THE GENUS XANTHORIA (FR.) TH.FR. IN NORTH AMERICA

LOUISE LINDBLOM

ABSTRACT. The lichenized ascomycete genus Xanthoria (Fr.) Th. Fr. (Teloschistaceae) in continental United States and Canada is revised. The following 15 species are recognized: Xanthoria borealis, X. candelaria, X. concinna, X. elegans, X. fallax, X. fulva, X. hasseana, X. mendozae, X. montana, X. oregana, X. paretina, X. polycarpa, X. sorediata, X. tenax, and X. ulophyllodes. The morphology, anatomy, secondary chemistry, ecology, and distribution of these species is discussed. A key for the identification of the species is presented together with distribution maps and illustrations of all species. Two taxa are described as new: Xanthoria montana and X. tenax. In addition to the newly described species, X. concinna and X. mendozae are reported for the first time from the study area. A number of taxa are reduced into synonymy and all names treated are typified.

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Sweden.
INTRODUCTION

Members of the genus *Xanthoria* (Teloschistaceae, Ascomycota) are among the most conspicuous and beautiful lichens that exist. They constitute a prominent part of the lichen vegetation in various open and nutrient-enriched environments, such as seashores, roadsides, and sites affected by bird droppings. The genus is very widespread, known from all continents of the world, and often grows in abundant colonies. Thus, it is likely that one of the first lichens that a novice lichenologist identifies and collects belongs to *Xanthoria*. Representatives of the genus, mainly the type species *X. parietina*, have frequently been used in investigations concerning, e.g., ecology and physiology of lichens, and in a discussion at the XV International Botanical Congress concerning the choice of a group of “model lichens”, *X. parietina* received most votes (Smith 1993). The circumstances mentioned above, contribute to the genus being well represented in most herbaria. Although the genus is considered easy to identify, it often causes trouble to determine a collected specimen to species. Two significant reasons for this are that the species of *Xanthoria* are morphologically variable and that the taxonomy of *Xanthoria* has generally not been well understood. A world monograph of the genus *Xanthoria* has never been carried out, but in recent time taxonomically important contributions concerning some particular groups have been published (e.g., Steiner & Poelt 1982, Poelt & Petutschnig 1992a, 1992b, Giralt et al. 1993).

My research interest in the genus *Xanthoria* began in 1992 when I was introduced to various taxonomic problems as subject for a doctoral thesis. In the autumn of 1993, I decided to concentrate my studies to a monograph of the species of *Xanthoria* in a geographically limited area, namely North America (continental United States and Canada). It was obvious that *Xanthoria* had been a source of confusion and frustration among lichenologists in that area. Several of the species known in the genus, from several of the commonly recognized intrageneric groups, were represented in North America. A large number of collections were deposited in the herbaria, which ensured that my conclusions concerning, e.g., distribution, would be possible to consider as well founded.

During the course of the study I have chosen to keep the traditional delimitation of the genus *Xanthoria*. I have considered it unnecessary to challenge the generic concepts, because such work should be carried out on a world-wide scale. Additionally and importantly, it demands an immense experience of the entire family Teloschistaceae, as well as the species within the different genera. Considering that *Caloplaca*, the largest genus of the family, comprises at least 500 species, great care should be taken in any reconsideration of the generic boundaries within the family. The relationships between both previously described genera and potentially new ones should be carefully analysed with appropriate methods.

ACKNOWLEDGEMENTS

First of all, I wish to thank my supervisor Ingvar Kärnefelt for suggesting the
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The genus *Xanthoria* as the subject for my thesis, and for giving me advice and support throughout the work.

I would like to express my sincerest gratitude to Irwin Brodo, Thomas Nash and Clifford Wetmore for carefully reading the manuscript and making many suggestions for improvements. I also wish to thank them, as well as Bruce McCune, Jan-Eric Mattsson, Roland Moberg, the late Josef Poelt, Roland Santesson, Ulrik Söchting, Einar Timdal, Shirley Tucker, and William Weber for valuable advice and discussions regarding my work.

For help and hospitality during my visits to North America, I am especially grateful to Irwin Brodo, Bruce McCune, Charis Bratt, William Weber, Katherine Glew, and Patricia and James Hinds.

Furthermore, I would like to express my sincerest gratitude to my colleagues and friends at the Department of Systematic Botany for always being helpful and ready to discuss various problems. I especially want to thank Ulf Arup, Stefan Ekman, Lars Fröberg, Patrik Fröden, Arne Thell, and Martin Westberg for fruitful discussions on lichenological and other matters, constructive criticism, and help in many different ways. Per Lassen kindly provided the Latin diagnoses and helped me with matters concerning nomenclature, translations of Latin texts, and arranging loans. Stefan Andersson gave me advice regarding statistical problems, and Ulf Arup made the drawings in this work. Henrik Dagnegård, Sigvard Svensson, Kurt Lindberg, and Kristina Holmin are thanked for technical assistance.

I am indebted to Doris Baltzo, Charis Bratt, James Hinds, Douglas Ladd, Roger Rosentreter, Göran Thor, Leif Tibell, and Shirley Tucker for lending me material from their private herbaria, and to the curators of all public herbaria sending material on loan. Ulrik Söchting kindly carried out HPLC analyses of some specimens included in this study.

Financial support was received from The Royal Swedish Academy of Sciences (Hierta-Retzius stipendiefond), The Royal Physiographic Society of Lund, The Lund Botanical Society, Lund University (Anna och Svante Murbecks minnesfond, Bokelunds fond, Landshövding Per Westlings minnesfond, Nordstedts fond, Ove Almborns fond), and Anna Christenssons Fond.

Finally, I wish to thank Harald Moritz-Olsen for being a supportive assistant during the field work and for continuous encouragement throughout this study.

**OBJECTIVES**

This study has two primary objectives: The first is to provide a taxonomic revision of the North American taxa of the genus *Xanthoria* (in the present sense) and a sound morphological basis for species identification. The second is to provide the basis for future research concerning *Xanthoria* in the fields of population studies, taxonomy on larger geographical scales, phylogeny including related taxa, and detailed floristics, among others.
HISTORICAL BACKGROUND

The genus Xanthoria

Linnaeus (1753) recognized two species that presently belong to the genus Xanthoria: Lichen candelarius and Lichen parietinus. Much later, Link (1791) recognized Lichen elegans and a few years thereafter Hoffman (1796) described Lobaria polycarpa. The four taxa were included by Elias Fries (1825) in his new subgenus Xanthoria of the already existing genus Parmelia. The circumscription of the subgenus included taxa with a foliose thallus and yellow apothecial disk, and a few other taxa now belonging to other genera, e.g., Squamarina and Teloschistes, were included. Th. M. Fries (1860) elevated Xanthoria to genus level, and distinguished two subgroups. The first ("Physcia") comprised four species with asci containing eight spores, and the other ("Candelaria") comprised two species with asci containing many spores. Later Fries (1871) transferred X. elegans, originally included in Xanthoria, to the new genus Caloplaca. Over the years, numerous taxa were described in Xanthoria. Hillmann (1920) listed 75 epithets which had been described for forms and varieties of X. parietina. He accepted 27 of these, while the rest were disregarded, recognized at species level or listed as uncertain. Later, Hillmann (1922) published an overview of the species of Xanthoria, where he attempted to compile the information scattered in the literature. In the overview 10 species were treated, five of which are still part of Xanthoria. The remaining five are now placed in Caloplaca, Teloschistes, or Xanthodactylon. Later, Hillmann (1935) accepted the separation of Xanthoria and Teloschistes Norman in the sense that is still used.

Poelt (1954) in a study of the lobate species of Caloplaca transferred C. elegans back to Xanthoria together with C. papillifera and C. sorediata. Xanthoria, compared with Caloplaca, was defined as having a lobate to foliose thallus with a well developed lower cortex, more or less developed rhizines, and very loose medulla. By that, he introduced the present commonly accepted delimitation of the genus Xanthoria from Caloplaca. He later transferred three species of Xanthoria, viz., X. lobulata, X. persica, and X. polycarpoideae, into Caloplaca (Steiner & Poelt 1982), further defining the concepts of Caloplaca and Xanthoria. Poelt has been involved in several other important contributions to the systematics of Xanthoria and related genera, e.g., regarding the genera in Teloschistaceae (Poelt & Hafellner 1980) and regarding the taxonomy of some species groups in Xanthoria (Poelt & Petutschng 1992a, 1992b, Giralt et al. 1993, Kondratyuk & Poelt 1997). Further investigations, especially regarding the phylogeny and evolution of Xanthoria and related genera in Teloschistales have been carried out by Kärnefelt (1989, 1990a, 1990b, 1991) and Kärnefelt & Thell (1994).

More detailed historical overviews concerning the family Teloschistaceae have been published by, e.g., Almborn (1963) and Kärnefelt (1989).

Presently, the genus Xanthoria as well as hypothesized groups of related species within Xanthoria are being re-evaluated by several researchers. The investigations are by necessity large and difficult, since the relations to all other genera in Teloschistaceae have to be considered. Having in mind that Caloplaca alone comprises at least 500
species, and that names at the genus level already exist for several of them, great care should also be taken not to unnecessary burden the field of nomenclature with new names.

Xanthoria in North America – a brief history

The first publication to my knowledge in which a taxon of Xanthoria (as presently delimitied) is possibly mentioned from North America is “Deutschlands Flora” by Hoffmann (1796). In the comments under “Lobaria” polycarpa, Hoffmann wrote that the apothecia of specimens from America had a more saturated colour. I have not been able to find out whether the collections to which he was referring originated from North or South America.

Edward Tuckerman published reports of Xanthoria species in several papers beginning with “An enumeration of some Lichenes of New England” (1839), where he stated that Parmelia (= X. parietina) was “very common” on rails, boarded buildings etc. A couple of years later, Tuckerman (1841) reported Squamaria (= X.) elegans from tombstones and pebbles in Cambridge. A very important contribution, and the first publication with a comprehensive treatment of Xanthoria (as Physcia) in North America was “Observations on North American and some other Lichenes” (Tuckerman 1860), where five varieties of Physcia (= X.) parietina were listed, including the taxa we now know as X. parietina, X. polycarpa, and X. candelaria. One new taxon was added, namely P. parietina var. ramulosa, which was later combined into Xanthoria by A. W. C. T. Herre (1910). Xanthoria ramulosa was also listed in the overview of the genus Xanthoria by Hillmann (1922). Tuckerman (1872) accomodated all species in Teloschistes, a view which was to become common among North American authors (e.g., Schneider 1898, Nearing 1947). Tuckerman’s taxonomic arrangement of 1862 was kept, principally, in “North American lichens”, but the genus Teloschistes was used, and the variety ramulosa was elevated to species (Tuckerman 1882). Like most authors, Tuckerman placed X. elegans in Placodium, a circumstance which he had already discussed in “Genera Lichenum” (Tuckerman 1872). This taxonomy was also followed by J. Macoun in “Canadian plants” (Macoun 1902).

The pioneering works of Tuckerman were followed by B. Fink and H. E. Hasse. In Fink’s account of the lichens of Minnesota (Fink 1910) three species were listed, and the posthumously published “Lichen Flora of United States” (Fink 1935) included five species: Caloplaca elegans, Teloschistes parietinus, T. candelarius, T. polycarpus, and T. ramulosus. Several of the papers on the lichen flora of California published by Hasse included notes on Xanthoria (Hasse 1898, 1903, 1906). In the comprehensive lichen flora of southern California (Hasse 1913) two species now placed in Xanthoria were included, Caloplaca elegans and Xanthoria lychna, with three varieties of X. lychna. Rasanen (1944) described the species X. hasseana based on the material which Hasse (1913) had named X. lychna var. laciniosa. Up to that time, only two taxa of Xanthoria had been described from North America. The third taxon to be recognized in North America was X. polycarpa var. maritima, which was recognized ten years later by I. M. Lamb (1954).
Table 1. Short historical survey of the treated species. Names on the on that line (boldface) or the name that specific author used for that taxon. I regard *X. ramulosa* (line 7) as conspecific with *X. polycarpa* (line 4).

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<thead>
<tr>
<th>Linnaeus (1753)</th>
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<th>Hoffmann (1796)</th>
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same line (1–16) are either nomenclatural synonyms of the taxon first presented. There are 16 lines although only 15 species are treated in this paper, because

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Two species of *Xanthoria*, viz., *X. parietina* and *X. polycarpa* were mentioned in Degelius's (1940) paper on lichens from Maine, and their low frequencies compared with Europe were commented upon. In the same paper, a summary of the lichenological research of America was provided.

The most comprehensive study of the genus in North America was carried out by Rudolph (1955). He revised the entire family Teloschistaceae, and accepted 6 taxa in *Xanthoria*. The work was never published, however, and it seems that some *Xanthoria* species were misunderstood in Rudolph's attempt to apply existing old-world names to North American material. This caused some difficulties for subsequent lichenologists working with North American collections, especially regarding the concepts of *X. polycarpa* and *X. ramulosa*. Nevertheless, it is a helpful guide summarizing the knowledge of all species of *Xanthoria* on the continent.

One new species of *Xanthoria* was described from North America after the revision by Rudolph. *Xanthoria alaskana* was described in a report of the lichens of Tuxedni Wilderness, Alaska (Talbot et al. 1992). The latest North American study concerning *Xanthoria* was published by Hinds & Hinds (1993a, b). The first paper treated the species occurring in Maine and in the second paper the taxonomy regarding the *X. fallax* group was updated following Poelt & Petutschnig (1992a).

The number of taxa in the checklist of lichens of North America by Egan (1987) was 10. Eight years later, in the latest checklist (Esslinger & Egan 1995), 17 taxa in 15 species of *Xanthoria* were listed. Of these, I accept 13 species in this treatment, and describe 2 as new.

**Species Concept**

In the taxonomic studies of lichens where species concepts are discussed, it is generally concluded that the taxonomic species concept reflects the "truth" in an acceptable way, and in addition is most practical (e.g., Kärnefelt 1979, Timdal 1991, Arup 1995a, Ekman 1996). In some studies where the species concept is discussed, the concepts are described in terms of evolution and phylogeny (e.g., Mattsson 1993, Wedin 1995), and it is stated that species are evolutionary lineages that are monophyletic, i.e., share derived characters. Mattsson (1993) adds that species rank is assigned to the smallest monophyletic group that can easily be identified. Hawksworth (1974) concludes that marked discontinuities in several unrelated characters should separate species, but that the interpretation of what constitutes such a well marked discontinuity must rest with the individual taxonomist and varies in different groups.

My approach in this work is similar to those cited above. I follow for example Hawksworth (1974), Arup (1995a), and Ekman (1996) in that species should be separated by discontinuities in a number of characters, and in practice I follow Mattsson (1993) by assigning species rank to the smallest monophyletic group that can easily be identified. I agree with for example Mattsson (1993) and Wedin (1995) that species should represent hypothesized evolutionary lineages. I have refrained from using the rank of subspecies, although it may have been considered appropriate by some authors to reflect geographical differentiation within *X. fulva* and *X. oregana* (see the Discussion.
for these species).

**MATERIAL AND METHODS**

*Study area*

The study includes the continental United States and Canada, which in this publication is referred to as “North America”.

*Material*

The study is based on both herbarium material and my own field collections. About 5,000 specimens were examined, including all or sets of relevant material in the following institutional herbaria (abbreviations follow Holmgren et al. 1990): ASU, BM, CANL, COLO, C, FH, GZU, H, KR, LD, MIN, MSC, NY, O, OSC, PC, UBC, UPS, US, UWO, and WIS. In addition, collections from several private herbaria were included: D. E. Baltzo, C. C. Bratt, J. W. Hinds, D. Ladd, R. Rosentreter, G. Thor, L. Tibell, and S. C. Tucker. Type material and scattered collections from BP, BM, GOET, GZU, H, FH, M, O, SFSU, STU, TUR-V, UPS, US, and WIS have been studied. My own material comprises c. 300 specimens and is deposited in LD. Some duplicate collections are deposited in ASU, CANL, MIN, and US.

*Field work*

The main part of the field work was carried out in North America on two occasions: (1) in Ottawa (Ontario), Oregon, California, Arizona, Utah, and Colorado in June-July 1993, and (2) in Connecticut, Rhode Island, Massachusetts, New Hampshire, Maine, New Brunswick, Nova Scotia, and Vermont in September 1995. I also made a few collections in Vancouver, British Columbia, in August 1994. Twelve out of 15 taxa of *Xanthoria* treated have been studied in the field in North America.

*Morphology and anatomy*

Morphological studies were carried out on dry material using a dissecting binocular microscope with up to 40 × magnification. Measurements were performed on mature thalli, and if the collection consisted of more than one specimen only one was chosen for study. Lobe width was measured in up to three different ways, at the outermost tips, at the widest point, and just inside the widest point. Measurements from the latter place were generally used in the descriptions, except for *X. borealis* and *X. mendozai*, where the measurements from the widest point were used.

Most anatomical studies were made on hand-cut sections or squash preparations mounted in water or in lactophenol-cotton blue. Detailed anatomical studies were made on sections, usually 15–20 μm thick, cut with a freezing microtome and mounted in lactophenol-cotton blue. Characters were studied under a light microscope with and/or without interference contrast. When studying soredia or other structures with heavy pigmentation, a 10% aqueous solution of KOH (K) followed by additional water was sometimes used to dissolve and wash off the anthraquinone crystals.

