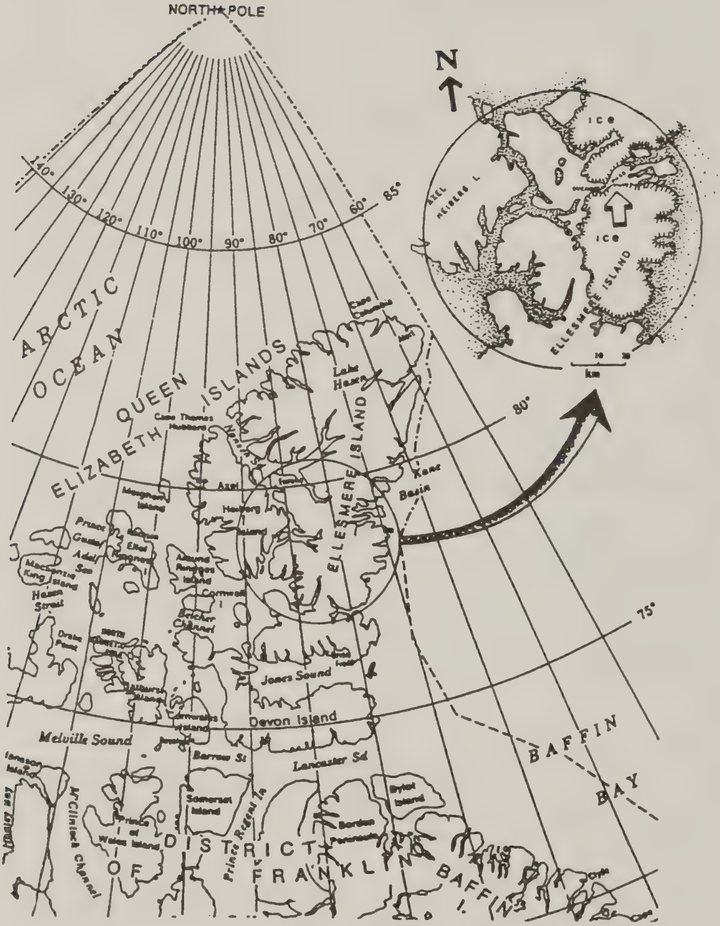

Fig. 1. Map showing the relationship to Ellesmere and other islands in the Queen Elizabeth chain, in the eastern Canadian Arctic. The location of Sverdrup Pass is indicated by a large white arrow to the right of centre in the inset.

in High Arctic lichens and to make comparisons between sites at different altitudes within the same mountain system.

## Materials and methods

Physical separation of thallus into vegetative and reproductive components is time-consuming, and precision is low because of the small size of young fruiting bodies as well as the close adhesion between thallus and substrate. Therefore, to approximate the extent of ascocarps, close-up photography was used instead of microdissection. It was assumed that the proportion of thallus surface area involved in generating propagules was a reflection of biomass devoted to reproduction and that such a measure provided at least one valid indication of reproductive effort.

Field reconnaissance was undertaken on a granitic mountain slope near a valley glacier and ice field on the south side of Sverdrup Pass in Central Ellesmere Island (Fig. 1) in the high Arctic regions of eastern Canada (79°10'N,79°45'W). For the study it was necessary to select lichen species that occurred at both higher and lower elevations and bore visually distinct ascocarps that were easily identifiable in photographs. The species finally chosen were *Rhizocarpon superficiale* (Schaerer) Vainio subsp. *boreale* Runem. and *Lecidea tesselata* Flörke s. lato, and specimens identified by I.M. Brodo and P.Y. Wong were deposited in the National Herbarium of Canada (CANL), Ottawa. Both lichens were saxicolous species that generated apothecia, but no specialized vegetative reproductive structures, such as soredia or isidia.

Within each of twelve areas selected to be as homogeneous as possible in respect to both geological and biological features, one 10 X 10 m study site (Fig. 2) was positioned randomly. The altitudes of the sites ranged from approximately 240 m above sea level, that is, just above the valley floor, to 895 m which was nearer the top of the mountain. Dry granitic rock substrate predominated in all. The entire study area had been covered by ice during the Wisconsin Period of glaciation, but escaped glaciation during the subsequent Little Ice Age, 1550-1850 AD (Alt 1985). The dimensions of thalli in these sites were not compared statistically, but sizes were not noticeably different between sites.

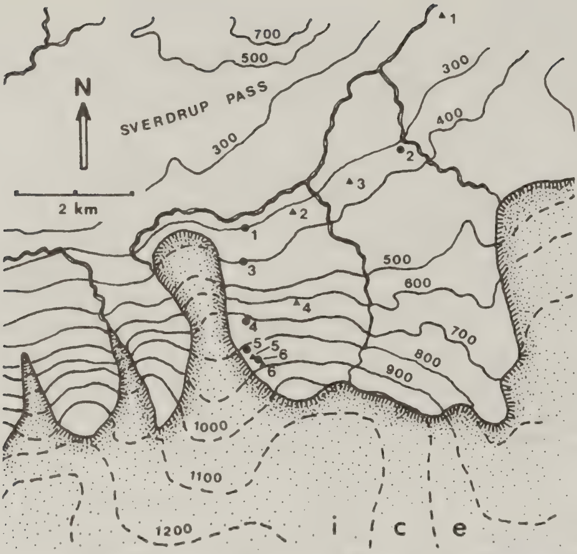

Fig. 2. Study sites in central Sverdrup Pass.• = collection sites for *Rhizocarpon superficiale* subsp. *boreale* and ▲ = sites for *Lecidea tesselata*. Elevational contours are shown in m and the ice cap and glaciers are shown with stippling.

Table 1. Characteristics of study sites in central Ellesmere Island, Canada where *Rhizocarpon superficiale* subsp. *boreale* and *Lecidea tesselata* were evaluated.

| Species | Site Number | Altitude (m) | Distance to nearest ice (km) | Cover% | |
|---|---|---|---|---|---|
| | | | | Vascular | Lichen |
| *Rhizocarpon* | 1 | 300 | 0.70 | 20 | 60 |
| *superficiale* | 2 | 320 | 2.00 | 30 | 40 |
| ssp. | 3 | 400 | 0.40 | 10 | 40 |
| *boreale* | 4 | 730 | 0.30 | 10 | 40 |
| | 5 | 825 | 0.07 | <1 | 30 |
| | 6 | 885 | 0.15 | <1 | 30 |
| *Lecidea* | 1 | 240 | 3.50 | 30 | 55 |
| *tesselata* | 2 | 320 | 1.80 | 15 | 70 |
| | 3 | 340 | 2.80 | 30 | 40 |
| | 4 | 640 | 1.30 | 40 | 40 |
| | 5 | 870 | 0.10 | <1 | 40 |
| | 6 | 895 | 0.15 | <1 | 60 |

Each lichen was assessed in six sites. At least one specimen per species was collected in each site and 10 of the larger thalli from amongst those in each site were chosen on the basis of random numbers. However, thalli that were eroded or extensively intergrown with other lichen species were excluded. Selected thalli were photographed along with a metric scale using a 35m camera equipped with a macrolens and loaded with Kodachrome film ASA 64.

Thalli of *Rhizocarpon superficiale* ssp. *boreale* were projected from 35mm transparencies to 6 times their actual size, and two non-overlapping 1 X 1 cm plots (enlarged size 6 X 6 cm) were randomly chosen on the upper surface of each image. All apothecia in each plot on the projection were traced onto a clear acetate sheet with a black Staedler medium-point waterproof pen, and then rendered opaque. Each of the two acetate tracings based on one thallus was read 10 times in a Li-cor Portable Area Meter, model LI-3000 (error 2-5%). The extent of apothecia in each sample thallus was expressed as a mean of the 20 readings, 10 of each tracing. The relationship between actual area of objects and meter readings was established using planar forms of known areas, and on the basis of the standard curve thus generated, mean thallus readings were converted to $cm^2$ and then to a percentage of the total plot area.

For *Lecidea tesselata*, with thalli sometimes too small or irregular to accomodate 1 X 1 cm plots, all apothecia on each thallus were traced from the enlargement onto acetate and blackened, and an outline of the whole thallus was traced onto opaque paper. Tracings and outlines were each read 10 times in the area meter and the mean of these readings used to characterize the extent to which apothecia were produced by any given sample. Both thallus and apothecia readings were converted to area ($cm^2$) and the percentage of thallus area devoted to ascocarps was then calculated.

In order to assess the significance of differences in apothecial areas between sites the percentage data were arcsin squareroot transformed and subjected to one-way analysis of variance (ANOVA) and Duncan's Multiple Range test. The statistics package used was SPSS/PC+ for IBM PC (SPSS Inc., V5.0.2, Chicago, IL).