The limits of the subhymenial layers are often difficult to distinguish. For practical reasons the subhymenium was included in the measurements of the hypothecium.
The amyloid reaction of asci was studied on gently squashed preparations of small fragments of apothecia in modified Lugol's solution (water replaced by 50% lactic acid) after treatment with 10% KOH-solution and water. Generally, 0.3% Lugol's solution was used, but various concentrations were tested to examine if lower concentrations staining less heavy would reveal variable structures.

Only released spores and conidia were measured, mounted in water. Care was taken to measure only mature and dead spores. The spores were considered mature if a distinct and narrow isthmus could be recognized. In a few cases, when the specimen studied had been recently collected, I was forced to kill viable spores by heating the preparation according to Steiner & Peveling (1984). Curved, inflated, or otherwise abnormal spores were not included in the study. The septum was measured near the narrowest point, i.e., approximately corresponding to the length of the isthmus.

The number of specimens (N) from which measurements have been obtained is about 20 in common species. In species where the number of collections is low I have used the available number of specimens. When possible, I tried to use specimens from various parts of the distribution area in North America. The number of observations per specimen (n) depends on the character studied. Characters like size of thallus, apothecium, or hymenium thickness were recorded once per specimen, while 10 measurements per specimen were recorded for soredia, spores, and conidia.

The values recorded are generally presented as (minimum value recorded-)lowest specimen arithmetic mean observed-arithmetic mean of all observations-highest specimen arithmetic mean observed (-maximum value recorded) (s, N, n), where s is the standard deviation of all observations, N is the number of specimens studied and n is the number of observations per specimen. Thus, the total number of observations is N × n. If not otherwise stated, n = 10. In some cases, the maximum and minimum value observed has been left out. For characters which were found not to meet the normal probability assumption or where detailed measurements were difficult to obtain and/or of little use, the values recorded are given as “minimum value observed-maximum value observed”. A discussion on different methods of presenting measurements is found in Ekman (1996).

**Chemistry**

For the identification of secondary substances, high performance thin layer chromatography (HPTLC) was used (Arup et al. 1993).

The following three solvent systems were used. Solvent A: Toluene : dioxane : acetic acid, 45 : 15 : 2. Solvent B: Cyclo-hexane : methyl tert.-butyl ether : formic acid, 6.5 : 5 : 1. Cyclo-hexane was used instead of hexane since the latter is known to cause damage to the nervous system. Solvent C: Toluene : acetic acid, 20 : 3. The solvents were always used fresh. Atranolignin and norstictic acid from a mixture of *Platismatia glauca* (L.) W. L. Culb. & C. F. Culb. and *Pleurosticta acetabulum* (Neck.) Elix & Lumbsch were used as references for determining Rf classes (Culberson & Kristinsson 1970). Authentic substances for the anthraquinones: emodin, fallacinal, parietin, parietinic acid, and teloschistin were supplied by Dr. J. Elix, Canberra (same as in Arup 1995a). All
reference substances were applied at least once on each of the opposing sides of the plates.

At least two specimens of each of the studied taxa were analysed. Two to three apothecia and small pieces of young exposed parts of the thalli were cleaned and extracted with acetone for about 15 min. 3–5 µl were applied one µl at a time on Merck HPTLC silica gel 60 F254 glass plates (Art. No. 5629) with a 0.20 mm thick silica gel layer. The spots were kept as small as possible and a Nanomat III (Camag Art. No. 022.4710) was used to ensure that every sample application was made at the right position.

The HPTLC plates were dried in c. 50°C and allowed to cool before they were developed in 10 × 10 cm Horizontal developing chambers (Camag Art. No. 022.8500). Saturation configuration of the chamber was used. The chromatograms were viewed in UV light (254 and 366 nm), lightly sprayed with 10% sulphuric acid (H2SO4), heated to 110°C for 5–10 min, and again viewed in UV light (366 nm). Drying and heating of the plates was carried out with a TLC plate heater (Camag Art. No. 022.3306).

Twelve specimens of X. tenax were analysed by U. Söchting with the HPLC method as described in Söchting (1997).

**Distribution**

The distribution maps and phytogeographic descriptions presented here are based exclusively on material seen by me, except for one report of X. parietina in Oregon which was provided by Bruce McCune (in litt.). One symbol on the maps may represent one or more collections and/or localities. The diameter of a dot on the map is approximately 70 kilometres.

**Statistical and numerical methods**

The distinctness of Xanthoria borealis vs. X. mendozae, X. fallax vs. X. ulophyllodes, two geographical subpopulations of X. fulva, three geographical subpopulations of X. parietina, and three geographical subpopulations of X. polycarpa were investigated using statistical and numerical methods. The methods used were Student’s t-test, canonical variate analysis (CVA), and principal components analysis (PCA). The t-test is equivalent to one-way ANOVA when only two variables are compared. Prior to all analyses, the distribution of each character was examined to ensure that it met the normality assumption. All calculations were performed using the programme Statistica (StatSoft 1994) on a Macintosh computer.

Student’s t-test is a commonly used method to evaluate differences in the mean for a quantitative character between two groups. PCA is a method used to summarize multivariate data by assigning the majority of variance to a smaller number of uncorrelated composite orthogonal axes, termed principal components (Dunn & Everitt 1982). These are arranged in order of decreasing amount of variance explained. CVA is similar to PCA but the first axis is required to be in the direction of greatest variability between the means of predefined taxa, or groups (Dunn & Everitt 1982). The axes found in a CVA are termed canonical variates. Wilks’ Lambda gives the proportion
of total variance due to variation within groups. The Wilks' Lambda value obtained is used to denote the discriminatory power of the model, with a range from 1.0 (no discriminatory power) to 0.0 (perfect discriminatory power). Missing values in the data matrices were handled in either of two ways available in the Statistica programme: casewise deletion or mean substitution (StatSoft 1994). If casewise deletion is selected, cases with one or more missing values are deleted from the analysis. When mean substitution is selected, all cases are retained, and any missing value is replaced by the calculated mean for the respective variable, or in this case, character. The main disadvantage of the latter method is that it artificially decreases the variation of scores, and this decrease is proportional to the number of missing data. Additionally, it may decrease the values of very strong correlations, because the artificially created data points are, by definition, uncorrelated. As no explicit "rules" for when each method should be applied are given, I have used the principle of only using the mean substitution option when the number of missing values is very low. Three of the quantitative characters measured (width of the paraphyses, width of the paraphyses tips and width of the thalline margin) were excluded in all cases because the data did not meet the normality assumption and the overall variability was low. In the various analyses of each of the four cases, one or more characters were occasionally left out, because the variation was too low, the normality assumption was not or just barely met, or simply because I decided that it was inappropriate to include it. The latter reason is proper when such methods are used in taxonomic studies, since the aim is not to describe the entire variation in all characters.

**Nomenclature and citations**

The abbreviations of authors follow Brummitt & Powell (1992).

The specimen citations usually include only selected specimens, but at least one locality for each state/province are always given. For rare species, all specimens used in this study are cited. The citations are kept in a very abridged form. I have used the following information available from the labels: county (comté), parish, or equivalent division, followed by year of collection, collector, collection number, and herbarium. If county/parish has not been specified, I have used any other information available from the labels, except for the Fink collections in MIN, for which county information has been added by C. M. Wetmore (Wetmore 1978). In the collection lists, I have on one occasion included a specimen that occur mixed in a collection of another species. This is preceded by a "++", and the name of the species under which the collection is being filed is indicated by "filed with". A complete list of all examined specimens is available from the author on request.

**Morphology and Anatomy**

*Thallus*

Growth form—The thalli of all species of *Xanthoria* are foliose or (in *X. candelaria*) foliose to subfruticose. The thalli occur separately or tend to coalesce into small to widespread stands composed of more than one individual. In some species (for example,
X. elegans, X. fallax, X. parietina) the lobes are mostly horizontal and appressed to the substrate giving the thallus a flattened and rosette-like appearance. Specimens of X. elegans sometimes exhibit an almost fruticose habit with more or less terete and inflated lobes, especially when growing among bryophytes or in other humid sites. In other species (X. borealis, X. candelaria, and X. mendozae) the lobes are semi-erect to erect and mainly attached near the lobe base, giving the thallus a cushion-like or shrubby appearance. Lobes of (very) young thalli are invariably horizontal and appressed in all species. Lobes are basically dorsiventral. Even X. candelaria, which has partly (sub)terete lobes, is dorsiventral in the lower portions of the thallus. The branching of the lobes is usually frequent and regular. In several of the sorediate species, young lobes are richly branched, but the lobe apices gradually become eroded as soredia are produced on the lower side.

Surface—The colour of the thallus varies from light yellow to orange to reddish orange or occasionally greenish to grey, as a result of anthraquinone crystals in the cortex. In the species treated here, the variation in colour depends on differences in the concentrations rather than the composition of the various substances. The colour is variable within each species, but general differences between species do in fact exist. For example, X. borealis is mainly dark orange to reddish, while X. candelaria basically is yellow to light orange. Parts of the thalli exposed to the sun are usually more intensely pigmented than shaded parts.

A whitish farinose pruina is formed by some species, viz., X. concinna, X. tenax, X. mendozae, and X. borealis and sporadically also in X. elegans. In X. borealis and X. mendozae the pruina is most prominent on the outer (younger) parts of the thallus. The amount of pruina produced varies within all species, and is probably connected to environmental factors (Poelt 1973, Wadsten & Moberg 1985). The surface of non-pruinose specimens varies from smooth to coarse or wrinkled.

Pseudocyphellae and similar structures are known from a few species of Xanthoria (Karnefelt 1989, Karnefelt et al. 1995). In the North American species, however, they are lacking. Sometimes, X. elegans has a tendency to form thin patches on the upper cortex, that may resemble pseudocyphellae.

The lower surface is mainly white to yellowish (yellow when exposed) and smooth to somewhat wrinkled.

Cortex—The upper cortex is paraplechtenchymatous, c. 10–20 µm thick, and composed of c. 3–5 layers of somewhat elongated or isodiametric cells, anticlinally oriented (Fig. 1A–B). The cells closest to the surface or algal groups are more rounded and frequently have thinner walls. The anatomy and thickness is uniform among the species of Xanthoria investigated.

The lower cortex is similar to the upper cortex in most species, except for X. tenax and X. mendozae. In X. tenax, a lower cortex is developed only under the outermost part of the lobes. In X. mendozae, the lower cortex is anatomically similar to the prosoplechtenchymatous cortex of the species of Teloschistes, with more or less periclinal hyphae.

Photobiont—The photobionts are green, unicellular, and spherical with a diameter
<table>
<thead>
<tr>
<th>Species</th>
<th>Thallus diameter (mm)</th>
<th>Lobe width (mm)</th>
<th>Attachment organ</th>
<th>Soredium diameter (µm)</th>
<th>Apothecium diameter (µm)</th>
<th>Spore length (µm)</th>
<th>Spore width (µm)</th>
<th>Spore septum (µm)</th>
<th>Pycnidium diameter (µm)</th>
<th>Conidium shape</th>
<th>Conidium length (µm)</th>
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<td>rhizines</td>
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<td>5.4-8.0</td>
<td>2.9-5.7</td>
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<td>bacilliform</td>
<td>3.8-4.7</td>
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<td>0.9-4.0</td>
<td>ellipsoid</td>
<td>41-96</td>
<td>0.1-0.2</td>
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<td>5-6</td>
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<td>2.9-3.6</td>
</tr>
</tbody>
</table>
up to c. 25 µm. The taxonomy of the photobiont has not been studied by me, but according to Ahmadjian (1993) it belongs to the genus *Trebuoxia*. The photobiont layer is about 40–80 µm thick, more or less continuous in most species and composed of coalesced algal colonies, which are sometimes separated by strands or bundles of hyphae. In, for example, *X. candelaria* the algal colonies are distinctly spread in the medulla.

**Medulla**—The structure of the medulla is rather variable. Some species have a medulla with uniformly thick, elongated and sparsely branched cells (*X. parietina, X. elegans, X. sorediata*) (Fig. 1A). The hyphae are arranged in bundles, which run below the algal layer, often close to the lower cortex, and individual hyphae or bundles may reach the cortex. In other species (*X. fallax, X. fulva, X. hasseana, X. polycarpa, X. montana, X. ulophyllodes*) the cells are mainly shorter, rounded or somewhat irregular, and frequently branched (Fig. 1B). The hyphae are loosely interwoven and more randomly orientated. *Xanthoria candelaria* probably also belongs in the latter group, but closer studies are needed to fully understand the medullary structures of *Xanthoria*.

**Attachment**—The thallus is attached near or by the lobe bases or with specialized structures. Developed attachment organs can generally be referred to as hapters or (true) rhizines. Previously, both hapters and rhizines have commonly been termed rhizines. Anatomically they are similar, composed of hyphae originating in the lower cortex. The cells are elongated and narrow, with a thick wall.

Hapters are short, more or less thick, and have a “foot”, viz., a terminal width extension, that improves the ability to attach firmly. Such structures occur in, for example, *X. elegans, X. parietina, and X. polycarpa* (Fig. 1E).

Rhizines are short to long, more or less slender, pointed or frayed, with only a faint or small terminal width extension. Such structures occur in, for example, *X. fallax and X. hasseana* (Fig. 1F). According to Poelt & Petutschneg (1992a) and Poelt & Kondratyuk (1997), hapters only develop after initial contact with the substrate, i.e., always are attached, while rhizines develop whether or not such initial contact has been established. Previous authors (Hannemann 1973) have not included ontogenetic criteria in the definitions. Furthermore, Hannemann (1973) classified the attachment organs in *X. parietina* as rhizines (and those in *X. elegans* as hapters (“Hafter”)), while later authors have classified them as hapers.

Hapters and rhizines are originally white, but turn yellow when exposed to light. Because rhizines are longer and consequently more exposed, they are more frequently yellow than hapters.

**Vegetative dispersal**—Specialized structures for vegetative dispersal are formed in about half of the species treated, namely *X. borealis, X. candelaria, X. fallax, X. fulva, X. mendozae, X. oregana, X. sorediata, and X. ulophyllodes*. All these North American species produce soredia, never isidia, although isidia do occur in species of *Xanthoria* outside North America. The soralia vary with respect to position, structure/morphology, and the developmental type of the soredia. Soredia may be produced laminally, as in *X. sorediata*; marginally, as in, for example, *X. fallax*; or on the lower side of the thallus, as in *X. mendozae*. In several species the soralia are actually situated
marginally to submarginally as well as on the lower side, for example, *X. fulva* and *X. oregana*. The structure of the soralia is closely connected to the morphology of the soredia. Two principal types of soredia can be recognized:

a) Blastidia: basically formed from the cortex as well as the medulla and are generally more or less irregular and concolorous with the thallus. According to Poelt & Petutschnig (1992a), a blastidium can produce new blastidia by budding. Typical blastidia can be seen in *X. ulophyllodes*.

b) Soredia in a narrow sense: produced only from the medulla (in cracks or holes in the cortex) and are usually less strongly pigmented (i.e., paler) than the thallus. *Xanthoria fallax*, with soredia produced from crescent shaped slits (“bird nests”) in the cortex on the lobe margins, and *X. fulva*, with soredia produced from openings on the lower surface are examples of this.

As a rule, blastidia can be recognized by being concolorous with the upper surface of the thallus, while soredia are lighter coloured, usually with a tinge of green. In addition, blastidia have a smoother surface and often appear irregular, probably because they are producing new blastidia by budding. Soredia are usually spherical and more powdery, with a soft surface. Sometimes it is difficult to conclude which soredial type that a particular specimen produces, and it is necessary to study several specimens of a species.

Previously, the anatomy of individual soredia was not studied to a great extent in *Xanthoria*. Poelt & Petutschnig (1992a) showed that anatomical differences between soralia and blastidia exist. My experience is that these differences are very difficult to observe. Both blastidia and soredia are composed of one to several algal cells, which are separated and surrounded by fungal cells. Each soredium begins with one algal cell surrounded by fungal cells. Soon, the algal cell starts to divide, forming a tetrad. The cells of the tetrad then separate, and each cell divides again. The fungal cells seem to vary slightly with respect to shape, and usually there are 2–4 layers of hyphae covering the soredium.

**Apothecium**

Most of the species in North America are, at least occasionally, found with apothecia. Apothecia are often abundantly produced in favourable habitats. *Xanthoria borealis* and *X. mendozae*, however, have never been found with apothecia.

Morphology—The apothecia are laminal, sessile to stipitate, rounded, and concave to plane, or somewhat convex. The shape is affected by the presence of neighbouring apothecia. The size is very variable, and sometimes extremely oversized apothecia occur, probably because of environmental factors. The colour of the disk varies from yellow to orange, but is mostly somewhat darker than the thallus. A white pruina occurs in variable amounts on the disk of two species, namely *X. concinna*, and *X. tenax*. The (proper) exciple is visible to varying extent from the outside as a proper margin between the disk and the thalline margin, and is concolorous with the disk.

A thalline margin is always present and has the same colour as the thallus. It is smooth to uneven, and sometimes crenulate. The thalline margins in some species (for
example, *X. fallax* and *X. hasseana*) bear structures similar to rhizines. They can be free or attached to the cortex of the thallus or neighbouring apothecia. Such structures were reported very early from North American material of *Xanthoria*, by Tuckerman (1882). Similar structures are found in the family Physciaceae, and are characteristic in the genus *Phaeophyscia* (Moberg 1977). The rhizines on the thalline margin are probably not homologous with the fibrils that occur in certain species of *Teloschistes*, as the latter structures almost never seem to be attached by the tips. Species lacking rhizines (for example, *X. parietina* and *X. polycarpa*) can have thalline margins attached by very short hapter-like structures or by direct cortex-cortex contact. In *X. candelaria*, the thalline margins sometimes produce lobules, which may become sorediate. Soralia occur regularly on the thalline margins of the sorediate species.