## Results

The means and standard deviations for apothecial area per $cm^2$ of surface of all thalli analyzed in each site are shown in Figs. 3a and b. Mean apothecial area in sampling sites ranged from approximately 16-38% for *R.*

*superficiale* and from 8-17% for *L. tesselata*. According to ANOVA there were highly significant differences between sites ($P \leq 0.002$)for both lichen species. The same letter on bars in each of the histograms indicates no significant difference ($P = 0.05$) according to Duncan's multiple range test.

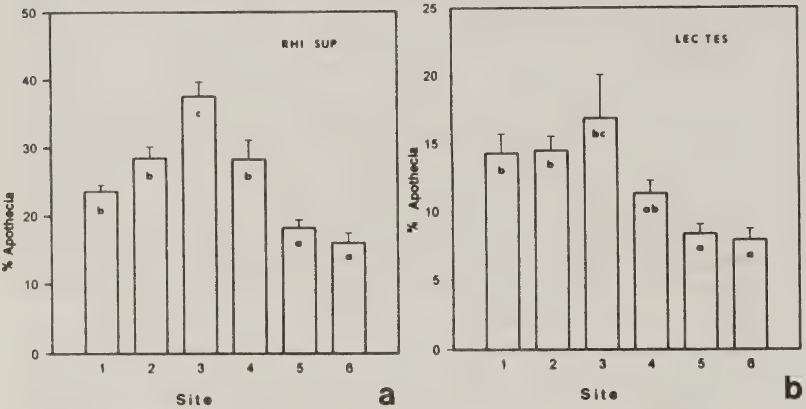

Fig. 3. Percentage of thalli covered by apothecia in sites on the north face of granitic mountains in central Ellesmere Island. Sites for each lichen species are arranged in order of altitude from lowest (site 1) to highest (site 6). The vertical line on each bar indicates standard error of the mean, and letters on bars indicate homogeneous subsets ($P = 0.05$) according to Duncan's multiple range test. a) *Rhizocarpon superficiale* subsp. *boreale*, b) *Lecidea tesselata.*

In *Rhizocarpon superficiale* subsp. *boreale*, apothecial area was highest at elevation 400m, less than one-quarter of the way up the mountain and significantly lower at the sites located both above and below. The four lower sites were between 300m and 2 km from the nearest ice mass. Apothecial extent in this species was least of all at the higher elevations of 825 and 885m where in each case the distance from the ice field was 150 m or less and the cover of vascular plants failed to achieve 1%.

In *Lecidea tesselata* there was greater thallus area covered by apothecia at low altitude sites, with no significant differences among the four lowest. However, reproductive effort was significantly less at the highest altitudes, 640m or above, than in the two lowest sampling sites. The least apothecial area in this species was observed 100 to 150m from the ice edge, in sites with elevations of 800m or more where vascular plant cover was low.

## Discussion

Few spores were found in samples collected from any of the sites, but rarity of spores in the collections might be explained by the fact that all sampling was done within a few days in mid-summer, and it may have been a time that did not coincide with peak sporulation. Because spore production could not be properly assessed or compared between sites, analysis of spore-bearing structures was the only available means of judging reproductive effort. Nevertheless, even if thalli had been truly sterile, establishment in the general area could have been accomplished through spores introduced form elsewhere.

Because spores are widely broadcast, all study sites had probably been exposed to a similar assortment of ascospores. One indication of successful long distance wind dispersal of lichens is the colonization of geologically new islands (Lindsay 1977). Spores of lichens are particularly well adapted for wind dispersal and the strong winds in mountainous terrain (Barry & Chorley 1982), such as in Sverdrup Pass, would facilitate dispersal (Longton 1988). Spores apparently belonging to species of *Solorina* were observed on rock surfaces in the pass (Fahselt and Sweet 1991), and because *Solorina* was not found during an extensive study of the immediate area, it appears that the landscape was in fact subject to propagules from more distant points. Thus, it was probably reasonable to assume that the study locations, located on the same N-facing mountain slope and mostly less than 6 km from one another, were all exposed to a similar spore rain.

Lichens in study sites closer to ice masses on mountain tops must have experienced lower temperatures than those situated further from the ice or those at lower elevations, and temperature is an important factor, if not the most important influencing cryptogams in polar regions (Longton 1988). At higher altitudes lichens would also have been more exposed to the force of prevailing winds (Barry & Chorley 1982), and thus more subject to dessication. Total lichen cover on rock surfaces showed no consistent trend in relation to altitude, but the increased severity of growing conditions at higher elevations was clearly indicated by the extemely low vascular plant cover in sites nearest the mountain top (Table 1). Thus, it may be that the environmental restrictions at higher elevations may also have played a role in reducing the reproductive output of lichens. The high apothecial area observed in *R. superficiale* at 400m, exceeding that at two of the lower sites, represented somewhat of a departure from the overall pattern and suggested mitigating circumstances at this level, such as local protection from the force of winds.

The explanation for reduced representation of reproductive structures at higher altitudes was not determined, but initiation or expansion of fruiting structures could have been restricted by more limiting growing conditions. A previous transplant experiment with *Xanthoparmelia cumberlandia* indicated that significantly more apothecia were present per unit area of thallus in sites where annual snowfall was less and where the mean annual growing season was somewhat longer (Fahselt 1977). In one of these warmer sites, apothecial area was also significantly increased in comparison to a more northerly location. In any event, in Sverdrup Pass the surface area of thallus devoted to ascocarps clearly differed from site to site on the same mountain slope and, for both *Rhizocarpon superficiale* and *Lecidea tesselata*, it least where growing conditions were most limiting.

Longton (1988) indicated that considerable reproductive effort is maintained by certain Antarctic endemics, but also that sexual reproduction is low in polar lichens, either through lack or rarity of sexual fruiting or failure to sporulate normally. Reduced production of spores in less favorable sites was also reported by Hale (1987) and Lindsay (1977). The present study indicates that reproduction of at least some apotheciate crustose taxa in central Ellesmere Island is significantly curtailed under the harshest cold and windy conditions over distances of only a few kilometeres. This is parallel to the situation in higher plants where flowering and seed set may be impaired if stress is sufficiently severe (Hopkins 1995).

## Acknowledgments

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# THE TERRICOLOUS LICHEN FLORA OF THE SAN RAFAEL SWELL, EMERY COUNTY, UTAH, U.S.A.

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## ABSTRACT

Twenty-three species of terricolous lichens in sixteen genera are reported from the San Rafael Swell in east-central Utah. The San Rafael Swell is an anticlinal uplift 165 km from north to south and up to 65 km wide. The crest of the anticline has eroded down to Permian Limestone; while peripheral areas consist of massive ridges of tilted, eroded Triassic and Jurassic sedimentary rocks. This unusual geologic setting presents a unique opportunity for studying terricolous lichens from a variety of soil types. *Gypsoplaca macrophylla*, a rare gypsophilous lichen, is a new species record for the state of Utah. *Acarospora schleicheri* and *Lecanora argopholis,* typically found on rock substrates in lower to middle elevation sites on the Colorado Plateau, were collected from undisturbed sandy soils. *Cladonia pyxidata, Leproloma membranaceum,* and *Physconia muscigena,* previously unknown from lower to middle elevation sites on the Colorado Plateau, were collected from protected, rocky micro sites. A rare and rather unusual crustose lichen, found only on gypsiferous soils on the San Rafael Swell, is described as new to science (*Lecanora gypsicola* sp. nov.). Vagrant lichens appear to be absent from the San Rafael Swell.

Keywords: terricolous lichens, soil crusts, microbiotic soil crusts, gypsiferous soils, San Rafael Swell, Utah

## INTRODUCTION

**Previous work-** Lichens are important components of soil crust communities in western North America. In some habitats lichens account for a significant percentage of the ground cover, often stabilizing the soil surface and enhancing soil fertility (Harper and Pendleton 1993, Belnap and Gardner 1993). Over the last 25 years soil crust-related research in arid and semiarid western North America has increased our understanding of the various biological components and ecological roles of microbiotic soil crusts. Early studies described various components of soil crust communities (Anderson and Rushforth 1976, Johansen et al 1981); while later workers studied various aspects of soil crust ecology (Belnap and Harper 1995, Brotherson and Rushforth 1983, Kleiner and Harper 1977, St. Clair et al. 1984, Skujiņš and Klubek 1978). The effects of various types of human-related disturbance (grazing, fire and vehicular activity) have also been studied (Belnap 1996, Johansen et al. 1984, Johansen and St. Clair 1986). Natural recovery and reclamation of damaged soil crust communities have also been researched (Anderson et al. 1982, Belnap 1993, Buttars et al. in press, St. Clair et al. 1986).

Anderson and Rushforth (1977) published the first list of terricolous lichens from Utah. Specimens were collected from 34 sites in three general areas. Most of the sites (24) were located in the Great Basin, five were in gypsiferous areas of Washington County; while the balance were located in pristine, open grassy areas in Canyonlands National Park. They reported a total of 17 species in 11 genera; however, three species were saxicolous, while six were misidentified. St. Clair and Warrick (1987) reported *Acarospora nodulosa* (Duf.) Hue var. *nodulosa,* a squamulose lichen collected from gypsiferous soils in southern Utah, as a new species record for North America. McCune and Rosentreter (1992) described habitat conditions associated with the rare soil lichen *Texosporium sancti-jacobi.* Timdal (1990) described a new and rare squamiform lichen genus and family (*Gypsoplaca* of the Gypsoplacaceae) from gypsiferous soils in southwestern Colorado. Included in Timdal's paper was a list of 21 soil crust species commonly associated with *Gypsoplaca macrophylla.* Many of the species on Timdal's list are frequently found on gypsiferous soils throughout the state of Utah. Rosentreter and McCune (1992) described distribution patterns of vagrant species of the foliose genus *Dermatocarpon* in Idaho, Montana, Wyoming and eastern Oregon and Washington. Three recent monographic works (Thomson 1987, 1989, Timdal 1986, Breuss and McCune 1994) have added valuable taxonomic and ecological information about two of the more abundant soil genera in western North America (*Psora* and *Catapyrenium*). Finally, St. Clair et al. (1993) published a summary paper describing the lichens of soil crust communities in the Intermountain Area of the western United States. They cited a total of 34 species in 17 genera from soil crust communities throughout the Intermountain Area.

**Geology of the study area-** The San Rafael Swell is a major domal uplift which dominates the geologic structure of east-central Utah (Figure 1). The anticline is 165 km long from north to south and up to 65 km wide, east to west. The uplift occurred during the Eocene and exposed strata from the Triassic, Jurassic and Cretaceous periods. Moving from east to west across the "swell" you first encounter the Mancos Shale, followed successively by the Dakota, Carmel, Navajo, and Wingate sandstones, and finally the Moenkopi and Chinle formations; with the crest of the swell dominated by the flat-lying Kaibab Limestone.

## MATERIALS AND METHODS

**Collection, identification and deposition of specimens-** Soil lichens were collected from many locations across the San Rafael Swell. Specifically, sites representing various soil and vascular plant community types were identified and systematically collected.

Specimens were identified using standard keys, taxonomic treatises and by making comparisons with herbarium material. Standard chemical spot tests, and where necessary , thin-layered chromatography were used to finalize species identifications. Only one collection is cited for each species. Nomenclature follows Esslinger and Egan (1995). All specimens are currently housed in the Herbarium of Nonvascular Cryptogams at Brigham Young University (BRY) in Provo, Utah.

Fig. 1. Map of the San Rafael Swell in east-central Utah.

## RESULTS

A total of twenty-three lichen species in sixteen genera were collected from various sites on the San Rafael Swell. *Gypsoplaca macrophylla* is reported as a new species record for the state of Utah. Two species which commonly occur on sandstone substrates on the Colorado Plateau, *Acarospora schleicheri* and *Lecanora argopholis,* were collected from stabilized sandy soils on the San Rafael Swell. In addition three taxa, not previously reported from arid lower to middle elevation sites on the Colorado Plateau (*Cladonia pyxidata, Leproloma membranaceum,* and *Physconia muscigena* , were collected from protected micro sites on the San Rafael Swell. A rare and unknown, crustose *Lecanora* sp. was collected from gypsiferous soils derived from the Carmel Formation. This taxon (*Lecanora gypsicola* sp. nov.) is described as new to science in this paper.

Following is an alphabetical list of all terricolous lichen species collected on the San Rafael Swell. The information for each species includes: relative abundance (rare<common< abundant), substrate information, as well as herbarium and collection numbers. Assignment of relative abundance categories is based on the following criteria: rare = 1-2 encounters, common = 3-9 encounters, and abundant ≥ 10 encounters.

ACAROSPORA NODULOSA var. NODULOSA. Common on gypsiferous soils. BRY C-28001 (Rajvanshi 0001). This species has also been collected from gypsiferous sites in Washington County, Utah.

ACAROSPORA SCHLEICHERI. Rare on stabilized, protected sandy soils. BRY C-28002 (Rajvanshi 0002). This species occurs on sandstone boulders in canyon sites on the San Rafael Swell. It also occurs commonly on alpine tundra sod in higher elevation sites in western North America, as well as open, lower to middle elevation, grassy shrub lands in Idaho. Recently, I have also collected this species from soils in lower montane grassy sites in southwestern Colorado.

BUELLIA ELEGANS. Common on protected sandy soils. BRY C-28003 (Rajvanshi 0003).

CATAPYRENIUM DAEDALEUM. Common on gypsiferous soils. BRY C-28004 (Rajvanshi 0004).

CATAPYRENIUM SQUAMULOSUM. Abundant at all sites. BRY C-28005 (Rajvanshi 0005). This species is broadly distributed across the entire intermountain western United States. It occurs in a wide variety of habitat types, ranging from Great Basin valleys to alpine tundra sod. It occurs on soil or soil over rock.

CLADONIA PYXIDATA. Rare on sandy soils in protected, shaded micro sites. BRY C-28009 (Rajvanshi 0006). This species is common on soil and detritus in upper montane and subalpine habitats throughout the western United States. However, it is generally absent from lower to middle elevation arid sites on the Colorado Plateau.

COLLEMA TENAX. Abundant at all sites. BRY C-28010 (Rajvanshi 0007). This species is broadly distributed across the intermountain western United States.

DIPLOSCHISTES DIACAPSIS. Common on gypsiferous soil; rare on sandy soils. BRY C-28013 (Rajvanshi 0008).

ENDOCARPON PUSILLUM. Rare on sandy soils. BRY C-28015 (Rajvanshi 0009).

FULGENSIA DESERTORUM. Abundant at all sites. BRY C-28017 (Rajvanshi 0010).

GYPSOPLACA MACROPHYLLA. Rare on gypsiferous soils. BRY C-21698 (Rajvanshi 0011). This species is found preferentially in steep-sloped areas of the contact zone between the Carmel Formation and the Page Sandstone; in close proximity to the base of a dead shrub (usually *Atriplex confertifolia*).

HEPPIA LUTOSA. Rare on sandy soil. BRY C-28020 (Rajvanshi 0012).

LECANORA ARGOPHOLIS. Rare on stabilized, protected sandy soils. BRY C-28021 (Rajvanshi 0013). This species occurs commonly on sandstone rocks in Buckhorn Wash. The movement of this taxon from rock to stabilized soil surfaces is most likely caused by several factors including: 1) the protected status of the location; 2) the close proximity of rock specimens to soil substrates; and 3) the high degree of similarity, in terms of chemistry and texture, between the sandstone and adjacent stabilized sandy soils.

LECANORA GYPSICOLA St. Clair & Newberry sp. nov. Common on gypsiferous soils derived from the Carmel Formation (Figures 2-5). BRY C-28022 (St. Clair 4829).

Thallus cretaceous ad cinereus, crustaceus, solum arcte adhaerens, crassus, usque ad peripheriam omnino areolatus. Hypothallus invisus. Areolae verruciformae aut bullatae aut extra sursumve irregulariter expansae, spisse coacervatae, apice tumescentes, cortici crasse pruinoso, farinaceo-tartareo, interdum excavato. Apothecia lecanorina. Margo thallo concolor et crasse pruinosus, mox sinuosus. Discus fuliginosus, tenuiter pruinosus, mature planus ad vix convexus, mox saepe distincte convexus; vetus, saepe crateratus aut fissuratus, hyphis nivalibus per orificia erumpentibus. Hypothecium incoloratum; hymenium hyalinum, c. 80-90 µm crassum; epithecium melleus; paraphyses septatae, ramosae, interdum anastomosantes, 3-4 µm latae, cellulis proximaliter strictis, distaliter moniliformibus-tumescentibus; asci clavati, 60-70 x 15 µm trans latissimum medium, apparatu apicali simili Bacidiae; sporae 8, hyalinae, nonseptatae, late ellipticae, 10-14 x 8-10 µm. Cortex acidum norstictum continens. Ad solum gypsiferum, Emery Comitas, Utah, C.F.A.

Thallus chalky-white to ashy gray, crustose, adhering tightly to the soil, thick, areolate throughout. Hypothallus not seen. Areoles verruciform to bullate to irregularly expanded upwards and outwards, tightly heaped together, apically swelling, the cortex thickly pruinose, mealy to crumbly rough, occasionally excavated. Apothecia lecanorine. Margin concolorous with thallus, thickly pruinose, soon becoming sinuous. Disk fuliginose, weakly pruinose, at first flat to scarcely convex, soon often distinctly convex; when old, often cratered or fissured, with white hyphae erupting through. Hypothecium colorless; hymenium hyaline, ca. 80-90 µm high; epithecium yellow-brown; paraphyses septate, branching, occasionally anastomosing, 3-4 µm wide, proximally straight, distally moniliform-swelling; asci clavate, 60-70 x 15 µm at the widest, the apical apparatus of the Bacidia-type; spores 8, hyaline, nonspetate, broadly elliptical, 10-14 x 8-10 µm. Cortex containing norstictic acid. On gypsiferous soil, Emery County, U.S.A.