Thalline margin—the cells of the cortex of the thalline margin are similar to the cortex cells of the rest of the thallus. The algae occur close to the cortex in more or less distinct groups. Where the algal groups occur adjacent to the cortex, the cortex cells become more rounded and the cell walls thinner. The algal layer in the thalline margin is continuous with the algal layer enclosing the excipulum.

Proper exciple—the proper exciple of *Xanthoria* has been defined previously as annular (Henssen & Jahns 1973). The hyphae of the proper exciple in the mature apothecium, however, actually form a cupular structure which encloses the hypothecium and the hymenium (Fig. 1C). This structure has also been observed in species of *Caloplaca* (Arup 1995a, Jahns et al. 1995). Below the hypothecium, this structure varies in thickness from undiscernible to thin (for example, *X. polycarpa*) or thick (for example, *X. elegans, X. parietina*), up to c. 60 µm. The hyphae radiates from below the hypothecium outwards and upwards to the rim of the proper margin, but single hyphae or bundles may also extend through the algal layer reaching the cortex of the thalline margin. The cells are smooth, mostly heavily gelatinized, and the lumina are more or less elongate (rounded in cross section). Close to the rim of the exciple, the lumina are generally shorter, slightly elongate and similar to the cells of the upper cortex of the thallus.

Hypothecium—the hypothecium is formed between the exciple and the hymenium. It is colourless to pale brown, and consists of irregularly oriented hyphae with thin walls. The cells stain dark blue in cotton blue (Fig. 1C). Occasionally, in *X. fulva*, oil droplets occur in the hypothecium and may be abundant.

Hymenium—the hymenium varies in thickness, generally c. 50–110 µm, and is colourless, except for the upper part, where yellow anthraquinone crystals occur in a ± distinct layer.

Paraphyses—the paraphyses are straight, simple or branched, but mostly with 1–3(–4) branches. Within North America the number of branches varies very little, but paraphyses may have up to six branches in the South African species *X. capensis* (Kärnefelt et al. 1995). The paraphyses are 1–3 µm wide in the mid-hymenium. The tips are more or less capitate and up to 8 µm wide. In *X. fulva*, the uppermost cells regularly contain oil droplets, c. 3–4 µm wide. I have occasionally observed them also in other species, mainly *X. elegans, X. polycarpa*, and *X. sorediata*. Oil droplets in the

Paraphyses have previously been reported from X. novozelandica (Kondratyuk & Poelt 1997) and are not uncommon in Caloplaca (Arup 1995a). The oil droplets gradually vanish when the lichen material is kept dry in the herbarium. The exact nature of the substance in the oil droplets is not known.

Asci and spores—The asci are cylindrical to broadly cylindrical, c. 40–65 × 10–20 µm, and normally each ascus contains eight spores. The apical structure seems to be homogenous within Xanthoria with respect to the amyloid reaction. The ascus structure corresponds to the Teloschistes type (sensu Honegger 1978), which was based on investigations of X. parietina. The Teloschistes type ascus has an apical dome composed of a non-amyloid inner and a strongly amyloid outer part. According to Honegger (1978) and Letrouit-Galinou (1973), there is no special mechanism for spore discharge, but the apex simply splits prior to spore release.

The spores are polaribilocular, hyaline, and c. 10–20 × 4–10 µm. The spore shape varies from cylindrical to narrowly ellipsoid or ellipsoid (Fig. 2). The septum varies from narrow to wide, 1–10 µm. The shape and size of the spores together with the width of the septum constitute valuable taxonomic characters.

Pycnidium

Pycnidia are found in all species occurring in North America, including those which are never or rarely found with apothecia. They are laminal, generally occur on young parts of the thallus, and are sometimes observed on the thalline margin of apothecia. In X. sorediata, pycnidia are usually found among the soredia. When normally abundantly apotheciate species lack apothecia, pycnidia are often developed frequently over the entire thallus.

The pycnidia are laminal and are more or less immersed in the thallus. The ostiole area is pigmented as the upper cortex (for example, in X. candelaria) or darker, concolorous with the apothecial disks (for example, in X. hasseana and X. parietina). Pycnidia can be detected as small orange dots on the upper surface even in early stages
of development. Mature pycnidia are larger, often forming small "warts" and generally are easily found.

Pycnidia in North American species are multilocular and correspond to type VIII (Xanthoria-type) in Vobis (1980) (Fig. 1D). The outer wall consists of layers of somewhat angular cells and is not pigmented. The conidiogenous cells are somewhat angular, c. 4–8 µm long and form the inside walls. The intercalary conidiogenous cells produce conidia laterally near the upper end, whereas the terminally situated cells produce conidia terminally (type VII/VIII in Vobis 1980). Oil droplets have been observed in the conidiophore cells of a few specimens of X. fulva.

The conidia are ellipsoid, bacilliform, or varieties of these two shapes (Fig. 3). The length of the conidia ranges from 1.5 to 5.5 µm, with the smallest being ellipsoid (X. candelaria and X. polycarpa) and the largest being bacilliform (X. borealis and X. mendozae). Usually, only one shape of conidia, with small variation, occurs in the pycnidia of a species. In X. oregana, however, conidia of several shapes occur in one pycnidium (Fig. 3). Mixed conidial types have previously not been reported in Xanthoria, or the Teloschistaceae. Conidial shape is probably a valuable character to separate groups within Xanthoria, but the case in which mixed shapes can occur within a single pycnidium should be kept in mind.

So-called macroconidia have been reported to occur in X. fulva (Poelt & Petutschnig 1992a). Macroconidia seem to be known only from the type specimen, and I have never observed such structures in the North American collections. The structures on the type specimen of X. fulva should be studied further, because it is important to establish whether or not a parasite is involved.

Notes on morphological variability

Species of Xanthoria generally exhibit great morphological variability. It has not been shown if the variation depends on phenotypic plasticity or on genetic variability. Probably, the causes are a combination of both. There is a tendency for different species to behave in similar ways in certain habitats. For example, in dry habitats on smooth substrates, lobes tend to be closely pressed to the substrate, and rhizines become more scarce and short. In moist and rough habitats, such as bryophyte cushions or on seashores, lobes often become numerous, more or less inflated and loosely attached to the substrate. Other characters such as the number of lobes, the width of the lobes and length of the rhizines also are influenced by environmental factors. A frequently described phenomenon is that thalli of almost all species of Xanthoria become less pigmented when growing in less sun-exposed sites (Hillmann 1922, Hill & Woolhouse 1966, Richardson 1967). Grazing by various kinds of herbivores is a further reason why thalli may appear morphologically aberrant. This has been shown and discussed by Poelt & Petutschnig (1992a). Direct damage is usually possible to detect and interpret, but after the thallus, or parts of it, has regenerated, the morphology is much more difficult to interpret.

Geographically correlated, infraspecific, genetic differentiation probably does exist, as shown for example for populations of X. parietina in Spain (Reyes et al.
1996). Tendencies to infraspecific differentiation are also shown for X. parietina and X. polycarpa in the chapter Statistical and numerical treatment in this work. At present, this variation is difficult to estimate and is poorly understood. It has been suggested, for example by Wedin (1995), that morphological plasticity could explain existing taxonomic confusions within variable groups, and that new taxa should be studied with great care before being described. Careful studies of the lichens in the field are helpful to understand the morphological variation and its causes. It is often very difficult to summarize the morphological variation in a simple, comprehensive way, and the descriptions of the taxa of Xanthoria in this work should be read with this in mind.

CHEMISTRY

The secondary chemistry of the genus Xanthoria is characterized by the production of anthraquinones. This character is shared with the majority of species in the family Teloschistaceae. The secondary chemistry in Xanthoria has only been thoroughly studied in limited investigations (e.g., Steiner & Hauschild 1970, Hauschild et al. 1971, Fahselt & Krol 1989, Arnold & Poelt 1995), but recently a project has been initiated to investigate the secondary chemistry within the Teloschistaceae (Sochting 1997).

Substances and chemosyndromes

Altogether five secondary substances, all anthraquinones, were found (Tab. 3, Fig. 4): emodin, fallacinal, parietin, parietinic acid, and teloschistin.

In all specimens parietin occurred as a major substance, while emodin, fallacinal, teloschistin, and parietinic acid occurred in lower concentrations. The studied taxa can be divided into two chemical groups that are separated by different concentrations of mainly teloschistin, but also fallacinal (Tab. 4). Taxa with high concentrations of teloschistin and fallacinal belong to group A3 (sensu Sochting 1997) while taxa with “normal” concentrations belong to group A (sensu Sochting 1997). The high concentrations of teloschistin and fallacinal characteristic for the A3 syndrome was reported for X. calcicola (as X. aureola) by Steiner & Hauschild (1970). Group 1 in Arup (1993) probably refers to both A and A3. The “Elegans” and “Sorediata” groups found by Arnold & Poelt (1995) were not distinguished in my investigation.

One species, X. mendozae, was impossible to refer to either of the chemosyndromes
Table 3. HPTLC data for lichen secondary substances found in the North American material of *Xanthoria*. The division of the chromatogram into Rf classes follows Arup et al. (1993) and Culberson & Kristinsson (1970).

<table>
<thead>
<tr>
<th>Substance</th>
<th>Rf class A</th>
<th>Rf class B</th>
<th>Rf class C</th>
<th>Rf value (mm) A</th>
<th>Rf value (mm) B</th>
<th>Rf value (mm) C</th>
<th>Colour after heating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parietinic acid</td>
<td>3-4</td>
<td>5</td>
<td>6</td>
<td>23.5-24</td>
<td>21.5-23</td>
<td>19.5-20.5</td>
<td>yellow</td>
</tr>
<tr>
<td>Norstictic acid</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>25-26</td>
<td>19-20</td>
<td>11-12</td>
<td>golden yellow</td>
</tr>
<tr>
<td>Teloschistin</td>
<td>4-5</td>
<td>3</td>
<td>4-5</td>
<td>25-26</td>
<td>16-17</td>
<td>13-14</td>
<td>yellow</td>
</tr>
<tr>
<td>Emodin</td>
<td>5</td>
<td>6</td>
<td>5</td>
<td>28-29</td>
<td>16-17.5</td>
<td>15-16</td>
<td>yellow – bright orange</td>
</tr>
<tr>
<td>Fallacinal</td>
<td>6-7</td>
<td>5</td>
<td>6-7</td>
<td>34-35</td>
<td>22-24</td>
<td>24.5-25.5</td>
<td>dull yellow–beige</td>
</tr>
<tr>
<td>Parietin</td>
<td>7</td>
<td>6-7</td>
<td>7-8</td>
<td>35-36</td>
<td>27-28</td>
<td>29</td>
<td>yellow</td>
</tr>
<tr>
<td>Atranorin</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>36-37</td>
<td>28-29</td>
<td>27-28</td>
<td>buff to yellow</td>
</tr>
</tbody>
</table>

Fig. 4. HPTLC chromatograms in the solvent systems A and C. Rf – reference substances; A – chemosyndrome A; A3 – chemosyndrome A3. at – atranorin; em – emodin; fa – fallacinal; no – norstictic acid; pa – parietin; pc – parietinic acid; tel – teloschistin. Shaded spots indicate that the particular substance occur in higher concentrations. Distances between the samples are not drawn in correct scale.

A or A3, and seems to be intermediate. In *X. tenax* both chemosyndromes occur, but in different thalli.

Discussion

Anthraquinones are derivatives of the acetate-polymalonate pathway. The anthraquinones found in the North American material differ only slightly in chemical structure from each other (cfr. Huneck & Yoshimura 1996). Hypotheses for the pathways have been discussed by Arup (1993), Steiner & Hauschild (1970), and
Table 4. The chemosyndromes (sensu Söchting 1997) occurring in North American species of *Xanthoria*.

<table>
<thead>
<tr>
<th></th>
<th>A</th>
<th>A3</th>
<th>Intermediate</th>
<th>A + A3</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Xanthoria</em> borealis</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>candelaria</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>concinnia</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>elegans</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>fallax</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>fulva</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>hasseana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>mendozae</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>montana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>oregana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>parietina</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>polycarpa</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>sorediata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>tenax</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>ulophyllodes</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


Little is known about the biological function of anthraquinones in the lichens. It has been suggested that lichen products may have a protective function against herbivore attacks in nature (e.g., Culberson 1970, Lawrey 1983, 1986). Regarding anthraquinones, however, this seems highly unlikely: I have frequently noticed *Xanthoria* thalli damaged by herbivores in both herbarium collections and in nature. Furthermore, it has been experimentally shown that *X. parietina* can provide all essential elements and nutrients necessary for snail growth and reproduction (Baur & Baur 1997).

It has also been suggested that lichen products may serve as filters that shades photophobic lichen photobionts (like *Trebouxia*) from the sunlight (e.g., Henssen & Jahns 1973, Ertl 1951). Rikkinen (1995) supported this view and stated that although it has been shown that the anthraquinones (parietin) mainly occur as crystals on the surface and between hyphae in outer layers of the cortex, there is every reason to believe that they have a significant effect on the spectral composition of the light that penetrates through the lichen cortex. In addition to this, anthraquinones may have a secondary value in protecting the lichen thallus from excessive UV irradiation (Elix 1996).

Taxonomic value—Hitherto, anthraquinones have not been considered taxonomically valuable at the species level within *Xanthoria*. My investigation of the North American taxa supports this view. One interesting pattern is visible, however,
concerning which species has the same chemosyndrome. The species in group A, in addition to chemistry, share several morphological characters, such as presence of hapters and ellipsoid conidia. All species that belong to group A3 share the corresponding characters, presence of true rhizines (absent in *X. concinna*, however) and bacilliform conidia. In North America, these groups seem well delimited. Two European species, *Xanthoria calicina* and *X. resendei*, also belong to chemosyndrome A3 (Steiner & Hauschild 1970, Sochting 1997), but they have hapters and ellipsoid conidia like the North American species belonging to chemosyndrome A. Thus, although the pattern in North America probably is relevant for the relationships within *Xanthoria*, general conclusions concerning the whole genus should be made with great care.

*Xanthoria mendozae* was impossible to interpret regarding chemosyndromes. Its taxonomic position remains unclear for several other reasons, mainly because of the structure of its lower cortex. More sensitive methods may show whether it should be assigned to any of the chemosyndromes A or A3.

No far-reaching taxonomical conclusions should be drawn based on this chemical investigation, which was limited geographically as well as regarding the number of specimens examined. Still, it is possible that the chemical syndromes could be used as supportive characters for groups on some taxonomic level in the future.

**ECOLOGY AND DISTRIBUTION**

**Ecology**

Substrate—A majority of the taxa of *Xanthoria* are only slightly selective in their substrate choice. In addition to the naturally occurring substrates most taxa are often found on various anthropogenous substrates, e.g., fences, walls, roofs, and tombstones. One single collection of *X. polycarpa* was made on an abandoned car!

Eleven taxa are both corticolous and saxicolous, while four species are never or very rarely corticolous (Tab. 5). Of the species that are corticolous and saxicolous, *X. fallax*, *X. fulva*, *X. hasseana*, *X. oregana*, *X. montana*, and *X. ulophyllodes* are mainly corticolous, while *X. candelaria*, *X. parietina* and *X. polycarpa* are found about equally as corticolous and saxicolous specimens. When corticolous, *X. parietina* is mainly collected on trunks of the phorophytes, while *X. candelaria* and *X. polycarpa* are collected mostly on twigs. *Xanthoria tenax* is corticolous and lignicolous, while *X. concinna* is only found on twigs.

*Xanthoria mendozae* is the only exclusively saxicolous species. *Xanthoria borealis*, *X. elegans*, and *X. sorediata* are mainly saxicolous, but often grow on soil or among bryophytes. Occasionally, *X. elegans* and *X. sorediata* are collected on other substrates, for example bark, lignum, and bones.

The corticolous ones occur on a large variety of phorophytes (Tab. 5). From the collections of corticolous specimens for which the phorophyte is indicated on the label (c. 70%), we know that in North America *Xanthoria* has been collected on at least 85 different phorophyte genera. In more than half of these 85 cases, only one species of the phorophyte genus is involved. *Xanthoria polycarpa* and *X. fulva* are the two species...
Table 5. The percentage of occurrences on different kinds of substrates (if higher than 1.0%) for the North American species of *Xanthoria*. Occurrences on substrate classified as "various" are not shown. For the corticolous specimens the percentages on bark and twigs are presented as well as the minimum number of phorophyte genera. \( n = \) the number of collections with known substrate type.

<table>
<thead>
<tr>
<th>Xanthoria</th>
<th>Saxicolous</th>
<th>Terricolous</th>
<th>Lignicolous</th>
<th>Corticolous</th>
<th>Bark</th>
<th>Twigs</th>
<th>Min. no. of phorophytes</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>borealis</td>
<td>61</td>
<td>26</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td>23</td>
</tr>
<tr>
<td>candelaria</td>
<td>37</td>
<td>2</td>
<td>18</td>
<td>42</td>
<td>50</td>
<td>50</td>
<td>20</td>
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</tr>
<tr>
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<td>0</td>
<td>100</td>
<td>0</td>
<td>100</td>
<td>1</td>
<td>2</td>
<td>306</td>
</tr>
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<td>96</td>
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<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
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<td>2</td>
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<td>93</td>
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<td>2</td>
<td>38</td>
<td>551</td>
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<td>93</td>
<td>98</td>
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<td>41</td>
<td>681</td>
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<td>hasseana</td>
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<td>99</td>
<td>89</td>
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<td>90</td>
<td>90</td>
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<td>83</td>
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<td>tenax</td>
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<td>86</td>
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<tr>
<td>ulophyllodes</td>
<td>9</td>
<td>1</td>
<td>86</td>
<td>86</td>
<td>86</td>
<td>86</td>
<td>86</td>
<td>58</td>
</tr>
</tbody>
</table>

with collections from most phorophyte genera (Tab. 5). Although the diversity of phorophytes is high, the majority of collections for each *Xanthoria* species are made on about three phorophyte genera. The phorophyte genera richest in *Xanthoria* species are *Acer, Juniperus, Populus, Quercus, Ulmus,* and *Salix*. Several other phorophytes constitute important substrates for one or more *Xanthoria* species when the number of records per phorophyte is considered.

The saxicolous species occur on various types of rock. Most species do not exclusively grow on either calciferous or non-calciferous rock, although some species tend to favour one of them. For example, most collections of *X. sorediata* are made on calciferous rock, while *X. elegans* occurs on more acidic rock as well as on calciferous rock. Rock is an important substrate, e.g., along the Atlantic coast where *X. elegans, X. parietina,* and *X. polycarpa* can be found in mixed populations. The seashore rocks along the Pacific coast are poorer in *Xanthoria* species; the only species regularly found on this substrate is *X. candelaria*.

Habitat—The habitats of *Xanthoria* in North America cover a range from sea level to an altitude of c. 3000 metres (*X. mendozae*). Most species grow in open or semi-open situations, more or less exposed to sunlight, moist to rather dry (low air humidity at least seasonally), and nutrient rich. One species, *X. mendozae*, is almost
entirely confined to shaded vertical rock faces. Several species are able to grow in extreme (exposed) environments, for example seashore or tundra habitats. *Xanthoria* species are often found growing together with one or two other *Xanthoria* species, or species of the genera *Caloplaca*, *Candelaria*, *Candelariella*, and *Physcia*, among others.

Several species are enhanced by human activities shaping the landscape and providing substrates, for example, establishment of buildings, walls, and churchyards, or planting of trees in dust-enriched environments (avenues, churchyards, park grounds etc.).

The species of *Xanthoria* are strong competitors, and once established on a substrate the lichen grows and reproduces vigorously and may soon cover large areas (see, for example, Sharnoff & Sharnoff 1997, p. 58).

**Distribution**

Most species of *Xanthoria* have a wide distribution in North America. As most species are able to grow on a variety of substrates, no species seems to have a distribution limited by the availability of suitable substrates. Instead, their distributions are limited by other ecological, climatic and historic factors. The majority of the species are widespread in the arctic-alpine, boreal and temperate regions in North America and, consequently, they may belong to more than one floristic Element. The classification of the distribution patterns has been adapted from Brodo (1968, 1984), Brodo & Hawksworth (1977), Ekman (1996), and Hale (1961). The terminology regarding classification of the geo-biosphere into zonobiomes follows Walter & Breckle (1984).

1. Arctic-alpine element: *X. borealis*.
   The main distribution of *X. borealis* lies within the arctic tundra zonobiome (IX), with extensions into the cold-temperate, boreal zonobiome (VIII).

2. Arctic-Alpine and Boreal elements: *X. elegans*, *X. sorediata*.
   These species have a tendency to be coastal in the east, but not in the west. In the temperate regions in the west, they are widespread at high altitudes.

3. Western (Arctic-alpine to Temperate elements): *X. candelaria*.

4. Boreal to Temperate elements: *X. hasseana*.
   *Xanthoria hasseana* belongs to the north Temperate to southern Boreal, plus western Temperate elements. The main distribution area is south of the arctic zonobiome (IX), but one locality is known from the transition of zonobiomes VIII and IX, in Alaska.

5. Temperate element: *X. fallax*, *X. fulva*, *X. ulophyllodes*.
   These species have their main distribution south of the arctic zonobiome (IX). *Xanthoria fallax* and *X. ulophyllodes* occur mainly in central and western grasslands and dry areas with extensions into the east. *Xanthoria fulva* has an important part of its distribution range belonging to the Eastern temperate subelement, but is also distributed in the west.

6. Temperate element; Oceanic subelement: *X. parietina*, *X. polycarpa* (?)
   *Xanthoria parietina* has a typical oceanic distribution, whereas *X. polycarpa* is
more widespread, has a boreal tendency and is absent from the southeast.

7. Western Temperate element to Western montane: *X. montana*, *X. oregana*.

*Xanthoria oregana* extends from the western montane areas (approximately corresponding to zonobiome VII) to the Pacific coastal area (mediterranean zonobiome IV). *Xanthoria montana* has a wider distribution and is known also from the boreal zonobiome (VIII) in Alaska.

8. Western montane: *X. mendozae*.

The distribution range lies within the arid-temperate zonobiome (VII). Species with a western montane distribution type have commonly been regarded as belonging to the Boreal element.

9. Californian: *X. tenax*.

*Xanthoria tenax* is exclusively known from the Pacific coastal region in California, Baja California, and Sonora. Its distribution lies entirely within the mediterranean zonobiome with winter rain (IV). This lichen could belong to the Madrean element, but bryophyte and lichen species with this distribution type have previously sometimes been referred to a Californian element. Because California is a complex area where several elements occur (Raven & Axelrod 1978), the total distribution area and possible evolutionary origin of *X. tenax* should be investigated before a reliable analysis and classification can be made.

10. Texan: *X. concinna*.

In the United States, *X. concinna* is known from one locality in Texas. Its main distribution, however, is in Nuevo Leon and San Luis Potosi, Mexico. Probably, it belongs to the Madrean element (corresponding to the Mexican element of Hale 1961), but my knowledge of the species is at present too poor to allow a reliable interpretation.

**STATISTICAL AND NUMERICAL TREATMENT**

I have chosen to investigate some interesting or taxonomically complicated cases that I found during my studies of the genus *Xanthoria* using various numerical and statistical methods to summarize the variation and to test the distinctness of some particular taxa. Four such studies were carried out. The first two of these were similar in the way that the two more or less clearly separated taxa were involved, and I wished to study whether there were further discontinuities in quantitative characters. The three latter cases were similar in the way that one variable taxon was studied with the purpose to describe the variation and to test the distinctness of various predefined groups, which may motivate taxonomic recognition. Methods like these have previously been used and discussed in lichen taxonomy by, for example, Arup (1992, 1993), Ekman (1996), and Martinez & Burgaz (1996).

For details on the methods used, see Material and methods.

*Xanthoria borealis* and *X. mendozae*

Background—*Xanthoria borealis* was recently described on Swedish material by Santesson & Poelt (Poelt & Petutschnig 1992a). In the same publication material of this taxon from the United States also was cited. My investigation showed that these...
collections belong to *X. mendozae*. Material from North America was heterogenous and originated from two disjunct distribution areas, one northern and one western. The specimens from the northern distribution area correspond to *X. borealis*, whereas those from the west correspond to *X. mendozae*. Both taxa have a peculiar thallus morphology with more or less upright and aggregated lobes that are attached by the base from a central point. Sometimes the lobes are supported by short rhizines. They also share other remarkable characters: large bacilliform conidia, frequently pruinose upper cortex, and soredia produced from the lower surface. There are, however, obvious differences in thallus colour, appearance of the pycnidia and soredia, and structure of the lower cortex. I analysed the quantitative characters to statistically investigate whether there are any other discontinuities that might support the taxonomic recognition of the two taxa.

**Methods**—Almost all specimens discovered in the studied herbarium material of *Xanthoria* were included, in total 17 specimens of *X. borealis* and 22 specimens of *X. mendozae*. No apothecial characters were studied since no fertile specimens were found. The following six characters were measured for each specimen:

1. Thallus size. The maximum diameter of the thallus as seen from above. This measurement is difficult to estimate because the thalli are frequently fragmented (THALLUS).
2. Lobe width. The width at the widest point of one fully developed lobe per specimen (LOBEMAX).
3. Lobe base. The width near the point of attachment of one lobe per specimen (LOBEBAS).
4. Pycnidium size. The diameter of one pycnidium per specimen (PYCNID).
5. Conidium length. An average of 10 conidia from one pycnidium per specimen (CONIDIA).

The differences between *X. borealis* and *X. mendozae* were investigated with t-tests performed on each of these characters. The distinctness of the taxa regarding quantitative characters was investigated with a CVA including characters 2 and 4–6. Characters 1 and 3 were excluded because they were difficult to estimate and data were lacking for several specimens. There were c. 8% missing values in the matrix and they were handled with the casewise deletion option.

**Results**—Descriptive statistics and the significance of the t-values are presented in Tab. 6. *Xanthoria borealis* and *X. mendozae* differ significantly in the sizes of pycnidia, conidia, and soredia, although none of the studied characters separate entirely the taxa.

The canonical variate histogram is shown in Fig. 5., and the canonical loadings are presented in Tab. 7. *Xanthoria borealis* and *X. mendozae* show little overlap along the single canonical variate separating the groups (Wilks' Lambda 0.266; F = 17.20; p < 0.00001).

**Conclusions**—It is obvious that *X. borealis* and *X. mendozae* are separated by
Table 6. Descriptive statistics and the significance of differences between means, as revealed by t-tests comparing *X. borealis* and *X. mendozae*. Abbreviations of characters are explained in the text. s.d. is standard deviation, significance levels of t are denoted *** for \( p \leq 0.001 \), and ns (not significant) for \( p > 0.05 \).

<table>
<thead>
<tr>
<th>Character</th>
<th><em>X. borealis (N = 17)</em></th>
<th><em>X. mendozae (N = 22)</em></th>
<th>Significance of t</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>s.d.</td>
<td>min-max</td>
</tr>
<tr>
<td>THALLUS (mm)</td>
<td>10.8</td>
<td>3.3</td>
<td>7.0–15.0</td>
</tr>
<tr>
<td>LOBEMAX (mm)</td>
<td>1.5</td>
<td>0.32</td>
<td>1.1–2.2</td>
</tr>
<tr>
<td>LOBEBAS (mm)</td>
<td>0.7</td>
<td>0.3</td>
<td>0.3–1.3</td>
</tr>
<tr>
<td>PYCNID (mm)</td>
<td>0.14</td>
<td>0.04</td>
<td>0.07–0.20</td>
</tr>
<tr>
<td>CONIDIA (µm)</td>
<td>4.35</td>
<td>0.25</td>
<td>3.85–4.68</td>
</tr>
<tr>
<td>SOREDIA (µm)</td>
<td>53.0</td>
<td>12.4</td>
<td>40.7–96.0</td>
</tr>
</tbody>
</table>

Fig. 5. Canonical variate histogram of 12 specimens of *Xanthoria borealis* (white) and 18 specimens of *X. mendozae* (black) from North America.

Table 7. Character loadings for the four characters on the canonical variate (\( \times 100 \)) in a CVA performed to investigate the distinctness of *X. borealis* and *X. mendozae*. All characters contribute positively to the canonical variate separating the taxa.

<table>
<thead>
<tr>
<th>Character</th>
<th>Canonical variate I</th>
</tr>
</thead>
<tbody>
<tr>
<td>LOBEMAX</td>
<td>15</td>
</tr>
<tr>
<td>PYCNID</td>
<td>86</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>44</td>
</tr>
<tr>
<td>SOREDIA</td>
<td>37</td>
</tr>
</tbody>
</table>
correlated discontinuities in several quantitative and qualitative characters. Although they are superficially very similar, they are probably not very closely related.

Xanthoria fallax and X. ulophyllodes

Background—Xanthoria fallax and X. ulophyllodes were recently revised by Poelt & Petutschng (1992a, 1992b) and were mainly distinguished by differences in the morphology of soralia and soredia. Several important characters are shared, however. For example, both taxa have bacilliform conidia and true rhizines from the lower cortex as well as from the thalline margin of the apothecia. The distribution areas of the taxa in North America are wide and overlapping. Statistical analyses were carried out to determine if additional quantitative characters support the taxonomic recognition of X. fallax and X. ulophyllodes.

Methods—Twenty-two specimens of X. fallax and 21 specimens of X. ulophyllodes were included in the study. Specimens with developed apothecia only were included, since my aim was to analyse characters connected to sexual reproduction as well as vegetative characters. For X. ulophyllodes it was impossible to keep my intention of using specimens from various parts of the distribution range: most apotheciate specimens collected originated from Minnesota.

The following 13 characters were measured for each specimen:

1. Thallus size. The maximum diameter of the thallus (THALLUS).
2. Lobe width. The width of one lobe per specimen (LOBEWID).
3. Pycnidium size. The diameter of one pycnidium per specimen (PYCNID).
4. Conidium length. An average of 10 conidia from one pycnidium per specimen (CONIDIA).
5. Apothecium size. The maximum diameter of the largest apothecium (APOTHEC).
6. Hymenium thickness. One measurement per specimen (HYMENIUM).
7. Hypothecium thickness. One measurement per specimen (HYPOTHEC).
8. Exciple thickness. One measurement per specimen (EXCIPLE).
10. Spore width. An average of 10 spores per specimen (SPWIDTH).
12. Algal layer thickness. The thickest part of the algal layer below the subhymenial layers (ALGLAYER).
13. Soredium size. An average of 10 soredia from one lobe per specimen (SOREDIA).

The differences between X. fallax and X. ulophyllodes were investigated with t-tests performed on each of these characters, followed by a CVA, which included all characters, except 5 (APOTHEC) and 13 (SOREDIA). Missing values (c. 12%) were handled with the casewise deletion option (StatSoft 1994).

Results—Descriptive statistics and the significance of the t-values are presented in Tab. 8. Xanthoria fallax and X. ulophyllodes differ significantly in 10 of the 13 characters examined but none of the characters separate entirely the taxa.
Table 8. Descriptive statistics and the significance of differences between means, as revealed by t-tests comparing \textit{X. fallax} and \textit{X. ulophyllodes}. Abbreviations of characters are explained in the text. s.d. is standard deviation, significance levels of t are denoted *** for \( p \leq 0.001 \), ** for \( 0.001 < p \leq 0.01 \), * for \( 0.01 < p \leq 0.05 \), and ns (not significant) for \( p > 0.05 \).

<table>
<thead>
<tr>
<th>Character</th>
<th>\textit{Xanthoria fallax} (N=22)</th>
<th>\textit{Xanthoria ulophyllodes} (N=21)</th>
<th>Significance of t</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>s.d.</td>
<td>min-max</td>
</tr>
<tr>
<td>THALLUS (mm)</td>
<td>14.9</td>
<td>6.8</td>
<td>5.0–28.0</td>
</tr>
<tr>
<td>LOBEWID (mm)</td>
<td>1.2</td>
<td>0.3</td>
<td>0.8–1.9</td>
</tr>
<tr>
<td>PYCNIID (mm)</td>
<td>0.12</td>
<td>0.02</td>
<td>0.10–0.18</td>
</tr>
<tr>
<td>CONIDIA (µm)</td>
<td>3.7</td>
<td>0.1</td>
<td>3.3–3.9</td>
</tr>
<tr>
<td>APOTHEC (mm)</td>
<td>1.4</td>
<td>0.4</td>
<td>0.7–2.3</td>
</tr>
<tr>
<td>HYMENIUM (µm)</td>
<td>74.0</td>
<td>12.3</td>
<td>53–110</td>
</tr>
<tr>
<td>HYPOTHEC (µm)</td>
<td>52.0</td>
<td>14.0</td>
<td>33–88</td>
</tr>
<tr>
<td>EXCIPLE (µm)</td>
<td>47.0</td>
<td>17.0</td>
<td>8–83</td>
</tr>
<tr>
<td>SPLength (µm)</td>
<td>14.1</td>
<td>0.9</td>
<td>12.5–15.4</td>
</tr>
<tr>
<td>SPWidth (µm)</td>
<td>6.3</td>
<td>0.3</td>
<td>5.7–7.1</td>
</tr>
<tr>
<td>SEPTUM (µm)</td>
<td>3.1</td>
<td>0.3</td>
<td>2.3–3.6</td>
</tr>
<tr>
<td>ALGLAYER (µm)</td>
<td>97.0</td>
<td>31.0</td>
<td>50–163</td>
</tr>
<tr>
<td>SOREDIA (µm)</td>
<td>40.3</td>
<td>5.4</td>
<td>31.8–50.8</td>
</tr>
</tbody>
</table>

Fig. 6. Canonical variate histogram of 15 specimens of \textit{Xanthoria ulophyllodes} (black) and 14 specimens of \textit{X. fallax} (white) from North America.

The results of the CVA are presented in Fig. 6 and Tab. 9. The discrimination of the taxa along the canonical variate is entirely discontinuous (Wilks' Lambda 0.081; \( F = 17.45; p < 0.00001 \)).

Conclusions—Apart from the structure of soralia and soredia, \textit{X. fallax} and \textit{X. ulophyllodes} are separated by correlated discontinuities among several characters. Spore length, septum, and the size of the conidia contributes most to the canonical variate...
Table 9. Character loadings for the eight characters on the canonical variate ($\times 100$) in a CVA performed to investigate the distinctness of *X. fallax* and *X. ulophyllodes*. The sign denotes whether the character is making a positive or negative contribution.