*Type:* U.S.A., Utah, Emery County, San Rafael Anticline, 8 km north of Wedge Overlook, alt. 1798 m, 3 September 1993. *St. Clair 4829* (holotype, BRY C28022; isotypes, COLO, MIN, US, WIS).

*Distribution:* U.S.A., Emery County, on gypsiferous soil derived from the Carmel Formation.

LEPROLOMA MEMBRANACEUM. Rare on sandy soils in protected, shaded micro sites. BRY C-28023 (Rajvanshi 0014).

PHYSCONIA MUSCIGENA. Rare on sandy soils in protected, shaded micro sites. BRY C-28024 (Rajvanshi 0015). This species is common in upper montane to alpine tundra habitats throughout the western United States. It has also been commonly collected beneath shrubs growing over and among bryophytes in middle elevation, grassy shrub lands in Idaho. However, it is generally absent from lower to middle elevation arid sites on the Colorado Plateau.

PSORA CEREBRIBFORMIS. Abundant at most sites. BRY C-28025 (Rajvanshi 0016).

PSORA DECIPIENS. Abundant at all sites. BRY C-28027 (Rajvanshi 0017).

PSORA GLOBIFERA. Rare on sandy soils. BRY C-28030 (Rajvanshi 0018).

PSORA TUCKERMANII. Common at most sites. BRY C-28031 (Rajvanshi 0019).

SQUAMARINA LENTIGERA. Common on both sandy and gypsiferous soils. BRY C-28032 (Rajvanshi 0020).

TONINIA SEDIFOLIA. Common at most sites. BRY C-28035 (Rajvanshi 0021).

TONINIA TRISTIS subsp. TRISTIS. Rare on sandy soils. BRY C-28038 (Rajvanshi 0022).

## DISCUSSION AND CONCLUSIONS

The terricolous lichen flora of the San Rafael Swell is diverse and well developed consisting of twenty-three species in 16 genera. Four species (*Catapyrenium squamulosum, Collema tenax, Fulgensia desertorum,* and *Psora decipiens*) were found at all collections sites. All four of these species are found commonly throughout the western United States from a wide range of habitat types. Four species (*Acarospora nodulosa var. nodulosa, Catapyrenium daedaleum, Gypsoplaca macrophylla,* and *Lecanora gypsicola*) were collected only from gypsiferous soils. Surprisingly, no vagrant lichens were collected at any of the sites on the San Rafael Swell. Vagrant species are typically absent from gypsiferous soils; however, other habitat types, many of which are common to the San Rafael Swell (e.g. Pinyon-Juniper Woodland and Saltbush Shrub land), are usually productive sites for vagrant species of *Xanthoparmelia* and *Aspicilia.* Vagrant species of both *Xanthoparmelia* and *Aspicilia* have been collected from various locations throughout east-central Utah; therefore, their absence from the San Rafael Swell is puzzling.

## ACKNOWLEDGMENTS

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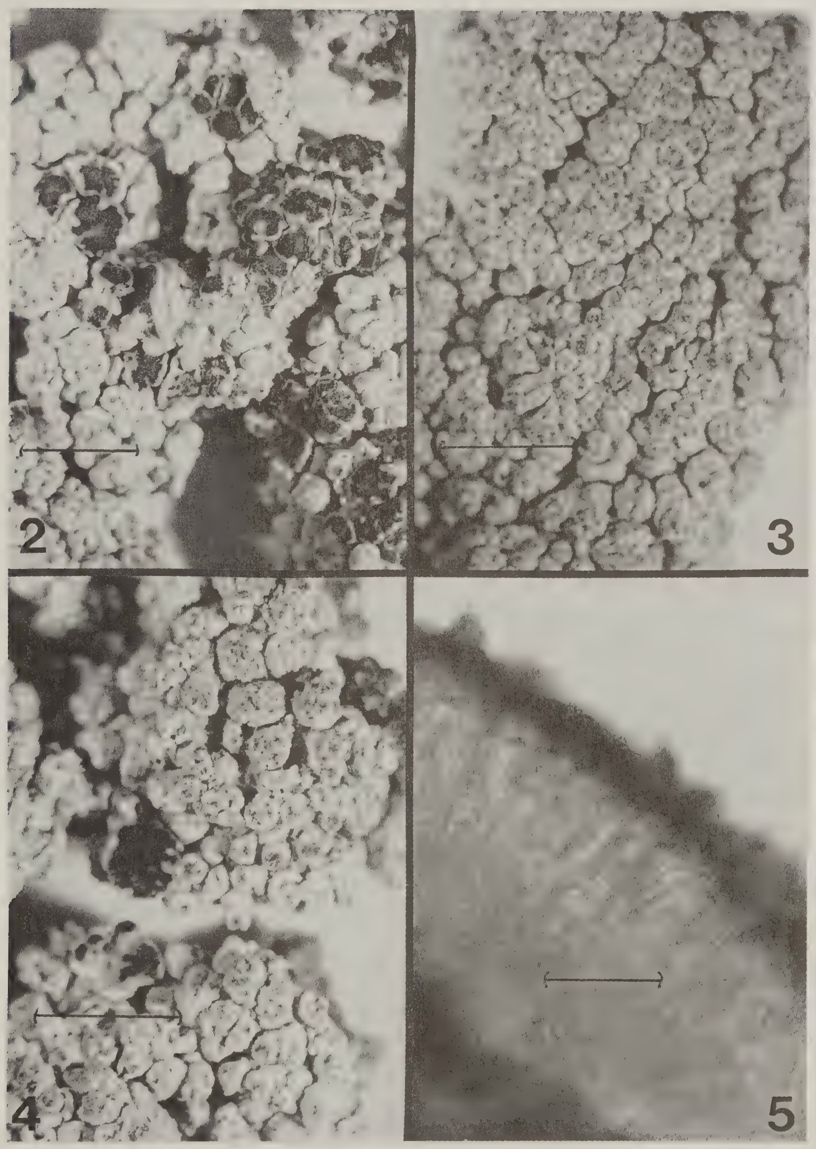

Figs. 2-5. *Lecanora gypsicola* (holotype). 2. Thallus with apothecia (bar = 5 mm). 3-4. Detail of thallus showing excavated areoles (bar = 6 mm). 5. Section through apothecium, showing hymenial structure and ascospores (bar = 50 µm).

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# CORTICOLOUS LICHENS AND BRYOPHYTES: PRELIMINARY SURVEYS OF OLD GROWTH AND MANAGED NORTHERN HARDWOODS STANDS IN MINNESOTA

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**ABSTRACT**: In order to understand what biotic features of old growth forests are distinctive and thus vulnerable to disturbance, there is an urgent need for detailed comparisons of old-growth and managed forests. This project compares the corticolous epiphytes (lichens and bryophytes) of paired old growth and mature managed (partially logged) forests of two types of northern hardwoods (*Acer saccharum/Tilia americana* and *Quercus rubra/Acer saccharum/Tilia americana*) in northwestern Minnesota. The fertile crustose lichens had significantly higher cover and species richness in the old growth stand than in the paired managed stand, for the forest type with oaks. Conversely, macrolichens (foliose and fruticose) had lower cover and richness in old growth than in managed stand plots, for both forest types. Unlike the lichens, bryophytes did not differ significantly in total cover or richness when old growth and managed stands were compared; however, individual bryophyte taxa surfaced as indicator species in multivariate analysis. Cluster analysis (TWINSPAN) and ordinations (Canonical Correspondence Analysis and Non-metric Multidimensional Scaling) distinguished between the four individual stands more strongly than between management category (old growth versus managed) or substrate tree species. We conclude that a simple dichotomy of managed versus old growth categories does not fully capture the complex variation in stand history that influences the epiphyte assemblage, although it does correlate with general patterns of richness and cover. History, both natural and (primarily) anthropogenic, exerts a surprisingly strong influence on the structure and composition of epiphyte assemblages.

## INTRODUCTION

Concern has been mounting over the continued logging of ancient forests in the Pacific Northwest, forests that support threatened species and distinctive biotic assemblages. Biologists have also begun to scrutinize fragments of old-growth forest that remain in eastern North America (Davis, 1996), within a vast matrix of disturbed ground and second-growth (logged) forest. Once an old growth forest is logged, its ability to recover its pre-logging flora is in serious doubt. Duffy and Meier (1992) presented evidence that the Southern Appalachian vascular flora never returns to the old-growth condition following clearcut logging, a conclusion criticized by Johnson et al. (1993), but supported by others (Elliott and Loftis, 1993; Bratton, 1994; Matlack, 1994; Meier et al., 1995).