<table>
<thead>
<tr>
<th>Character</th>
<th>Canonical variate I</th>
</tr>
</thead>
<tbody>
<tr>
<td>THALLUS</td>
<td>-11</td>
</tr>
<tr>
<td>LOBEWID</td>
<td>17</td>
</tr>
<tr>
<td>PYCNIID</td>
<td>12</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>55</td>
</tr>
<tr>
<td>HYMENIUM</td>
<td>7</td>
</tr>
<tr>
<td>HYPOTHETIC</td>
<td>14</td>
</tr>
<tr>
<td>EXCIPLE</td>
<td>1</td>
</tr>
<tr>
<td>SPLWIDTH</td>
<td>-50</td>
</tr>
<tr>
<td>SEPTUM</td>
<td>-32</td>
</tr>
<tr>
<td>ALGLAYER</td>
<td>13</td>
</tr>
</tbody>
</table>

separating the taxa, and are consequently regarded as the most important distinguishing quantitative characters. The statistical and numerical investigation supports the separation of *X. fallax* and *X. ulophyllodes* at the species level.

*Xanthoria fulva*

Background—*Xanthoria fulva* has a wide distribution range in North America. There are slight morphological differences in the appearance of the thallus between specimens from the western parts of the range and specimens from the southeastern parts. The western morph is usually darker orange and has shorter lobes than the southeastern morph. Intermediate forms are not rare. Poelt & Petutschnig (1992a) in their discussion of *X. fulva* mentioned an unresolved taxon from North America and it is obvious that they were referring to the southeastern morph of *X. fulva*. The only difference mentioned by Poelt & Petutschnig (1992a), however, was that the southeastern morph lacked the upright lobes characteristic of *X. fulva*. This character is vague and western forms of *X. fulva* may have horizontal lobes, while southeastern forms, on the other hand, may have upright lobes. It is uncertain if the southeastern morph occurs outside of North America.

Methods—Sixteen specimens representing the western morph and ten specimens representing the southeastern morph were included in the investigation. My aim was to include only specimens with well-developed apothecia, because I wished to analyse characters connected to sexual reproduction as well as vegetative characters. Specimens with fully developed apothecia with mature spores were rare in the herbarium material, however, especially regarding the southeastern morph.
The following 13 characters were measured for each specimen:

1. Thallus size. The maximum diameter of the thallus (THALLUS).
2. Lobe width. The width of one lobe per specimen (LOBEWID).
3. Pycnidium size. The diameter of one pycnidium per specimen (PYCNID).
4. Conidium length. An average of 10 conidia from one pycnidium per specimen (CONIDIA).
5. Apothecium size. The maximum diameter of the largest apothecium (APOTHEC).
6. Hymenium thickness. One measurement per specimen (HYMENIUM).
7. Hypothecium thickness. One measurement per specimen (HYPOTHEC).
8. Exciple thickness. One measurement per specimen (EXCIPLE).
10. Spore width. An average of 10 spores per specimen (SPWIDTH).
12. Algal layer thickness. The thickest part of the algal layer below the subhymenial layers (ALGLAYER).
13. Soredium size. An average of 10 soredia from one lobe per specimen (SOREDIA).

The differences between the morphs were investigated with t-tests performed on each character. All characters were included in a PCA to summarize the total variation and to examine whether the morphs would form two clusters along the first principal axes. Missing values (c. 12%) were handled with the casewise substitution option.

Results—Descriptive statistics and the significance of the t-values are presented in Tab. 10. There are small significant differences in five of the 13 characters, viz., the size of conidia, spore length, spore width, septum and the thickness of the algal layer below the apothecium.

The character loadings for the PCA are shown in Tab. 11, and a plot of the principal components is presented in Fig. 7. The first three factors together explain 56% of the total variation. The plots show no clear clustering or separation of the two groups.

Conclusions—The distinctness of the two morphs is very low. The PCA plot of the first and third principal components even suggests that groups could be recognized in a totally different way (Fig. 7). Therefore, I choose not to make any taxonomic recognition of groups within X. fulva based on this investigation. One possible way to investigate them further would be to study the characters in the apothecia and pycnidia more thoroughly and to study the distribution of the two morphs on a wider geographical scale.

Xanthoria parietina

Background—Xanthoria parietina is common in southeastern Canada and northeastern United States, but occurs also in western Canada and United States, viz., British Columbia, Washington, Oregon, and California, as well as on a few scattered localities in Louisiana and southeastern Texas. It is also found in Mexico.
Table 10. Descriptive statistics and the significance of differences between means, as revealed by t-tests comparing two morphs of *X. fulva*. Abbreviations of characters are explained in the text. s.d. is standard deviation, significance levels of t are denoted ** for $0.001 < p \leq 0.01$, * for $0.01 < p \leq 0.05$, and ns (not significant) for $p > 0.05$.

<table>
<thead>
<tr>
<th>Character</th>
<th>Western morph (N=14)</th>
<th>Southeastern morph (N=10)</th>
<th>Significance of $t$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>s.d.</td>
<td>min-max</td>
</tr>
<tr>
<td>THALLUS (mm)</td>
<td>3.6</td>
<td>2.0</td>
<td>1.0-9.0</td>
</tr>
<tr>
<td>LOBEWID (mm)</td>
<td>0.4</td>
<td>0.1</td>
<td>0.2-0.6</td>
</tr>
<tr>
<td>PYCNID (mm)</td>
<td>0.11</td>
<td>0.03</td>
<td>0.08-0.18</td>
</tr>
<tr>
<td>CONIDIA (µm)</td>
<td>3.74</td>
<td>0.14</td>
<td>3.50-4.05</td>
</tr>
<tr>
<td>APOTHEC (mm)</td>
<td>1.7</td>
<td>0.7</td>
<td>0.9-3.6</td>
</tr>
<tr>
<td>HYMENIUM (µm)</td>
<td>81</td>
<td>12</td>
<td>50-100</td>
</tr>
<tr>
<td>HYPOTHEC (µm)</td>
<td>37</td>
<td>8</td>
<td>28-50</td>
</tr>
<tr>
<td>EXCIPLE (µm)</td>
<td>11</td>
<td>10</td>
<td>0-30</td>
</tr>
<tr>
<td>SPLENCH (µm)</td>
<td>16.1</td>
<td>1.4</td>
<td>12.9-17.8</td>
</tr>
<tr>
<td>SPWIDTCH (µm)</td>
<td>8.4</td>
<td>0.6</td>
<td>7.5-9.0</td>
</tr>
<tr>
<td>SEPTUM (µm)</td>
<td>5.4</td>
<td>1.0</td>
<td>3.9-6.8</td>
</tr>
<tr>
<td>ALGLAYER (µm)</td>
<td>78</td>
<td>23</td>
<td>38-125</td>
</tr>
<tr>
<td>SOREDIA (µm)</td>
<td>40</td>
<td>4</td>
<td>34-48</td>
</tr>
</tbody>
</table>

Table 11. Character loadings for the 13 characters on the first three principal components ($\times 100$) in a PCA performed to investigate patterns of variation within *X. fulva*. The sign denotes whether the variable is making a positive or negative contribution. The percentage of variance explained by each component is also given.

<table>
<thead>
<tr>
<th>Character</th>
<th>Principal component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>THALLUS</td>
<td>-26</td>
</tr>
<tr>
<td>LOBEWID</td>
<td>-4</td>
</tr>
<tr>
<td>PYCNID</td>
<td>10</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>67</td>
</tr>
<tr>
<td>APOTHEC</td>
<td>47</td>
</tr>
<tr>
<td>HYMENIUM</td>
<td>83</td>
</tr>
<tr>
<td>HYPOTHEC</td>
<td>-3</td>
</tr>
<tr>
<td>EXCIPLE</td>
<td>-35</td>
</tr>
<tr>
<td>SPLENCH</td>
<td>80</td>
</tr>
<tr>
<td>SPWIDTCH</td>
<td>87</td>
</tr>
<tr>
<td>SEPTUM</td>
<td>64</td>
</tr>
<tr>
<td>ALGLAYER</td>
<td>59</td>
</tr>
<tr>
<td>SOREDIA</td>
<td>-26</td>
</tr>
</tbody>
</table>

Variance explained: 29.1 14.5 12.8
When studying material of *X. parietina*, I became aware of slight differences in lobe structure between collections from the eastern and western plus southern areas. These differences could be a result of the substrate on which the specimens were growing: the southern collections were mostly from branches and dry twigs, while the collections from eastern North America were mainly from bark and rock. Statistical and numerical analyses were carried out to investigate if there were any significant differences between the regional populations. A small number of European and Mexican specimens was also included in the study in order to investigate their similarities to the North American specimens.

Methods—Twenty-three specimens from eastern North America, seven specimens from western and southern North America, four specimens from Mexico, and seven specimens from Europe (Finland, Hungary, Russia, Sweden, and Switzerland) were included in the study.

The following ten characters were measured for each specimen:

1. Thallus size. The maximum diameter of the thallus (THALLUS).
2. Lobe width. The width of one lobe per specimen (LOBEWID).
3. Pycnidium size. The diameter of one pycnidium per specimen (PYCNID).
4. Conidium length. An average of 10 conidia from one pycnidium per specimen (CONIDIA).
5. Hymenium thickness. The thickest part of the hymenium (HYMENIUM).
6. Hypothecium thickness. The thickest part of the hypothecium (HYPOTHEC).
7. Exciple thickness. The thickest part of the exciple (EXCIPLE).
8. Spore length. An average of 10 spores per specimen (SPLENGTH).
10. Septum width. An average of 10 spores per specimen (SEPTUM).
Table 12. Descriptive statistics and the significance of the differences between means, as revealed by t-tests comparing *X. parietina* in North America and Europe. Abbreviations of characters are explained in the text. s.d. is standard deviation, significance levels of *t* are denoted ** for 0.001 < *p* ≤ 0.01, * for *p* ≤ 0.05, and ns (not significant) for *p* > 0.05.

<table>
<thead>
<tr>
<th>Character</th>
<th>North America (N=30)</th>
<th>Europe (N=7)</th>
<th>Significance of <em>t</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>s.d.</td>
<td>min-max</td>
</tr>
<tr>
<td>THALLUS (mm)</td>
<td>44.4</td>
<td>18.2</td>
<td>15–100</td>
</tr>
<tr>
<td>LOBEWID (mm)</td>
<td>1.6</td>
<td>0.6</td>
<td>0.75–3.2</td>
</tr>
<tr>
<td>PYCNID (mm)</td>
<td>0.10</td>
<td>0.02</td>
<td>0.08–0.17</td>
</tr>
<tr>
<td>CONIDIA (µm)</td>
<td>3.1</td>
<td>0.2</td>
<td>2.7–3.6</td>
</tr>
<tr>
<td>APOTHEC (mm)</td>
<td>2.6</td>
<td>1.3</td>
<td>1.1–8.0</td>
</tr>
<tr>
<td>HYPOTHEC (µm)</td>
<td>73</td>
<td>9</td>
<td>53–90</td>
</tr>
<tr>
<td>HYMENIUM (µm)</td>
<td>30</td>
<td>9</td>
<td>15–48</td>
</tr>
<tr>
<td>EXCIPLE (µm)</td>
<td>25</td>
<td>11</td>
<td>10–55</td>
</tr>
<tr>
<td>SLENGTH (µm)</td>
<td>14.8</td>
<td>0.7</td>
<td>13.0–16.0</td>
</tr>
<tr>
<td>SPWIDTH (µm)</td>
<td>7.9</td>
<td>0.6</td>
<td>6.0–8.7</td>
</tr>
<tr>
<td>SEPTUM (µm)</td>
<td>6.2</td>
<td>0.8</td>
<td>3.8–7.9</td>
</tr>
<tr>
<td>ALGLAYER (µm)</td>
<td>80</td>
<td>18</td>
<td>50–113</td>
</tr>
</tbody>
</table>

The differences between the North American and the European populations were investigated with t-tests performed on each character.

Nine characters (2–10) were used in a PCA performed to summarize the variation pattern. Missing values (< 1%) were handled with the mean substitution option. The same nine characters were used in a CVA to further investigate the distinctness of the geographic groups, and to study if groups defined by substrate were distinct at any degree. Missing values were handled with the casewise deletion option.

Results—Descriptive statistics and the significance of the *t*-values are presented in Tab. 12. There are small significant differences in three of the characters, viz., lobe width, pycnidium size, and hymenium thickness.

The principal components plot is shown in Fig. 8 and the character loadings and the amount of variance explained is presented in Tab. 13. There seems to be some separation along the first principal component with respect to geographical origin. The European specimens form a distinct cluster with low values on the second and third principal component.

The canonical variates plot of specimens with different geographic origins including both North America and Europe is shown in Fig. 9 and the component loadings in Tab. 14. There is a pattern of more or less distinct clusters (Wilks’ Lambda 0.070; \( F = 4.53; \ p < 0.00001 \)), with a clear separation between the southwestern-western group and the eastern + European group along the first canonical variate. The pattern is similar when European specimens are excluded from the analysis (Wilks’
Fig. 8. Principal components plots of 41 specimens of *Xanthoria parietina* from eastern North America (circles), western North America (filled circles), Texas and Louisiana (crosses), and Europe (squares). The first three components (PC I–III) account for 65% of the total variance.

Table 13. Character loadings for the seven characters on the first three principal components (× 100) in a PCA performed to investigate patterns of variation within *X. parietina* with different geographic origins. The sign denotes whether the variable is making a positive or negative contribution. The percentage of variance explained by each component is also given.

<table>
<thead>
<tr>
<th>Character</th>
<th>Principal component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>LOBEWID</td>
<td>42</td>
</tr>
<tr>
<td>PYCNID</td>
<td>53</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>75</td>
</tr>
<tr>
<td>HYMENIUM</td>
<td>61</td>
</tr>
<tr>
<td>HYPOTHEC</td>
<td>-10</td>
</tr>
<tr>
<td>EXCIPLE</td>
<td>-7</td>
</tr>
<tr>
<td>SPLENGTH</td>
<td>70</td>
</tr>
<tr>
<td>SPWIDTH</td>
<td>90</td>
</tr>
<tr>
<td>SEPTUM</td>
<td>57</td>
</tr>
<tr>
<td>Variance explained</td>
<td>33.7</td>
</tr>
</tbody>
</table>

Lambda 0.152; F = 3.83; p < 0.0001, not shown).

Conclusions—The PCA and the CVA show that the groups defined by geographic origin form more or less distinct clusters. However, there also seems to exist a substrate induced variation, which is difficult to separate from the geographic pattern. This issue has previously not been investigated to any greater extent, but for instance, it has
Fig. 9. Canonical variates plot of 40 specimens of *Xanthoria parietina* from eastern North America (circles), western North America (filled circles), Texas Louisiana (crosses), and Europe (squares).

Table 14. Component loadings for the nine characters on the first canonical variates ($\times 100$) in a CVA comparing groups of *X. parietina* with different geographic origins in North America and Europe. The sign denotes whether the variable is making a positive or negative contribution.

<table>
<thead>
<tr>
<th>Character</th>
<th>Canonical variate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>LOBEWID</td>
<td>-19</td>
</tr>
<tr>
<td>PYCNID</td>
<td>-29</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>-35</td>
</tr>
<tr>
<td>HYMENIUM</td>
<td>-27</td>
</tr>
<tr>
<td>HYPOTHEC</td>
<td>-5</td>
</tr>
<tr>
<td>EXCIPLE</td>
<td>-11</td>
</tr>
<tr>
<td>SPLength</td>
<td>-12</td>
</tr>
<tr>
<td>SPWidth</td>
<td>-57</td>
</tr>
<tr>
<td>SEPTUM</td>
<td>-12</td>
</tr>
</tbody>
</table>

recently been shown that isozymic variation in *X. parietina* in Spain is correlated with climatic conditions as well as substrate (Reyes et al. 1996). As *X. parietina* is widely distributed in the world, there are reasons to be careful before making any taxonomical recognition of such differences, even if they are significant and clear-cut.

*Xanthoria polycarpa*

Background—*Xanthoria polycarpa* has been largely misunderstood in North America. For details on this problem and the taxa involved, see Discussion for this species. The material remaining in *X. polycarpa* after my taxonomic revision seemed homogenous, even though parts of it had been recognized at a taxonomic level (e.g., *X. polycarpa* var. *maritima* and *X. ramulosa*). I wished to carry out a study to see if
my impression was supported with regard to quantitative characters.

Methods—Twenty-eight North American specimens and six European specimens (Finland, Germany, Sweden) were included in the study. The European specimens grew on twigs as well as bark. Of the North American specimens, 16 were from western and southwestern North America and grew exclusively on twigs (material often determined to *X. ramulosa* and *X. alaskana*). The remaining 12 were from eastern North America and grew on both twigs and bark (4 specimens, previously determined to *X. polycarpa*), and rock (8 specimens, which should correspond to *X. polycarpa* var. *maritima*).

The following ten characters were measured on each specimen:

1. Thallus size. The maximum diameter of the thallus (THALLUS).
2. Lobe width. The width of one lobe per specimen (LOBEWID).
3. Pycnidium size. The diameter of one pycnidium per specimen (PYCNID).
4. Conidium length. An average of 10 conidia from one pycnidium per specimen (CONIDIA).
5. Hymenium thickness. The thickest part of the hymenium (HYMENIUM).
6. Hypothecium thickness. One measurement per specimen (HYPOTHEC).
7. Exciple thickness. The thickest part of the exciple (EXCIPLE).
8. Spore length. An average of 10 spores per specimen (SPLENGTH).
10. Septum width. An average of 10 spores per specimen (SEPTUM).

Table 15. Descriptive statistics and differences between means, as revealed by t-tests comparing *X. polycarpa* in North America and Europe. Abbreviations of characters are explained in the text. s.d. is standard deviation, significance levels of t are denoted * for \(0.01<p\leq0.05\), and ns (not significant) for \(p>0.05\).