Lichens and bryophytes are conspicuous components of ancient forests, and their persistence after logging is also of great concern (Rose, 1992). Previous work suggests the existence of distinctive assemblages and, in some cases, indicator taxa, within some old growth forests in western North America (Goward, 1994; Lesica et al., 1991), of the northeast (Selva, 1996; Cooper-Ellis, 1998), and in Europe (Soderstrom, 1988; Hyvarinen, et al., 1992). In southern Sweden, large old trees were necessary for the presence of sensitive lichen species found only in unmanaged stands (Gustafsson et al., 1992). Epiphytes are slow to invade and their abundance increases as forests age (McCune and Antos, 1982; McCune, 1993). Forest edges, which are analogous in some ways to logged or thinned forest stands, also support different epiphyte assemblages than do forest interiors (Chen et al., 1992; Sillett, 1994, 1995; Glenn and Webb, 1997; Glenn et al., in press). These differences between epiphytes of old growth and managed stands come as no surprise. Lichens and bryophytes are favored by those features that characterize the interior of an old growth forest: abundant coarse woody debris (Hale, 1996), high humidity, and old trees with favorable bark chemistry and structure (Cooper-Ellis, in press; Goward, 1994).

This project examines the corticolous (bark-dwelling) assemblages of lichens and bryophytes in northern hardwood forests. In the upper midwestern US, the northern hardwood forest type has lost more ground than any other forest type, with surprisingly rare remnants of primary forest still in existance (Frelich and Reich, 1996). Most remnants of this forest type contain cut stumps or other signs of anthropogenic disturbance (Rusterholz, 1996). Near the prairie-forest border in northwestern Minnesota, the majority of old growth forest stands are pine (*Pinus resinosa, Pinus strobus, Pinus banksiana*) forests of post-fire origin, with some pines reaching ages of >350 years (Frissell, 1973). Our work focuses on northern hardwood forests in this prairie-forest border region, southwest of today's pine zone, where the dominants are sugar maple (*Acer saccharum)* and basswood *(Tilia americana)*, with northern red oak *(Quercus rubra)* where large openings have occured (due to past fires or partial logging for pine). These forests differ from the better-studied northern hardwoods of the northeast because they lie far from the range limit for beech (*Fagus grandifolia)* and hemlock (*Tsuga canadensis)*, and because of other floristic differences related in large measure to a much drier climate and higher fire frequency. These factors could influence how disturbance by logging changes forest conditions and biota. Detailed quantitative studies of epiphytes in nearby Wisconsin (Hale, 1955; Culberson, 1955; Cole, 1977) provide a background framework for our inquiry into the consequences of forest management.

This project takes a comparative approach to elucidate the effects of forest management for corticolous lichen and bryophyte communities in northern hardwood forests in Minnesota. We contrast two mature managed (partially logged) stands with two intact, unmanaged stands that apparently represent old growth conditions. This comparative method has been used in many recent studies of other taxa and in other regions (see for example Gilliam and Turrill, 1993; Gilliam et al. , 1995; Kuusinen, 1994; Rominger, 1994; Halpern and Spies, 1995; Essen et al. , 1996; Davis, 1996; Webb, 1998).

Our study builds from two larger regional projects, one examining corticolous epiphytes as indicators of forest integrity, including regional and edge effects (Glenn and Webb 1997, Glenn et al., in press), and the other comparing structural and compositional features of old growth versus managed mature forests in 21 pairs of stands throughout Minnesota (Hale, 1996). We chose to sample intensively within a small number of stands in this exploratory research, because of the high variance of and multiple influences on epiphyte assemblages. The results show distinct patterns and suggest directions for future work.

## STUDY AREAS

Two pairs of stands were surveyed for corticolous epiphytes. Each pair includes one old-growth forest and one second growth ("managed") forest site, chosen for close geographic proximity and similarity of soils and forest dominants. The managed stands are mature forests that were partially logged recently. Both old growth forests show many characteristics of old growth including mound/pit topography, old trees (for this region;Table 1), and an uneven age distribution. Not surprisingly, basal areas were higher and tree densities lower than in the managed stands (Table 1; Hale, 1996). Coarse woody debris was abundant but also characterized the managed stands because of the logging practices utilized there (Hale, 1996).

All four sites are northern hardwood forests, with understories of sugar maple beneath canopies of sugar maple and basswood. The first pair (old growth stand plus managed stand) is distinguished by large northern red oaks; hence we call this the oak/maple/basswood forest type. The presence of light-demanding red oaks indicates a stand-opening disturbance in the past, probably fire in the old growth stand of oak/maple/basswood, but certainly logging in the younger managed stand of this type. The managed stand in this forest type was partially logged in 1992 with all branches left on site afterwards. It is possible that both stands were dominated by pines (*Pinus strobus, Pinus resinosa*) at one time, judging from the history of the region which includes frequent fires (Spurr, 1954; Frissell, 1973) and selective logging for pines around the turn of the century (Patterson, 1978; Aaseng, 1976).

The other pair of stands lacks oaks; this we call the maple/basswood forest type. Apparently American elm (*Ulmus americana*) played an important role until the arrival of Dutch elm disease; dead snags are abundant; living elm sprouts are still present; and overall densities of living trees are relatively low. Both stands have light colored, well-drained soils of loam over sand and loam, while the similarly colored soils of oak/maple/basswood stands were deep, well-drained loams (Hale, 1996). The managed stand has a high sapling density and low tree basal area, reflecting its young age; old pine stumps are still visible. The matching old growth maple/ basswood stand has the oldest trees in our study, reaching 167 years (Table 1) and exhibits no evidence of previous logging, fire, or pine dominance.

All four sites are located on generally level uplands within the Itasca moraine complex of Wisconsin glaciation. The climate is continental cold temperate, with nearby mean annual temperature of 3.7 degrees and mean annual precipitation of 640 mm (Keuhnast, 1972). As already noted, our study areas are part of a more extensive network of old growth/managed forest pairs throughout Minnesota whose other characteristics are compared in detail in Hale (1996). Table 1 gives locations and other features of these study areas.

## METHODS

Within Hale's releve plots (Hale, 1996) at each of the four study sites (Table 1), we sampled epiphytes on four randomly selected trees of each species (sugar maple, basswood, and northern red oak if present). Additional trees were randomly selected from those nearest the plots if needed to balance the sampling effort.

Epiphyte sampling utilized eight bark plots in "windows" (each 25 cm x 10 cm) on the bark of each tree, placed at the N, E, S, and W orientations. Like Hale (1955), we sampled both at the tree base and at a height of 1.5 m. All bryophytes and lichens, including crusts, were identified and their cover estimated. The 20 m x 20 m releve plots were also searched for additional epiphytes on fallen branches and logs to assess the total richness of corticolous epiphyte within a fixed area, because quantitative surveys can miss some components of the flora (McCune and Lesica, 1992). The identity of epiphytes was confirmed in the lab using microscopy and HPTLC (Camaq, Inc.) for characterization of lichen chemicals.

Tree diameters were measured and light measurements (in upper bark plots only) were recorded using an Accupar ceptometer, a multisensor light measuring wand, held at three different orientations. However, light data are only available for one pair of stands (sugar maple/basswood), because a massive blowdown struck the old growth stand of the other pair (red oak/maple/basswood) before measurements were taken, completely changing the light regime.

Data analysis used SPSS (Norusis, 1993) and PC-ORD (McCune and Mefford, 1995). To avoid pseudoreplication, all of our analyses pooled together each tree's four base bark plots and, for separate analysis, each tree's four upper bark plots. We did not combine upper bark and base bark plots because the environments and assemblages are so different. Instead we ran separate analyses for base bark plots, where bryophytes predominate, and for the upper bark plots, where lichens are most important.

We used simple t-tests to test for differences in cover and richness between different management types. Beyond these univariate statistics on summary variables, we used multivariate analyses to interpret entire assemblages of epiphytes within the bark plots. To search for epiphyte species or assemblages that serve to distinguish managed from old growth stands, we used TWINSPAN (version of McCune and Medford, 1995), a divisive method of classification. We next ran two kinds of ordination analyses: canonical correspondence analysis (CCA; Ter Braak, 1986, 1987; Palmer, 1993), and non-metric multidimensional scaling (NMS) (Kenkel and Orloci, 1986; Kent and Coker 1992; McCune and Mefford, 1995; McCune et al., 1997). Canonical correspondance analysis is a method of direct ordination that uses the measured environmental variables to explain the variation in species composition of the samples. In this analysis the variables used were management status (managed vs. old growth), species of the substrate tree, tree diameter, inclination of the trunk, site, and where available, light. In non-metric multidimensional scaling (NMS; Kent and Coker 1992; McCune and Mefford 1995), the epiphyte plots are arranged in a multi-dimensional 'ordination space' with plots that are most similar closest together. Only the species composition of each plot, and not the environmental factors, is used in arranging the plot; thus NMS is a technique of indirect ordination.