<table>
<thead>
<tr>
<th>Character</th>
<th>North America (N = 30)</th>
<th></th>
<th></th>
<th>Europe (N = 6)</th>
<th></th>
<th></th>
<th>Significance of t</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>mean</td>
<td>s.d.</td>
<td>min-max</td>
<td>mean</td>
<td>s.d.</td>
<td>min-max</td>
<td></td>
</tr>
<tr>
<td>THALLUS (mm)</td>
<td>11.9</td>
<td>3.7</td>
<td>5.0–25.0</td>
<td>10.3</td>
<td>3.3</td>
<td>7.0–15.0</td>
<td>ns</td>
</tr>
<tr>
<td>LOBEWID (mm)</td>
<td>0.37</td>
<td>0.13</td>
<td>0.2–0.7</td>
<td>0.49</td>
<td>0.08</td>
<td>0.38–0.60</td>
<td>*</td>
</tr>
<tr>
<td>PYCNID (mm)</td>
<td>0.097</td>
<td>0.026</td>
<td>0.05–0.18</td>
<td>0.075</td>
<td>0.016</td>
<td>0.05–0.10</td>
<td>ns</td>
</tr>
<tr>
<td>CONIDIA (µm)</td>
<td>2.52</td>
<td>0.18</td>
<td>2.2–2.9</td>
<td>2.46</td>
<td>0.14</td>
<td>2.3–2.7</td>
<td>ns</td>
</tr>
<tr>
<td>APOTHEC (mm)</td>
<td>1.9</td>
<td>0.8</td>
<td>1.0–4.5</td>
<td>1.5</td>
<td>0.4</td>
<td>1.1–2.0</td>
<td>ns</td>
</tr>
<tr>
<td>HYMENIUM (µm)</td>
<td>68</td>
<td>10</td>
<td>43–90</td>
<td>69</td>
<td>11</td>
<td>57–87</td>
<td>ns</td>
</tr>
<tr>
<td>HYPOTHEC (µm)</td>
<td>33</td>
<td>10</td>
<td>18–50</td>
<td>36</td>
<td>8</td>
<td>25–50</td>
<td>ns</td>
</tr>
<tr>
<td>EXCIPLE (µm)</td>
<td>8</td>
<td>9</td>
<td>0–28</td>
<td>12</td>
<td>19</td>
<td>0–38</td>
<td>ns</td>
</tr>
<tr>
<td>SPLENGTH (µm)</td>
<td>13.0</td>
<td>1.0</td>
<td>11.3–15.0</td>
<td>13.8</td>
<td>0.6</td>
<td>13.4–14.8</td>
<td>ns</td>
</tr>
<tr>
<td>SPWIDTH (µm)</td>
<td>6.7</td>
<td>0.6</td>
<td>5.4–7.9</td>
<td>6.6</td>
<td>0.2</td>
<td>6.4–7.0</td>
<td>ns</td>
</tr>
<tr>
<td>SEPTUM (µm)</td>
<td>4.2</td>
<td>0.8</td>
<td>2.8–6.2</td>
<td>4.5</td>
<td>0.1</td>
<td>4.4–4.6</td>
<td>ns</td>
</tr>
<tr>
<td>ALGLAYER (µm)</td>
<td>75</td>
<td>18</td>
<td>50–123</td>
<td>94</td>
<td>21</td>
<td>75–125</td>
<td>*</td>
</tr>
</tbody>
</table>
The differences between the North American and the European populations were investigated with t-tests performed on each character. Nine characters (2–10) were used in a PCA to investigate the pattern of variation between specimens originating from different parts of North America and Europe. There was one missing value in the data matrix and it was handled with the mean substitution option. The same nine characters were also used in a CVA to investigate the distinctness of the three groups. The missing value was handled with the casewise deletion option.

![Figure 10](image)

Fig. 10. Principal components plots of 36 specimens of *Xanthoria polycarpa* from eastern North America on bark (circles) and on rock (squares), western North America (crosses), and Europe (filled circles). The first three components (PC I–III) account for 61% of the total variance.

Table 16. Character loadings for the seven characters on the first three principal components (×100) in a PCA performed to investigate patterns of variation within *X. polycarpa*. The sign denotes whether the variable is making a positive or negative contribution. The percentage of variance explained by each component is also given.

<table>
<thead>
<tr>
<th>Character</th>
<th>Principal component</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>LOBEWID</td>
<td>−3</td>
</tr>
<tr>
<td>PYCNID</td>
<td>−37</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>−6</td>
</tr>
<tr>
<td>HYMENIUM</td>
<td>63</td>
</tr>
<tr>
<td>HYPOTHEC</td>
<td>−22</td>
</tr>
<tr>
<td>EXCIPLE</td>
<td>17</td>
</tr>
<tr>
<td>SPLENGTH</td>
<td>81</td>
</tr>
<tr>
<td>SPWIDTH</td>
<td>65</td>
</tr>
<tr>
<td>SEPTUM</td>
<td>81</td>
</tr>
<tr>
<td>Variance explained</td>
<td>26.3</td>
</tr>
</tbody>
</table>
Results—Descriptive statistics and the significance of the t-values are presented in Tab. 15. There are very small significant differences in two characters, viz., lobe width and thickness of the algal layer.

The principal components plot is shown in Fig. 10, while the character loadings and the amount of variance explained are presented in Tab. 16. No distinct clusters with respect to distribution area are apparent in the PCA plot, but it is evident that the morph growing on rock in the eastern distribution area tends to have the lowest

![Canonical variates plot](image)

Fig. 11. Canonical variates plot of 35 specimens of *Xanthoria polycarpa* from eastern North America (circles), western North America (crosses), and Europe (filled circles).

<table>
<thead>
<tr>
<th>Character</th>
<th>Canonical variate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>LOBEWID</td>
<td>19</td>
</tr>
<tr>
<td>PYCNID</td>
<td>-38</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>-13</td>
</tr>
<tr>
<td>HYMENIUM</td>
<td>6</td>
</tr>
<tr>
<td>HYPOTHEC</td>
<td>-7</td>
</tr>
<tr>
<td>EXCIPLE</td>
<td>6</td>
</tr>
<tr>
<td>SPLength</td>
<td>67</td>
</tr>
<tr>
<td>SPWidth</td>
<td>4</td>
</tr>
<tr>
<td>SEPTUM</td>
<td>32</td>
</tr>
</tbody>
</table>

Table 17. Component loadings for the nine characters on the first canonical variates ($\times 100$) in a CVA comparing groups of *X. polycarpa* with different geographic origins in North America and Europe. The sign denotes whether the variable is making a positive or negative contribution.
values on the first and second principal components. A PCA performed without the European specimens gave basically the same pattern (not shown).

The canonical variates plot of the groups from different distribution areas is shown in Fig. 11, and the component loadings are presented in Tab. 17. The CVA shows a weak geographic pattern with overlapping clusters (Wilks' Lambda 0.333; F=1.95; p < 0.033).

![Canonical variates plot](image)

Fig. 12. Canonical variates plot of 30 specimens of *Xanthoria polycarpa* from eastern North America on bark (circles) and on rock (filled circles), and from western North America (crosses).

<table>
<thead>
<tr>
<th>Character</th>
<th>Canonical variate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>I</td>
</tr>
<tr>
<td>LOBEWID</td>
<td>45</td>
</tr>
<tr>
<td>PYCNID</td>
<td>-15</td>
</tr>
<tr>
<td>CONIDIA</td>
<td>4</td>
</tr>
<tr>
<td>HYMENIUM</td>
<td>17</td>
</tr>
<tr>
<td>HYPOTHEC</td>
<td>23</td>
</tr>
<tr>
<td>EXCIPLE</td>
<td>-9</td>
</tr>
<tr>
<td>SPLength</td>
<td>31</td>
</tr>
<tr>
<td>SPWidth</td>
<td>18</td>
</tr>
<tr>
<td>SEPTUM</td>
<td>5</td>
</tr>
</tbody>
</table>

Table 18. Component loadings for the nine characters on the first canonical variates (×100) in a CVA comparing groups of *X. polycarpa* with different geographic origins within North America. The sign denotes whether the variable is making a positive or negative contribution.
The canonical variates plot of the North American specimens is shown in Fig. 12, and the component loadings in Tab. 18. In particular, the morph growing on rock in the northeastern distribution area is separated from both the southeastern population on bark and twigs and the western group, which grows mainly on twigs (Wilks’ Lambda 0.154; F = 3.27; p < 0.001). In an attempt to exclude the potential influence of the substrate, I repeated the analysis with only two groups, the eastern and the western. The result of the CVA indicates little separation of the groups (Wilks’ Lambda 0.504; F = 2.18; p < 0.070).

Conclusions—The PCA and the CVA show that the groups defined by geographic origin form more or less overlapping clusters. In the CVA, the groups show some separation, especially if only North American populations are considered. However, the geographic differences are difficult to separate from substrate induced variation.

The morphological variation between geographical populations and specimens growing on different substrate observed by me in both *X. parietina* and *X. polycarpa* should be studied more in detail. At this point, no taxonomic changes based on the measured variation seem justified.

**TAXONOMY**

The genus *Xanthoria* in the sense used in this work is heterogenous and at least two species are only provisionally kept in *Xanthoria* awaiting further treatment. I have chosen not to break up the genus for several reasons. To begin with, it would have been necessary to consider many more species in *Xanthoria* as well as related genera. In addition, such a project would best be carried out on a worldwide scale. Finally, I have considered it practical to keep all treated taxa in *Xanthoria*, because the material, including the species described here as new, has mostly been determined to one or another species in this genus. Bearing this in mind, I still think that it is meaningful to briefly summarize the characteristics of the genus *Xanthoria* in North America.

*Caloplaca lobulata* was previously kept in *Xanthoria*, but Steiner & Poelt (1982) transferred it to *Caloplaca* sect. *Xanthoriella* together with two more species, all of which lack a continuous lower cortex as well as any kind of attachment organs. The taxon is not treated in this work. *Caloplaca lobulata* in the sense of North American authors is not synonymous with *C. lobulata* (Florke) Hellbom. The collections from North America are mainly on rock, while *C. lobulata* s. str. is corticolous. The North American material, which lacks a valid name, is currently being investigated by U. Arup and C. M. Wetmore.

*Xanthoria* (Fr.) Th.Fr.


Thallus foliose to subfruticose, forming separate rosettes or coalescing into stands ± covering the substrate. Lobes dorsiventral to subterete, ± horizontal to semierect to erect, smooth to ± wrinkled, mostly frequently branched. Upper surface in variable yellow to orange colours, occasionally greenish or grey, sometimes with a
white pruina. Lower surface white to yellow, smooth to somewhat wrinkled. Attachment organs mostly present, submarginal to laminal, simple, white to yellow, developed as hapters (± short and attached with more or less pronounced terminal extensions) or (true) rhizines (short to long, free or attached, pointed to somewhat frayed). Soralia present in about half of the species, laminal or marginal to submarginal, blastidious or soredious, concolorous with the upper surface or lighter yellow to greenish yellow.

Cortical layers paraplectenchymatous (apart from one species, X. mendozae, with prosoplechtenchymatous lower cortex), composed of c. 3–5 layers of isodiametric to somewhat elongated cells, colourless apart from external crystals of anthraquinones. Medulla with hyphae arranged in bundles or more lax, reticulate, cells short to long, c. 3–5 µm thick, smooth. Photobiont in a ± continuous layer near the upper cortex or in groups spread throughout the medulla, of Trebouxia type, green, unicellular, up to c. 25 µm diam.

Apothecia present or lacking, laminal, sessile to ± stipitate, disk darker than the thallus, occasionally with a white pruina. Thalline margin concolorous with the thallus, sometimes with short hapters or short to long rhizines, smooth to sorediate, occasionally with lobules. Exciple cupular (sensu Arup 1995a, Jahns et al. 1995), thin to thick, gelatinous, colourless, cells with thick walls and ± elongate lumina, which are shortest laterally near the surface where they become similar to the cortex cells. Hypothecium colourless to pale brown, irregular, cells with thin walls, sporadically with oil droplets. Hymenium usually colourless in lower part and with anthraquinone crystals in a ± distinct layer in the upper part. Paraphyses simple or branched, often also with scattered anastomoses in the lower part, apices ± capitate, occasionally or regularly with oil droplets in the uppermost cells. Asci of Teloschistes type (sensu Honegger 1978), clavate, with eight spores. Spores polaribilocular, hyaline, usually ellipsoid, sometimes cylindrical to narrowly ellipsoid, c. 10–20 × 4–10 µm, septum narrow to wide, c. 1–10 µm.

Pycnidia usually present, ± conspicuous, laminal, immersed to protruding, concolorous with the thallus or darker, cavity rounded with several chambers (± conform with the Xanthoria type sensu Vobis 1980), cells in the pycnidium wall as well as conidiogenous cells angular, isodiametric to slightly elongated, c. 3–5 µm. Conidia ellipsoid, bacilliform, or, in the single case of X. oregana, of several shapes within the pycnidium, c. 2–5 × 1–2 µm.

Secondary chemistry characterized by anthraquinones (emodin, fallacinal, parietin, parietinic acid, and teloschistin). Thallus and apothecia K + purple, C-, Pd-.

Key to the species

Most of the species of Xanthoria can with some training be recognized by gross morphology only. Sterile, young, or in some way extreme thalli may, however, be difficult or impossible to identify even for an experienced lichenologist. For some species, characteristics of the spores and/or conidia are necessary to reach a conclusive identification. Material collected for identification should preferably consist of healthy, fully developed, i.e., not too small, thalli. Great care must be taken when identifying
the collection, because two or several species of *Xanthoria*, and occasionally *Teloschistes*, may grow intermingled.

**Lobe structure.** This is a somewhat variable character, and generally some practise is needed to evaluate the lobe structure. In most cases, it is feasible to compare the lobes with the photographs of the species (Figs. 13, 14 & 29).

**Attachment organs.** Hapters and rhizines have been used as key characters. Hapters are typically short and attached, and often have a terminal foot. Rhizines are longer, free or attached, and the tip is pointed to somewhat frayed.

**Spores.** Only (dead) spores released from the ascus should be studied. The septum is measured close to the isthmus.

**Conidia.** There is usually some variation in shape, which is not indicated in the key. Only the predominant shape is given.

Measurements in the key are given as “arithmetic mean minus standard deviation-arithmetic mean-arithmetic mean plus standard deviation”. In addition, minimum and maximum values are given in a few cases.

For more details on the characters, see Morphology and anatomy.

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6b. Lobes wider, c. 0.8–1.1–1.4 mm wide; soredia produced marginally to submarginally; pycnidia light orange to orange; cells of paraphyses without oil droplets; rhizines sparse or (mostly) abundant: ......................... 7

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8b. Conidia ellipsoid, oblong ellipsoid, bacilliform, or irregular (variable within a single pycnidium), (3.0–)3.4–3.6–3.8(–4.0) μm long; soralia marginal to submarginal or from the lower side of the lobe apices, which often become helmet-shaped; laminal soralia absent; lobes horizontal to slightly erect, rhizines rarely visible from above; chemosyndrome A: .................. X. *oregana*

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11b. White pruina present; conidia bacilliform. Southern parts of the area: ................................................................. X. *concinna*

12a. Conidia ellipsoid; lower surface with short, attached hapters; thalline margin without rhizines but sometimes with short attached hapters; thallus up to 100 mm: .......................................................... 13

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13b. Lobes convex, narrow to wide (up to c. 1.5 mm); thallus ± firmly attached; with extremely short hapers: ........................................... X. *elegans*
14a. Spores ellipsoid, with a wide septum, 5.6–6.5–7.4 µm; upper surface yellow to orange: ..............................................X. hasseana
14b. Spores cylindrical to ellipsoid, with a narrow septum, 1.6–2.2–2.8 µm; upper surface light orange to dark orange: ..............................................X. montana

1. Xanthoria borealis R. Sant. & Poelt
(Figs. 15, 29A)
Torneträsk, Abiskosuolo, på de fägelgådslade, vertikala klippväggarna på önns SW-sida.
Alt. 350 m. Regio subalpina.”, 1943, Santesson 3481 (UPS, holotype; GZU, LD, isotypes).

Thallus small, up to 15 mm, foliose, forming small patches or sometimes extensive colonies covering the substrate, attached ± centrally, by lower parts of lobes, sometimes with supporting rhizines. Lobes narrow-wide, 1.1–2.2 mm (s = 0.3, N = 17, n = 1) at widest point, short, ± erect, revolute, with or without thin terminal branches, apices down-turned. Upper surface dark orange to reddish orange, ± coarse, often slightly pruinose. Lower surface white, smooth. Rhizines scattered, mostly near lobe bases, white, thin, short, pointed to somewhat frayed. Soredia blastidious, produced submarginally and, later, from the apical (terminal) parts of the lower surface, orange to greenish orange, small, often lumped, 41–53–96 µm (s = 12, N = 17). Photobiont layer discontinuous, ± spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia not seen.

Pycnidia common, scattered, ± immersed, reddish orange, c. 0.1–0.2 mm diameter. Conidia bacilliform, (3.5–)3.8–4.3–4.7–(5.25) µm long (s = 0.2, N = 12), c. 1.5 µm wide.

Chemistry—Parietin (major), fallacinal (major), emodin, teloschistin (major), and parietinic acid. (Chemosyndrome A3).

Ecology—Saxicolous and terricolous among bryophytes, a few specimens on antlers and bones on the ground. The saxicolous specimens were growing on gneiss as well as calcareous rock, and several of them were collected in extremely nutrient rich sites, e.g., near bird nests or on bird rocks.