Authorities for nomenclature are Esslinger and Egan (1995) and Harris (1977) for lichens; Anderson et al. (1990) for mosses; Stotler and Crandall-Stotler (1977) for liverworts and hornworts; and Gleason and Cronquist (1991) for vascular plants.

## RESULTS AND DISCUSSION

### *Comparison of the Paired Stands*

Table 1 presents the comparison of cover and species richness for each stand, with individual species aggregated into structural groups and with results from all tree species combined to give a stand-level assessment. For both the oak/maple/basswood and the maple/basswood stands, the average cover and richness of macrolichens was significantly

| **Forest Type** | | **Oak / maple / basswood** | | | **Maple / basswood** | | |
|---|---|---|---|---|---|---|---|
| **Site Type** | | Old Growth | Managed | P-value | Old Growth | Managed | P-value |
| **Site Name** | | Arrowpoint | Bebensee | (t-test) | Sugarbush | Tamarac7 | (t-test) |
| | | | | *=significant | | | *=significant |
| **County** | | Mahnomen | Mahnomen | | Becker | Becker | |
| **Township** | | 143N | 144N | | 140N | 39W | |
| **Range** | | 38W | 38W | | 40W | se se s7 | |
| **Section** | | se ne s16 | sw sw s19 | | se s12 | USFWS | |
| **Stand Size** | (ha) | 40 | 16 | | 8 | 57 | |
| **Basal Area** | (sq m/ha) | 37.9 | 27.35 | | 31.1 | 24.6 | |
| **Tree Density** | (per ha) | 680 | 790 | | 390 | 400 | |
| **Sapling density (/ha)** | | 753 | 187 | | 617 | 1643 | |
| **Snags** | (per ha) | 50 | 60 | | 70 | 40 | |
| **Tree Ages** | (N) | 95-119 (11) | 58-77 (10) | | 80-167 (13) | 56-107 (11) | |
| **# Lichen Trees** | | 12 | 12 | | 8 | 8 | |
| **Macrolichens** | Cover | 155 | 248 | 0.10 (0.03**) | 19 | 116 | 0.02* |
| | Richness | 3.6 | 5 | 0.06* | 1 | 2.9 | 0.02* |
| **Fertile crusts** | Cover | 32 | 12 | 0.02* | 54 | 34 | 0.6 |
| | Richness | 3 | 2.2 | 0.04* | 1.7 | 2.5 | 0.3 |
| **Bryophytes** | Cover | 240 | 259 | 0.8 | 389 | 339 | 0.7 |
| | Richness | 2.1 | 2.4 | 0.6 | 2.1 | 1.4 | 0.2 |
| **All epiphytes** | Cover | 492 | 594 | 0.09 | 504 | 516 | 0.9 |
| | Richness | 8.8 | 9.5 | 0.3 | 4.8 | 6.8 | 0.09 |
| | | | | **base plots excluded | | | |

Table 1. Stand information and differences in epiphyte cover and richness between old-growth and managed stands. Epiphyte cover and richness are averages for the 2000 $cm^2$ bark surface area that results from pooling the eight 25 cm x 100 cm bark plots on each tree. Cover is thus given in $cm^2$ of epiphytes per 2000 $cm^2$ of bark.

less in the old growth than in the managed stands (t tests, $P<0.05$). In contrast, the cover and richness of fertile crustose lichens was significantly greater in the old growth oak/maple/basswood stand than in its matched managed stand; this pattern was not evident in the maple/basswood forest type. The sterile sorediate crustose taxa had too little presence to analyze alone, but were separated from the fertile crusts because of their very different ecology. Neither cover nor richness for bryophytes or for total epiphytes showed significant differences in the old growth vs. managed comparisons. Perhaps the crustose species present include some with humidity requirements not met in the managed stands, while some foliose lichens in this system respond positively to elevated light levels following selective logging.

### *Overall Species Richness*

Table 2 compares the total species richness among stands. Again the crustose lichens (including here both fertile and sterile sorediate crusts) have more richness in the old growth stands, in this case for both forest types. Total richness is comparable across management types. A stronger difference is that between the two forest types, with high richness in the oak/maple/basswood stand. This is due in part to the presence of a third tree species, red oak, in addition to the maples and basswoods found in both forest types, whose different bark structure and chemistry supports slightly different assemblages. A complete listing of epiphyte taxa by stand and substrate tree species is given in the Appendix.

**Table 2. Epiphyte species richness within each site ***

| Forest Type | Oak / maple / basswood | | Maple / basswood | |
|---|---|---|---|---|
| **Old Growth Status** | Old Growth | Managed | Old Growth | Managed |
| **Site** | Arrowpoint | Bebensee | Sugarbush | Tamarac |
| **N (trees sampled)** | 12 | 12 | 8 | 8 |
| **Total sq cm bark sampled** | 24000 | 24000 | 16000 | 16000 |
| **Total species /site** | 50 | 48 | 36 | 35 |
| **Macrolichens** | 14 | 13 | 13 | 12 |
| **Crustose lichens** | 16 | 13 | 15 | 11 |
| **Bryophytes** | 12 | 10 | 4 | 6 |
| **Species found only outside bark plots** | 8 | 12 | 6 | 6 |

* Species richness was based upon the counts of lichens and bryophytes in the bark plus those found in reconnaisance throughout the 20 x 20 m releve plots.

## *Cluster Analysis Results*

We analyzed community data from all 40 trees, to explore the many factors that might influence epiphyte assemblages on a given tree. Multivariate cluster analysis and ordination permit us to look beyond summary variables and consider the distribution of all epiphyte species present.

Results of the TWINSPAN cluster analysis show strong differences among stands but only weak further distinction between old growth and managed forests. Within this framework of environmental variation, the tree species are distinct from one another only secondarily, and more strongly at the tree bases than on the upper bark. The dendrograms from cluster analysis are unstable, shifting as minor parameters are modified in the model. Thus we do not present here the diverse dendrograms generated. This result indicates that the assemblages on the bark of a given tree are influenced by multiple factors and are not shaped by a single gradient.

For bark plots on the upper trunks, trees within a stand tend to cluster together even across different tree species. That is, a basswood in one stand clusters with maples in the same stand, not with basswoods from other stands. For example, most trees in the old growth maple/basswood site cluster together, because of shared high coverage by the moss *Anomodon minor* in the upper plots and the paucity of some 30 other epiphytes generally shared by other stands. This distinction explains both the first and second division of the dendrogram. The last subdivision separates into one cluster most of the trees in the managed oak/maple/basswood stand. This stand had more *Phaeophyscia pusilloides, Melanelia subaurifera* and *Candelaria concolor* but less of other species of *Melanelia* and less *Graphis scripta* as compared with other trees from the managed and old growth maple/basswood sites.

When the plots at tree bases are analyzed, the two maple/basswood stands cluster together, even though one is managed and the other old growth, because of high cover values of the bryophytes *Anomodon minor* (also an indicator species on upper trunks) and *Brachythecium acuminatum.* These are most abundant on the basswoods. Meanwhile most plots from the managed and old growth stands with oak also cluster together at the first division, sharing abundant *Amblystegium serpens, Xanthoria* sp., and *Physconia leucoleiptes.* Only at the second division of the cluster analysis do stands diverge on the basis of their management history, and then only in the pair of stands with oaks. The managed oak/maple/basswood stand had much less *Anomodon minor*, no *Graphis scripta*, and no *Platygyrium repens,* but more *Pylaisiella polyantha* and *Leskia polycarpa* as compared with its old growth counterpart. It is interesting to note that while these individual bryophytes showed responses to stand-level conditions, the summary variables of bryophyte cover and richness did not (Table 1).

These findings show how important the individual stand history can be. The distinctive upper-bark assemblages in the old growth maple/basswood stand probably reflect the breakup of elms and consequent higher light levels. Our light readings confirm much more light availability in this stand than in its managed counterpart. The recently logged oak/maple/basswood stand also splits off from the rest of the data set. Its floristic differences are strong and most likely influenced by management activity; for example, the lack of *Graphis scripta* probably results from inadequate humidity for this sensitive fertile crust.

## *Ordinations*

Canonical Correspondence Analysis (CCA): The direct ordination of epiphyte assemblages on environmental factors did not reveal a robust model of the interrelationships. Without light data, only 17% of the epiphyte species distribution in upper plots was explained by linear combinations of environmental factors, and for the base plots, 22%. In the CCA ordination for upper plots, the four sites were arrayed quite separately from one another, while management category (old growth vs. managed) was less important. For the base plots, site was also important but only because one stand (old growth maple/basswood) was so distinctive. The overall fit of these ordinations was so poor that we cannot draw conclusions about the strength of other relationships.

For the pair of sites with light data (maple/basswood stands), the fit of the CCA ordination improved significantly when light was included in the model. The ordination explained 38% of the epiphyte species variation in these two stands. In this case the first axis (explaining 17.2%) strongly distinguished between the two stands, which of course differed in management type (canonical coefficient=-.796). The second axis (explaining 13.8%) was most highly correlated with light (cc=-.539) while the third axis (explaining 8.1%) correlated highly with the tree species of the bark plot (cc=-.605). None of the three axes had strong relationships with tree size or slope of the trunk. Thus environmental measurements are important adjuncts for interpreting the role of stand history. Whether management type or other differences between the two stands are responsible for the variation this ordination detected is unclear in absence of replicate stands.

Nonmetric Multidimensional Scaling (NMS): The generally poor fit of the CCA model in the absence of light data for the full suite of sites led us to analyze the data using indirect ordination as well. On the NMS diagrams (Figures 1 and 2), each letter shows the placement of one tree's epiphytes, pooling each tree's four upper bark plots (Figure 1) and four lower bark plots (Figure 2). Note that the axes are not hierarchical in NMS. Thus the graphs utilize different numerical axes, in each case the two axes with the highest total correlation with the epiphyte assemblage data.

*Upper Plots, NMS*: The result of NMS analysis of the upper-bark epiphyte plots is shown in Figure 1. Epiphyte plots from trees in the two oak/maple/basswood stands are located in the upper left of the plot, set off by a boundary curve from the two maple/basswood stands to the right and below. There is one exception, a basswood, B**, that clustered with the old growth basswoods in the maple/basswood stand. In neither of the oak/maple/basswood stands was the species of tree an important factor in differentiating the epiphyte community, with the exception of the oaks in the old growth stand, upper case Q, which are clustered in the ordination. It is surprising that maples and basswoods are not distinguished in this analysis since they are generally recognized to support different lichen assemblages. Other factors are clearly playing a strong role.

More than tree species or even management history, the stand type (with oaks or not) has the most influence on the upper epiphyte assemblages, judging from the general segregation represented by the line on Figure 1. However, close examination of this graph reveals that management history shows some effect on basswood assemblages in particular. The trees in the old growth maple/basswood stand are grouped together in the lower part of the graph (four uppercase M and B below the curve). The four basswoods in this same stand form an especially tight cluster, together with one basswood from the other old growth stand (oak/maple/basswood). Within that same stand, maples and basswoods do segregate to some degree. In contrast, the other three stands have relatively similar epiphyte assemblages, as we also found through cluster analysis (above). The four basswoods from the managed maple/basswood stand fall into the upper zone of the plot, with the trees of both the oak /maple/basswood stands.

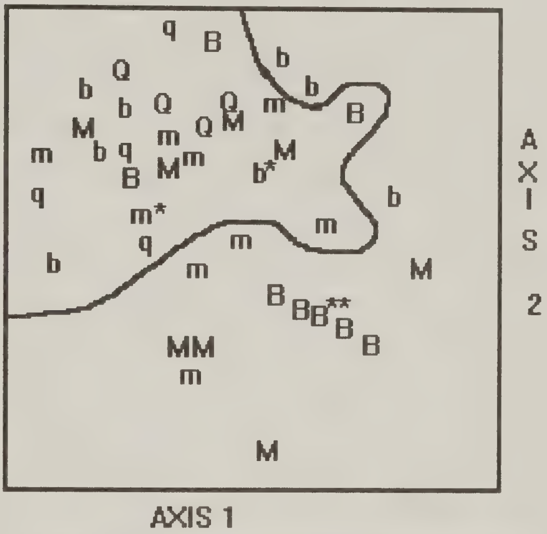

**Figure 1.** Upper bark plots: results of NMS ordination for epiphyte plots on upper bark. Each letter shows the placement of one tree's epiphyte assemblage from the upper bark plots. Trees from old growth stands are in upper case letters, while managed-stand trees are in lower case. The letters themselves represent species codes: M=sugar maple, B=Basswood, Q=oak. Trees of oak/maple/basswood stands lie to the upper left of the boundary curve, while trees of the maple/basswood stands lie to the right. The asterisks (*) denote exceptions, those trees that fall outside the region of the graph where other trees from its stand are found.

*m and b from maple/basswood stand
**B from oak/maple/bassswood stand

It is surprising that differences between forest types and between different stands were even stronger than differences between the substrate tree species. Without question the species of a tree exerts major influence on its epiphyte assemblage, because of interspecific differences in bark texture and chemistry (Hale, 1955; Cole, 1977; Culberson, 1955; Jesberger and Sheard, 1973). Our similar work at forest edges shows that the species of tree is a strong predictor of the epiphyte community within a stand (Glenn and Webb, 1997; Glenn et al., in press). However, the present old growth study shows that differences between forest stands can exceed differences between tree species. We note that our three tree species are quite similar to one other in bark texture and pH (Hale, 1955; Cole, 1977) and do not include trees with distinctive bryoflora (Cole, 1977). Others have shown that lichen species tend not to be obligate on single tree species because the epiphyte assemblage varies across interacting environmental gradients (Barkman, 1958; Schmitt and Slack, 1990). Thus it is an important result that forests in close proximity to one another diverge in their epiflora on the basis of stand history.

*Base Plots, NMS:* Epiphytes at tree bases exhibit a somewhat different pattern of ordination, with individual stands differing more strongly rather than forest types, at least for maple and basswood trees. For the base plots (Figure 2), NMS gives a clear clustering of the maple and basswood trees in the managed oak/maple/basswood stand (enclosed by an oval) and also separately for the old growth stand of the same type (sharp-cornered square). These clusters parallel the groupings from TWINSPAN analysis. However, the story is different for oaks; six of eight oaks are spread outside and between these within-stand clusters. The old growth maple/basswood stand forms a third cluster (in the square with curved corners) together with three plots from other stands. This diagram thus shows that the epiphyte community on the bases of maples and basswoods is more site-dependent than host-dependent. Conversely, for oaks, six of the eight trees (Q and q) have similar positions on axis 1, regardless of which stand they came from; therefore, the epiphyte community on oaks appears to be more host-dependent than stand-dependent. Apparent differences between managed and old growth stands are not strongly expressed by this analysis, which mixes management types in several parts of the graph.

Thus substrate tree species again interacts with stand history. For the bryophyte-dominated basal bark plots, the epiphytes of oaks are distinctive from those of the maples and basswoods. However as with the upper bark, we find stand history to be the major influence on the basal epiphytes for the maples and basswoods. The close compositional affinity of the old growth stand with oaks and the managed stand without oaks, an affinity also seen in the cluster analysis, suggests similar environmental conditions and perhaps a misclassification of the former stand, whose light-dependent oaks might have originated after logging rather than wildfire. More certainly the distinctiveness of one other stand, the old-growth maple-basswood site, results from elm mortality from the very recent pathogenic outbreak. Because the Dutch elm disease was introduced to the Americas by human agency, this event ultimately represents anthropogenic disturbance, though different in biotic consequences from logging.

## CONCLUSIONS

(1) The major characteristics of epiphyte assemblages differ between managed and old growth sites within the northern hardwoods forest types of northwestern Minnesota. The old growth forest sustains a significantly greater richness and cover of the fertile crustose lichens (for the forests with oaks) but, conversely, lower richness and cover of macrolichens (forest with and without oaks). These patterns reflect differences among lichen species in sensitivity to light (higher after logging) and humidity (lower after logging). Note that if we were to pool the lichen types for analysis, or omit crusts as is commonly done in lichen studies, this information would be obscured. For bryophytes, neither richness nor cover varied with management history in this survey; however, individual bryophyte species emerged as indicator species for analysis at the community level.

(2) Other individualistic aspects of stand history, such as pathogenic outbreaks (e.g., Dutch elm disease) and time since logging, help to explain surprisingly strong within-site affinity of epiphyte assemblages. One of our old growth sites and one managed site each formed rather discrete groupings when analyzed with both cluster analysis (TWINSPAN for upper plots) and ordination (NMS for plots at tree bases). Further scrutiny of structuring factors through direct ordination (CCA) also demonstrates the primacy of site, and also the importance of light. As with other biota, lichens and bryophytes exhibit complex multi-dimensional responses to how ancient and how undisturbed the forest is.