Distribution—Arctic, known from low altitudes in the Northwest Territories with an Alaskan disjunction. – Circumpolar, also seen from Greenland, Iceland, Norway, Sweden, Russia, Nepal.

Nomenclatural note—In the original description the label of the holotype was translated and cited as: “Torne Lappmark: Torneträsk, the island of Abisko-suolo off Abisko, on the vertical rocks on the W-side of the island. Bird rocks.”

Discussion—Xanthoria borealis is not very variable, but there are differences in the lobe morphology of young thalli (with shorter lobes) and mature thalli (longer lobes). Young lobes are mostly horizontal and narrow, and have very narrow branches with tips that are down-turned. Mature lobes are usually erect, very wide, flatter, and have a wide and scarcely incised terminal part.

Xanthoria borealis was described a few years ago from Sweden (Poelt & Petutschnig 1992a) and it was reported that apothecia had been found on one lobe. It is uncertain if the apothecia referred to were found on the type specimen or on some other specimen
investigated. The apothecia that occur in the holotype collection belong to intermixed lobes of *X. elegans*.

Poelt & Petutschng (1992a) reported *X. borealis* from two North American localities, one in Colorado and the other in Oregon. The cited specimens, however, belong to *X. mendozae*, which is superficially similar, mainly with regard to gross morphology and shape and size of the conidia. *Xanthoria borealis* can be distinguished from *X. mendozae* by its smooth blastidious soredia which are + concolorous with the thallus, more immersed and darker coloured pycnidia, and purer white, smooth lower surface. The soredia of *X. mendozae* are lighter, lemon yellow to greenish yellow, and have a woven surface reminiscent of a tennis ball. Furthermore, the pycnidia of *X. mendozae* are + concolorous with the thallus and slightly protruding as large, smooth warts, and the lower cortex is a dull dirty white. The two species are entirely allopatric in North America. For more details on the differences between *X. borealis* and *X. mendozae*, see the chapter Statistical and numerical treatment.

*Xanthoria candelaria* is morphologically somewhat similar to *X. borealis*, but it is separated mainly by having ellipsoid conidia, lighter orange thalli with richly branched lobes, and production of soredia also from margins and wrinkles of the lobes.

The Antarctic taxon *X. mawsonii* Dodge is very similar to *X. borealis*. It was not included in my studies, but according to Castello (1995) *X. mawsonii* differs from *X. borealis* by having ellipsoid conidia and flatter lobes. The most important differences between *X. mawsonii* and *X. candelaria*, according to Castello (1995), are that *X. mawsonii* has larger conidia, more reddish colour, and wider, pruinose lobes with soralia that are often labiform.

Selected specimens examined. CANADA. NORTHWEST TERRITORIES. Axel Heiberg Island, E side of island, 1980, Scotter 46053, 46301a, 46368 (WIS). Baffin Island, Cape Searle, 1950,

U.S.A. ALASKA. St. Mary's, Yukon River, 1980, Hoare 707 (WIS).

2. Xanthoria candelaria (L.) Th. Fr. (Figs. 13A, 16)


Thallus small, up to 30 mm, foliose-subfruticose, forming small cushions or extensive colonies covering the substrate, attached by lower parts of lobes, and hapters. Lobes narrow, 0.2–0.5 mm (s = 0.1, N = 4, n = 1), dorsiventral to subterete, ± erect, richly branched with narrow, subterete outermost branches, which probably function as vegetative dispersal units. Upper surface yellow to light orange, smooth-coarse, often wrinkled. Lower surface white to yellow, mostly somewhat wrinkled. Hapters very rare, white, thin, short, situated near lobe base, attached. Soredia blastidious, produced marginally, submarginally, at lobe tips, laminally along wrinkles, and from thalline margin, c. 29–38–49 µm (s = 6, N = 10). Photobiont layer discontinuous, spread throughout the medulla. Medulla reticulate, with short to somewhat elongate irregular hyphae.

Apothecia generally rare but may be abundant on some thalli, maximum diameter 0.9–1.0–4.0 mm (s = 0.9, N = 14, n = 1), concave to plane, laminal but often appear to grow terminal and embedded among lobe apices. Thalline margin 0.05–0.18 mm, smooth, often with lobules and soredia. Algal layer below exciple 38–64–88 µm (s = 15, N = 13, n = 1). Exciple visible from the outside, thickness below the hymenium 0–17–50 µm (s = 11, N = 16, n = 1), gelatinous, colourless, cell walls thick, lumina elongate. Hypothecium 25–39–68 µm (s = 11, N = 16, n = 1), colourless-pale brown, hyphae irregular, cell walls thin. Hymenium 58–71–90 µm (s = 8, N = 16, n = 1). Paraphyses sparsely branched (0–2 times), 1.5–2 µm wide, tips 5–7 µm wide, occasionally with oil droplets. Spores ellipsoid, (11.0–)12.1–13.5–14.8(–16.0) µm long (s = 0.8, N = 17), (5.0–)5.4–7.0–8.0(–9.0) µm wide (s = 0.8, N = 17), septum ± wide, (2.0–)2.9–4.3–5.7(–7.0) µm (s = 0.8, N = 17).

Pycnidia common, immersed, concolorous with the upper surface or slightly darker, c. 0.07–0.15 mm diameter. Conidia ellipsoid, (2.0–)2.3–2.6–2.9(–3.5) µm long
Fig. 16. Known North American distribution of *Xanthoria candelaria* (dots) and *X. concinna* (triangle). Collections of *X. candelaria* from the islands off the coast of Alaska and from Newfoundland not shown on the map.

(s = 0.2, N = 16), c. 1–1.5 µm wide.

Chemistry—Parietin (major), fallacinal, emodin, teloschistin, and parietinic acid. (Chemosyndrome A).

Ecology—Corticolous, saxicolous, and lignicolous. When corticolous, *X. candelaria* is found equally often on bark and twigs. The most important phorophytes by far are various species of *Picea*. Other important phorophytes are *Pseudotsuga* spp., *Abies* spp., and *Pinus* spp. A few collections have been made on deciduous phorophyte genera, e.g., *Betula* and *Populus*. The saxicolous specimens are from different kinds of rocks; acidic, calciferous, hard or soft. The sites where *X. candelaria* occurs are generally sunny and nutrient rich, e.g., open coniferous forests, by sea-shores or on the tundra.
Distribution—Widespread in the arctic to boreal region, and seems to be most frequent in the west. It occurs along the entire Pacific coast from Alaska to southernmost California. Also seen from Europe, Asia, Antarctica, South America.

Nomenclatural note—A neotype was selected by Santesson (in Moberg 1986). Jørgensen et al. (1994) supported this choice, as there is no relevant specimen in LINN.

Discussion—Xanthoria candelaria is clearly delimited from all other sorediate species with small thalli by having ellipsoid conidia. The morphology is variable, and it is frequently possible to observe much of the variation within one collection. The thallus cushions are sometimes very distinct, but they can sometimes coalesce into large patches. The orientation of the lobes varies from almost horizontal to erect, and the lobes are flattened, mainly in lower parts, to suberete, mainly in upper parts and the outermost branches. The soredia, which basically are blastidious, sometimes appear fine and powdery. Apothecia are usually rare and scattered, but may become very frequent and crowded on some thalli. The variation seems to depend on the substrate as well as nutrient conditions.

The variety X. candelaria var. finmarckica has been used for North American specimens until recently (Schindler 1990). The type collection of the variety consists of small, but otherwise typical specimens of X. candelaria.


3. **Xanthoria concinna** J. W. Thomson & T. H. Nash (Figs. 13B, 16)


Thallus small, up to 14 mm, forming ± distinct cushions. Lobes narrow, c. 0.3–0.5 mm, convex, somewhat revolute, horizontal to semierect, relatively richly branched. Upper surface bright yellow or greyish, mostly with a thick pruina. Lower surface white, smooth. Hapters rare, short, white, attached. Photobiont layer discontinuous, spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia frequent, usually abundant, maximum diameter 1–2 mm (N = 1, n = 1), rounded, plane, with a somewhat inflated appearance. Disk orange, lightly pruinose. Thalline margin c. 0.1 mm, thin, smooth, pruinose. Algal layer below hymenium c. 70–80 µm. Exciple not visible from the outside, thin, thickness below hymenium c. 15 µm. Hypothecium c. 50 µm. Hymenium c. 75 µm. Paraphyses simple or sparsely branched, c. 2 µm wide, tips c. 5 µm. Spores narrowly ellipsoid, 13–15 × 5–6 µm, septum 2.5–5 µm (N = 1).

Pycnidia common, immersed, concolorous with the upper surface or slightly darker orange. Conidia bacilliform, 3.5–4.0 × 1–1.5 µm (N = 1).

Chemistry—Parietin (major), fallacinal (major), emodin, teloschistin (major), and parietin acid. (Chemosyn drome A3). The KOH reaction becomes faint on parts of the thallus where the pruina is very thick.

Ecology—Corticolous on twigs in dry habitat.

Distribution—Known from one collection in southwestern Texas near the Mexican border. – Main distribution in Mexico.

Discussion—*Xanthoria concinna* is a largely unknown species, which has not been thoroughly investigated since it was described from Mexico. It was stated in the original description that the thallus is greyish (Thomson & Nash 1976). However, my studies of additional Mexican material have revealed that *X. concinna* normally has a bright yellow upper surface, and that the original material is unusually pale. The thick pruina enhances the impression of the thallus being gray.

The specimen from Texas is rather small and not as heavily pruinose as the Mexican material seen by me, but apart from that, the morphology and ecology corresponds well.
Superficially, *X. concinna* resembles *X. polycarpa*, mainly by the cushion-like growth form and the abundant apothecia. *Xanthoria concinna* is distinguished by having a pruinose thallus, narrower spores, bacilliform conidia, somewhat inflated apothecia, and a more robust habit.


4. *Xanthoria elegans* (Link) Th.Fr. (Figs. 13C, 17)


Thallus small-large, up to 55 mm, forming rosettes, sometimes coalescing. Lobes narrow to medium wide, 0.4–0.8–1.3 mm (s = 0.2, N = 22, n = 1), plane-convex, horizontal or rarely semi-erect, ± sparsely branched. Upper surface yellowish orange to bright orange to dark orange to dull red, ± coarse, occasionally slightly pruinose. Lower surface white, somewhat wrinkled. Hapters scattered, white, thick, very short and tightly anchoring the thallus. Photobiont layer more or less continuous near the upper cortex. Medulla with hyphae in bundles, cells regular, elongate.

Apothecia mostly frequent, sometimes sparse or lacking, maximum diameter 0.9–1.7–3.0 mm, (s = 0.5, N = 22, n = 1), slightly concave-plane or sometimes convex. Thalline margin 0.05–0.13 mm, smooth to ± crenulate. Algal layer below exciple 58–96–175 µm (s = 30, N = 22, n = 1). Exciple mostly visible from the outside, thickness below hymenium 12–32–50 µm (s = 11, N = 22, n = 1), gelatinous, colourless, cell wall thick, lumina elongate. Hypothecium 20–41–80 µm (s = 16, N = 21, n = 1), colourless-pale brown, irregular, cell walls thin. Hymenium 58–76–93 µm (s = 9, N = 21, n = 1). Paraphyses simple or sparsely branched (0–2 times), 2–2.5 µm wide, tips 5–6 µm wide, occasionally with oil droplets. Spores ellipsoid, (11.0–)11.8–13.4–15.8(–17.5) µm long (s = 0.9, N = 21), (5.5–)6.0–7.0–7.8(–8.5) µm wide (s = 0.4, N = 21), septum narrow, (1.0–)1.6–3.2–4.3(–5.0) µm (s = 0.6, N = 21).

Pycnidia sparse to abundant, immersed in thallus, somewhat darker than the upper cortex, c. 0.07–0.15 mm diameter. Conidia ellipsoid, (2.0–)2.6–2.9–3.2(–3.5) µm long (s = 0.2, N = 21), c. 1–1.5 µm wide.

Chemistry—Parietin (major), fallacinal, emodin, teloschistin, and parietinic acid. (Chemosyndrome A).

Ecology—Usually saxicolous, but occasional collections have been made on other
Fig. 17. Known North American distribution of *Xanthoria elegans*. A triangle denotes that the species is known from one locality only in the state, but the exact position is unknown. Collections from the islands off the coast of Alaska not shown on the map.

*substrates, e.g., soil, bone, antlers, and roofs. Xanthoria elegans* grows on various kinds of rock, both acidic and calciferous. Three collections from bark occurred in the material, on *Quercus* sp., *Salix* sp., and one unknown phorophyte. The habitats in which *X. elegans* is found are mainly open and nutrient rich (e.g., manured by birds); the humidity of the microhabitats ranges from dry to moist.

**Distribution**—Widespread, mainly in the arctic to boreal region, but also common in arid habitats of western North America. It occurs sporadically in the eastern temperate region with one find in Virginia and one in Louisiana. The western to southwestern collections are invariably from high elevations. – Widespread, earlier arctic-alpine, apparently spreading in modern time (Poelt & Petutschnig 1992a).

**Discussion**—This treatment of *X. elegans* should be regarded as tentative, as material from only a few herbaria has been studied. No great effort has been made
to separate morphological forms at any taxonomical rank. *Xanthoria elegans* is well-known for being morphologically very variable (e.g., Poelt 1969, Poelt & Petutschnig 1992a), and the taxonomy should be studied in more detail, preferably on a world-wide scale.

Three morphs of *X. elegans* have sometimes been recognized at some taxonomic rank in Europe (Poelt 1969) as well as in North America. One morph has orange, ± apotheciate thalli with lobes that are appressed to the substrate. It corresponds well with the type specimen. A second morph has yellow to bright orange, sparsely apotheciate thalli with semi-erect, ± inflated lobes. This morph has been referred to as *X. elegans* var. *splendens*. A third morph has very small, sparse apothecia and small, dark orange thalli with narrow and appressed lobes. It has been referred to as *X. elegans* var. *tenuis*. However, intermediate forms with respect to these characters are common, and it is probably not possible to recognize the morphs on any taxonomic level. The morphological plasticity of the morphs is illustrated, for example, on seashore rock, where thalli of the first morph often develop somewhat inflated and horizontal to semi-erect lobes. Fahselt & Krol (1989) have shown that the three morphs grow in different microhabitats, and that the first two do not vary significantly regarding chemistry or isozyme patterns in Arctic North America. Furthermore, Fahselt & Krol (1989) noted that intermediate forms occasionally occur in intermediate habitats.

*Xanthoria elegans* sometimes has been confused with *Caloplaca trachyphylla* (Tuck.) Zahlbr. In *C. trachyphylla*, however, a lower cortex occurs only under the outermost part of the lobes, no hapters are formed, the apothecia are more crowded and, instead of being folded, each apothecium fits tightly against its neighbours. In addition, the upper surface of the lobes of *C. trachyphylla* often, but not always, are somewhat verruculose. More detailed comparisons were made by Rudolph (1955).

A specimen of *Caloplaca cascadensis* H. Magn. (Cascade Mts, 1931, Grant, US isotype) was studied, because it had been suggested that it could be conspecific with *X. elegans* or another species of *Xanthoria* (Arup 1995b). The lobe morphology, however, indicates that it is not properly accommodated within the variation of *X. elegans*.


5. *Xanthoria fallax* (Hepp ex Arnold) Arnold (Figs. 18, 29C)


Thallus small to medium large, up to 30 mm, forming rosettes, sometimes coalescing. Lobes narrow to medium wide, 0.8–1.2–1.9 mm (s = 0.3, N = 21, n = 1), ± plane, horizontal or slightly raised, branched, with rounded, wide tips. Upper surface yellowish orange to orange, smooth to shiny. Lower surface white, smooth or slightly wrinkled. Rhizines frequent, white to yellow, medium thick, short-long, pointed or somewhat frayed, free or attached (with small foot). Soredia produced marginally, often on short side branches, in horizontal, ± crescent-shaped slits, with the upper cortex mostly persistent and forming a hood, common or rare (young thalli), small, distinct and ± spherical, powdery, lemon yellow to greenish yellow, c. 32–40–51 μm (s = 5, N = 15). Photobiont layer ± discontinuous and spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia rare, frequent on some thalli, maximum diameter 0.7–1.4–2.2 mm (s = 0.4, N = 22, n = 1), concave-plane or slightly convex, disk often with a central hollow. Thalline margin 0.04–0.18 mm, smooth, often breaking up with soredia, usually with vertical or ventral, white-yellow, pointed rhizines. Algal layer below exciple 50–97–163 μm (s = 31, N = 22, n = 1). Exciple not visible from the outside, thickness below hymenium 8–47–83 μm (s = 17, N = 22, n = 1), gelatinous, colourless, cell walls thick, lumina elongate. Hypothecium 33–52–88 μm (s = 14, N = 22, n = 1), pale
brown, irregular, cells with thin walls. Hymenium 53–74–110 µm (s = 12, N = 22, n = 1). Paraphyses sparsely branched (0–3 times), 1.5–2 µm, tips c. 4–6 µm. Spores ellipsoid, (11.5–)12.5–14.1–15.4(–17.0) µm long (s = 0.9, N = 18), (5.9–)5.7–6.3–7.1(–9.0) µm wide (s = 0.3, N = 18), septum wide, (2.0–)2.3–3.1–3.6(–5.0) µm (s = 0.3, N = 18).

Pycnidia common, immersed in thallus or slightly protruding, darker than the upper surface, 0.10–0.18 mm diameter. Conidia bacilliform, (3.0–)3.4–3.7–3.9(–4.5) µm long (s = 0.1, N = 21), c. 1 µm wide.