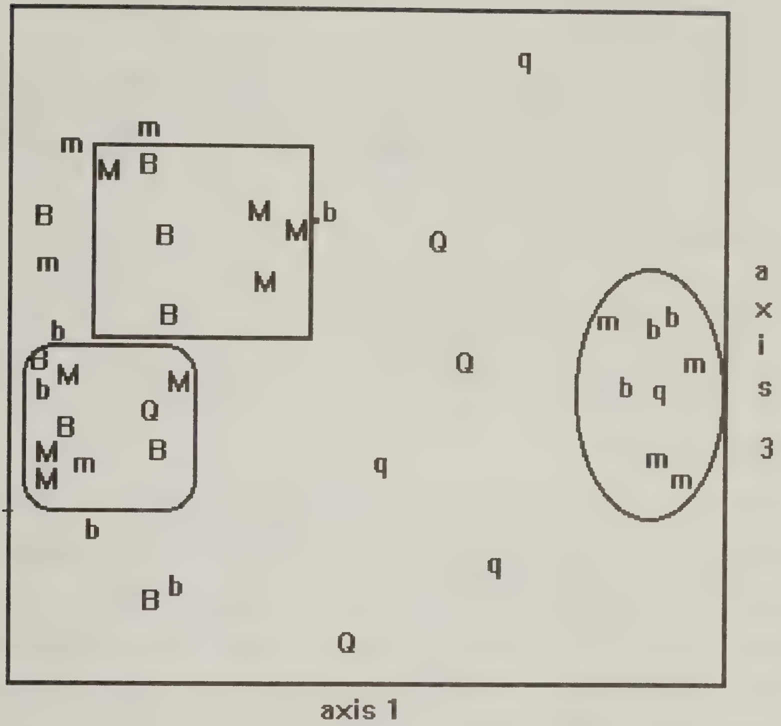

**Figure 2.** Base bark plots: results of NMS ordination for epiphyte plots on lower bark. As in Figure 1, each letter represents one tree's bark plots, but in this case for the tree base. Trees from old growth stands are in upper case letters, while managed-stand trees are in lower case. The letters themselves represent species codes: M=sugar maple, B=Basswood, Q=oak. The lines demarcate zones of the ordination where maple and basswood bark plots clustered together on the basis of which forest stand they occurred in. The oval encloses maples and basswoods in the managed oak/maple/basswood stand; the sharp-corned square encloses the old growth stand of the same type; the curved-corner square encompasses the bark plots in the old growth maple/basswood stand along with some others.

(3) Surprisingly, the species of the substrate tree was not as influential as the locality itself in these stands, with maples and basswoods within a site clustering together. Other research elsewhere suggests stronger influence of the substrate tree species upon the lichen assemblage (Culberson, 1955; Jesberger and Sheard, 1973) than we found, perhaps because all three of our tree species have similar bark pH (Hale, 1955; Cole, 1977), although basswood should be distinctive because its bark reatains more moisture (Hale, 1955; Cole, 1977). For the between-stand differences to dominate over between-tree-species differences, the environmental influence of historical events must be strong indeed. Thus the management

history of a specific site exerts important influence on the epiphyte assemblage as well as its cover and growth forms.

(4) The ability of this modest study to detect significant patterns suggests that a larger regional-scale survey would provide yet more insight into which aspects of forest history and composition contribute to high variance in epiphytes between stands. Our use of quantitative sampling and replication within stands, labor-intensive though they be, proved essential so that statistical and multivariate analyses could be used to test our hypotheses.

## ACKNOWLEDGEMENTS

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When I was a graduate student at the University of Minnesota, I had the good fortune to study plant taxonomy with John Thomson who was teaching "Plains and Boreal Flora" at the Lake Itasca Biological Station around 1980. While leading us deftly through the vascular flora, Dr. Thomson also inspired much interest in the lichens. In the field he often paused to pick up lichen specimens that had fallen from the forest canopy. I still use my training in plant taxonomy in my teaching and research, and I still use the wonderful twig-mounted dissecting needle that Dr. Thomson hand-crafted for each student. And in my present collaboration with Marian Glenn, partially presented in this compendium, I finally get to explore the lichens more fully, with gratitude to Dr. Thomson for sparking my curiosity about these strange, sensitive and beautiful organisms.

--- Sara Webb

## Appendix: Species list for sites and substrates

Substrates: B= basswood bark, M= sugar maple bark, O= northern red oak bark
R= found during reconnaisance in the plot, substrates vary.
Lichens: FC= fertile crustose, SC= sterile crustose, M= macrolichen

| **Species of epiphytes** | | **Oak/maple/basswood stands** | | **Maple/basswood stands** | |
|---|---|---|---|---|---|
| **1. Lichens** | | **Old growth** | **Managed** | **Old growth** | **Managed** |
| Acrocordia cavata | FC | | | B | B |
| Bacidia polychroa | FC | B, M | | M | B |
| B. rubella | FC | | | M | B |
| Biatora epixanthoides | SC | M | | M | |
| B. helvola | FC | | | M | |
| Caloplaca cerina | FC | | M | | |
| C. chrysophthalma | SC | B, M | B, M, O | M | B, M |
| C. holocarpa | FC | | O | | |
| C. ulmorum | FC | | | M | B, M |
| Candelaria concolor | M | B, M, O | B, M, O | M | B, M |
| C. fibrosa | FC | R | R | R | |
| Candelariella efflorescens | SC | O | | | |
| Cladonia sp. | M | | | | M |
| Eopyrenula intermedia | FC | B, M | M | M | B |
| Evernia mesomorpha | M | | R | | |
| Flavoparmelia caperata | M | R | R | | R |
| Flavopunctelia soredica | M | | R | | |
| Graphis scripta | FC | B, M, O | M | M | B, M |
| Leconora hybocarpa | FC | B | B, M | | |
| L. impudens | SC | | R | | |
| Lecidea plebeja | FC | M | | | |
| Lecidella euphoria | FC | R | B | | R |
| Lepraria sp. 3 (Harris 1977) | SC | | | B | |
| Lepraria sp. 4 (Harris 1977) | SC | | | B, M | |
| Melanelia exasperata | M | | R | | |
| M. subargentifera | M | B, M, O | B, M,O | | B, M |
| M. subaurifera | M | B, O | M, O | | B, M |
| Megaspora verrucosa | FC | M | B | | |
| Myelochroa aurulenta | M | | O | | |
| Parmelia sulcata | M | R | R | | |
| Parmeliopsis ambigua | M | R | | | |
| P. hyperopta | M | O | | M | |
| Pertusaria leioplaca | FC | O | O | | |

| Species of epiphytes | | Oak/maple/basswood stands | | Maple/basswood stands | |
|---|---|---|---|---|---|
| **1. Lichens (cont)** | | **Old growth** | **Managed** | **Old growth** | **Managed** |
| Phaeophyscia cernohorskyi | M | B, M, O | B, M, O | M | B, M |
| P. ciliata | M | B | M, O | R | B, R |
| P. hirtella | M | B, M | B, M | | B |
| P. imbricata | M | | | M | |
| P. orbicularis | M | M | | | M |
| P. pusilloides | M | B, M, O | B, M, O | B, M | B, M |
| Physcia aipolia | M | B, M | B, M, O | M | B |
| P. americana | M | R | | B, M | |
| P. millegrana | M | O | | M | |
| P. stellaris | M | R | B | R | |
| Punctelia bolliana | M | | O | R | |
| P. rudecta | M | | | R | |
| P. subrudecta | M | O | B, M | M | |
| Physconia leucoleiptes | M | B, M, O | B, M, O | M | B, M |
| Ramalina americana | M | | R | R | |
| Rinodina dakotensis | FC | R | R | | R |
| Scoliciosporum chlorococcum | FC | M | O | M | B, M |
| Strigula submuriformis | FC | B | | M | B, M |
| Xanthoria polycarpa | M | | | | B, M |
| Xanthoria spp. | M | B, M, O | B, M, O | M | |
| **2. Bryophytes** | | | | | |
| Amblystegium serpens | | M, O | B, M, O | B, M | |
| A. varium | | | O | | |
| Anomodon minor | | B, M, O | B, M, O | B, M | B, M |
| Brachythecium acuminatum | | B, M, O | O | B, M | B, M |
| B. salebrosum | | B, M, O | B, M, O | | M |
| Frullania eboracensis | | O | B, O | | B |
| Leskea gracilescens | | B, O | | | M |
| L. polycarpa | | | B, M, O | | |
| Lindbergia brachyptera | | M, O | | | |
| Mnium cuspidatum | | B, M, O | M | | R |
| Orthotrichum ohioensis | | B, O | | | |
| Platygyrium repens | | B, M, O | | | |
| Porella platyphylloidea | | B | O | B, M | B, M |
| Pylaisiella polyantha | | | B, M, O | | |

## Index to Scientific Names

Compiled by William R. Buck

Names in *italics* are synonyms; names in **boldface** are nomenclatural novelties. Page numbers followed by an asterisk (*) indicate a figure or map; page numbers in *italics* indicate that on that page the name is considered a synonym but on other pages within the volume the name is accepted. Names of substrates are not indexed.

# Index to Contributors

## CONTENTS, continued from back cover

## CONTENTS

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**Contents continued on p. 444.**

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