Chemistry—Parietin (major), fallacinal (major), emodin, teloschistin (major), and parietinic acid. (Chemosyndrome A3).

Ecology—Mainly corticolous on the trunks of trees, with a small number of collections made on rock, lignum, and twigs. When growing on bark, X. fallax has been found most often, by far, on the genus Quercus. Other important phorophytes include Populus spp., Ulmus spp., Acer spp., Robinia spp., and Fraxinus spp. Saxicolous specimens are from various kinds of rock, mainly sandstone, but also granite, basalt, limestone etc. The habitats in which X. fallax is found are open to semi-open, often more or less dry, but also more moist along rivers or lakes, and nutrient rich.

Distribution—Common and widespread in temperate regions of North America with extensions into boreal regions. Not known north of zonobiome VIII. – Also seen from Europe, Africa (?), Asia.

Nomenclatural note—Further synonyms to X. fallax are listed in Poelt & Petutschnig (1992a).
Discussion—In North America, the name X. fallax has been used in a collective sense for a number of sorediate species, e.g., X. fulva, X. mendozae, X. oregana, and X. ulophyllodes. Xanthoria fallax in the present, strict sense can be separated from all other species by the morphology of the soralia, which can be described as crescent shaped cups, or "bird nests" enclosed by the upper and lower cortex. The soredia are soft and powdery, produced from the medullary layer.

Xanthoria fallax is most similar to and certainly closest related to X. ulophyllodes, and they frequently are found growing together. Young thalli of these two species are impossible or at least difficult to determine until soralia are developed. In contrast to X. fallax, X. ulophyllodes produces blastidious soredia from the lobe margins and, on large thalli, also laminaly. The delimitation of X. fallax and X. ulophyllodes based on differences in morphology of the soralia and soredia is supported by other characters. For example, the thallus of X. fallax usually is flatter, with lobes ± appressed to the substrate, while the lobes of X. ulophyllodes are more loosely appressed and slightly uplifted, making the growth form appear less dense. Furthermore, significant differences in quantitative characters like spore length, septum width, and the size of the conidia are demonstrated. The quantitative differences between X. fallax and X. ulophyllodes are described in detail in the chapter Statistical and numerical treatment.

Xanthoria fallax is also likely to be confused with X. fulva. The latter, however, has distinctly narrower lobes with soredia produced from the lower surface, the pycnidia appear larger and the colour of the pycnidia is darker orange to red, and the rhizines are less frequent. The upper cortex around the soralia in X. fulva sometimes persists, and is thus similar to the "bird nest" soralia in X. fallax. In X. fulva, however, these soralia are distinctly smaller and situated at the tips of slightly raised narrow lobes.


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\begin{itemize}
\end{itemize}

6. \textit{Xanthoria fulva} (Hoffm.) Poelt \& Petutschnig (Figs. 13E \& F, 19)


\begin{itemize}
\end{itemize}

Thallus small, up to 9 mm, forming minute rosettes when young, coalescing with adjacent thalli and covering large parts of the substrate, attached by lower parts of lobes and with rhizines. Lobes narrow, 0.2–0.4–0.6 mm (s = 0.1, N = 24, n = 1), thin, plane-somewhat convex, horizontal as young to semierect-erect as mature, richly branched (most distinct on the youngest lobes), tips narrow, pointed or rounded. Upper surface yellow to light orange to orange to dark orange, smooth. Lower surface white, smooth. Rhizines rare to frequent, ± scattered, white-yellow, thin, ± short, mostly pointed, free or attached. Soredia produced at apices of lobes, marginally-submarginally in ± round cortex slits, upper cortex ± persistent, common, small, concolorous with the upper surface or somewhat lighter, c. 30–40–48 µm (s = 4, N = 23). Soralia often appear empty, since the soredia very easily fall out. Photobiont layer ± discontinuous and spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia rare, although abundant on some thalli, maximum diameter 0.7–1.5–3.6 mm (s = 0.7, N = 20), concave-plane or wavy, disk sometimes with central hollow. Thalline margin 0.05–0.1–0.18 mm, smooth, often soredious, rarely with ventral, short, mostly attached rhizines. Algal layer below exciple 38–72–125 µm (s = 22, N = 20, n = 1). Exciple not visible to visible from the outside, thickness below hymenium 0–12–30 µm (s = 9.2, N = 20, n = 1), gelatinous, colourless, with somewhat elongated lumina. Hypothecium 25–37–55 µm (s = 8, N = 20, n = 1), pale brown, irregular, cell walls thin, occasionally with oil droplets. Hymenium 50–75–100 µm
Fig. 19. Known North American distribution of Xanthoria fulva.

(s = 13, N = 20, n = 1). Paraphyses sparsely branched (0–2 times), c. 1.5–2.5 μm wide, tips c. 4–6 μm, mostly with one to several oil droplets in the uppermost cells. Spores ellipsoid, (11.0–)12.8–15.2–17.8(–20.0) μm long (s = 1.8, N = 18), (5.0–)5.7–6.2–7.1 (–9.0) μm wide (s = 0.7, N = 18), septum wide (2.5–)2.9–4.9–6.8(–9.0) μm (s = 1.1, N = 18).

Pycnidia sparse but almost always present, (immersed-) protruding, dark orange to reddish, 0.07–0.18 mm diameter. Conidia bacilliform, (3.0–)3.2–3.6–4.0(–4.5) long (s = 0.2, N = 22), c. 1 μm wide.

Chemistry—Parietin (major), fallacinal (major), emodin, teloschistin (major), and parietinic acid (minor). (Chemosyndrome A3).

Ecology—Mainly corticolous, but also on rock and lignum. Xanthoria fulva is one of two species in this study, the other species being X. polycarpa, with collections from an exceptionally large number of phorophyte genera. The most important phorophytes are Quercus spp., Ulmus spp., and Populus spp., followed by Celtis spp., Fraxinus spp., Acer spp., and Salix spp. The rock type of the saxicolous collections varies, but it seems like calciferous substrates, e.g., basalt and limestone are preferred. Xanthoria fulva is usually collected in open to semi-open habitats but the species seems to be able to also grow in more or less shaded sites.
Distribution—Widely distributed, mainly in the temperate region (mostly lowland localities), with a few boreal localities in the west. In the west, it seems to be somewhat montane. Most collections are made south of the arctic zonobiome (IX). *Xanthoria fulva* only reaches the coast in the northeast and along the Gulf coast. It has the most southeastern occurrence of the species treated here, with one find made in the Florida Panhandle. Also seen from Europe, Himalaya.

Discussion—Specimens of *X. fulva* from different parts of the distribution area differ slightly in morphology. The northern-western morph is generally darker orange and has rather short lobes, while the southeastern morph is lighter orange-yellow and often has longer lobes. I have not yet been able to find any clear-cut characters to distinguish them. Poelt & Petutschnig (1992a) in their discussion of *X. fulva* mentioned an unresolved taxon from North America and it is obvious that they were referring to the southeastern morph of *X. fulva*. In their opinion, it has more or less horizontal lobes, as opposed to *X. fulva* in the strict sense, which should have semi-erect to erect lobes. However, this is a variable character within all geographic populations of the species and more invariable and unequivocal characters should be investigated before a recognition of the morphs is made at any taxonomic level. For details on variation of quantitative characteristics within North American *X. fulva* see the chapter Statistical and numerical treatment.

Previous of the revision by Poelt & Petutschnig (1992a), specimens of *X. fulva* were commonly referred to *X. fallax*. Details on the distinctions from *X. fallax* are discussed under the latter species.

*Xanthoria fulva* is similar to *X. oregana*, but differs by usually having a smaller thallus, more wrinkled lobes, and more homogenous bacilliform conidia within the pycnidia.

*Xanthoria subramulosa* was described by Räsanen (1931) in a footnote to a key to the Estonian species of *Xanthoria*. Both the description and the type corresponds in all aspects with the morphology of *X. fulva*.

So-called macroconidia have previously been reported to occur in *X. fulva* (Poelt & Petutschnig 1992a). These macroconidia seem to be known from the type material, collected in Europe, only, and I have never observed such structures in the North American collections. There is a small probability of it being a case of a lichenicolous fungus.


7. Xanthoria hasseana Rässänen (Figs. 20, 29E)


Thallus small-medium large, up to 30 mm, forming rosettes, often coalescing, ± loosely attached with rhizines visible from above. Lobes narrow-medium wide, 0.3–0.6–0.9 mm (s = 0.1, N = 14, n = 1), ± plane, smooth, ± horizontal, frequently branched, with rounded apices. Upper surface yellow to light orange (to orange), smooth-shiny. Lower surface white, smooth to somewhat wrinkled. Rhizines frequent, white-yellow, medium thick, long, pointed to somewhat frayed (with small foot when attached), free or attached. Photobiont layer ± discontinuous and spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia almost always present, abundant, maximum diameter 1.9–2.5–3.1 mm (s = 0.4, N = 14, n = 1), slightly concave-plane. Thalline margin 0.07–0.15 mm,
smooth, with ± frequent, white-yellow, long, pointed, free or attached, vertical and ventral rhizines. Algal layer below exciple 38–83–150 μm (s = 34, N = 14, n = 1). Exciple sometimes visible from the outside, thickness below hymenium 20–35–63 μm (s = 11, N = 14, n = 1), colourless, gelatinous, cell walls thick, lumina ± elongate. Hypothecium 28–47–73 μm (s = 14, N = 14, n = 1), pale brown, irregular, cell walls thin. Hymenium 73–82–90 μm (s = 5, N = 14, n = 1). Paraphyses usually branched (0–3 times), c. 2 μm wide, tips c. 4–6 μm. Spores ellipsoid, (14.5–)15.4–16.7–18.0 (–20.0) μm long (s = 0.7, N = 14), (6.0–)7.5–8.3–9.5(–10.0) μm wide (s = 0.7, N = 14), septum wide, (4.0–)5.2–6.5–8.5(–10.0) μm (s = 0.9, N = 14).

Pycnidia common, immersed-protruding, darker than the upper surface, 0.10–0.18 mm diam. Conidia bacilliform, (3.0–)3.2–3.5–4.0(–4.25) μm long (s = 0.2, N = 14), c. 1 μm wide.

Chemistry—Parietin (major), fallacinal (major), emodin, teloschistin (major), parietinic acid. (Chemosyndrome A3).

Ecology—Corticolous, with occasional collections on rock and lignum. The corticolous collections are mainly from the trunks of the phorophytes. The most important phorophyte genus by far is Populus, and frequent collections have also been made on Quercus spp., and Aesculus spp. Xanthoria hasseana is mainly found in open to semi-open, nutrient rich habitats.

Distribution—Widespread in the southern boreal and northern temperate regions in the east, throughout California and in the Pacific Northwest. One locality, on the Pribiloff Islands, Alaska (not shown on Fig. 20), is considerably disjunct from the main distribution area. – Only seen from America.

Discussion—Xanthoria hasseana was described by Räsänen (1944), but the name
has not been frequently used. The original material was collected by Hasse in the Santa Monica mountains and filed as "Xanthoria lychnea var. laciniosa" (Hasse 1913). The type material is a little less apotheciate than is usual for X. hasseana. In most species of Xanthoria, however, abundance of apothecia is a variable trait. Xanthoria hasseana is recognized mainly by the frequent, long rhizines, which also occur on the thalline margin, more or less protruding orange pycnidia, and bacilliform conidia. The spores are ellipsoid with a wide septum. Xanthoria montana is very similar in gross morphology, but has spores that are cylindrical to narrowly ellipsoid, with a narrow septum. There are also statistically significant differences in the thickness of the hymenium, hypothecium, and exciple, as well as spore length and spore width. In addition, X. montana seems generally to be somewhat darker orange, and the rhizines are frequently shorter, and may be lacking on the apothecial margin.

Xanthoria hasseana has been confused with X. polycarpa in North America, mainly because both have a rather small thallus and abundant apothecia. Several characters separate them, however, such as the rhizines and the shape of the conidia. For a detailed discussion on X. hasseana and X. polycarpa, see the latter species.


8. *Xanthoria mendozae* Räsänen (Figs. 21, 29B)


Thallus small, up to 25 mm, foliose, forming small patches or extensive colonies covering the substrate, attached ± centrally, by lower parts of lobes, sometimes with supporting rhizines. Lobes ± wide, 0.8–6.0 mm (s = 1.4, N = 22, n = 1) at widest point, short, ± revolute, with or without thin terminal branches, apices curled downwards, mature lobes often ± fan-shaped and wavy. Upper surface yellow to orange, ± pruinose, often cracked near terminal parts. Lower surface dirty white, dull. Rhizines very rare, short, pointed or somewhat frayed, white. Soredia produced from lower surface, yellow to greenish yellow, large, spherical, with a dull, fuzzy surface ("tennis balls"), 46–70–84 µm (s = 10, N = 20). Photobiont layer discontinuous, ± spread throughout the medulla. Medulla reticulate, with short irregular hyphae. Lower cortex prosoplechtenchymatous, thin.

Apothecia not seen.

Pycnidia common, scattered, ± immersed, concolorous with the upper surface, or dark orange when overripe, c. 0.2–0.3 mm diameter. Conidia bacilliform, (3.8–) 4.2–4.6–4.9(–5.8) µm long (0.2, N = 20), c. 1.5 µm wide.

Fig. 21. Known North American distribution of *Xanthoria mendozae*.
Chemistry—Parietin (major), fallacinal, emodin, teloschistin, and parietinic acid. (Intermediate chemosyndrome A/A3).

Ecology—Saxicolous, mainly on volcanic rock, also on granite and sandstone. *Xanthoria mendozae* prefers shaded vertical rock faces, and is sometimes found among bryophytes.

Distribution—In montane areas of western North America, mostly at high altitudes (alt. 400–2900 m.). – Previously known from Mexico, South America, South Africa (map in Kärnefelt 1991).

Nomenclatural note—In the original description the locality data were cited as "Mendoza, Las Heras, Camino internacional, cerca de El Salto, 2,800 m. s. m.". The collection number is identical, however.

Discussion—In the North American herbaria, none of the specimens of *X. mendozae* found were filed under that particular name. *Xanthoria mendozae* has mainly been confused with *X. fallax* and, more recently, with *X. borealis*. *Xanthoria fallax* can be distinguished by having a rosette-formed thallus with ± appressed horizontal lobes, marginal soralia ("bird nests"), much more abundant rhizines, and shorter conidia. For details on the differences between *X. mendozae* and *X. borealis*, see the latter species and the chapter Statistical and numerical treatment.

*Xanthoria mendozae* and *X. borealis* vary in a similar way with regard to lobe structure of young vs. mature thalli. Young lobes are mostly horizontal and narrow, whereas mature lobes are usually more erect and wider. Apotheciate material of *X. mendozae* has never been reported. Apothecia were initially found in a few specimens, but these turned out to belong to fragments of intermixed *X. elegans*. Occasionally, structures resembling apothecial primordia were observed, but no asci or spores, only sterile hyphae, were found when I sectioned them.

Considering the western montane distribution pattern of *X. mendozae*, it is surprising that it does not seem to occur in the Alberta-B.C. border mountains. There is a small possibility that it is overlooked in that particular area.

The anatomy of the lower cortex of *X. mendozae* suggests that it perhaps should not be referred to the genus *Xanthoria*, as anatomy of the lower surface generally has been used as an important character separating genera within Teloschistaceae. The species had, at one time, been transferred to *Teloschistes*, but in recent years it has commonly been accommodated within *Xanthoria* (e.g., Kärnefelt 1989, 1991). *Xanthoria mendozae* and its taxonomic position is under investigation by Kondratyuk & Kärnefelt (1997).


9. Xanthoria montana L. Lindblom spec. nov. (Figs. 22, 29F)

Similis X. hasseanae sed differt sporis brevioribus et angustioribus, septo tenuiore,
(1.0–)1.6–2.2–2.8(–6.0) µm; hymenio, hypothecio, excipulo tenuioribus; lobis angustioribus.


Etymology: Montanus, montane. 

Thallus small-medium large, up to 30 mm, forming rosettes, often coalescing, loosely-firmly attached with rhizines often visible from above. Lobes narrow-medium wide, 0.2–0.3–0.5 mm (s = 0.1, N = 5, n = 1), ± plane, smooth, ± horizontal, frequently branched, with rounded apices. Upper surface yellow to light orange to dark orange, smooth-shiny. Lower surface white, smooth or somewhat wrinkled. Rhizines frequent, white to yellow, medium thick, short-long, pointed to frayed (with small foot when attached), free or attached. Photobiont layer ± discontinuous and spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia almost always present, abundant, maximum diameter 0.9–2.1–3.5 mm (s = 0.7, N = 18, n = 1), slightly concave-plane (-convex). Thalline margin 0.05–0.15 mm, smooth, with ± frequent white-yellow, short-long, pointed, free or attached, vertical and ventral rhizines. Algal layer below exciple 50–73–115 µm (s = 20, N = 18, n = 1). Exciple mostly not visible from the outside, thickness below hymenium 15–20–25 µm (s = 3, N = 17, n = 1), colourless, gelatinous, cell walls thick, lumina ±elongate. Hypothecium 10–23–63 µm (s = 12, N = 18, n = 1), pale brown, irregular, cell walls thin. Hymenium 58–71–95 µm (s = 9, N = 18, n = 1). Paraphyses usually branched (0–3 times), c. 2 µm wide, tips c. 4–7 µm. Spores cylindrical to narrowly ellipsoid, (12.0–)13.0–14.5–15.6–17.0(µm long (s = 0.8, N = 18), (4.5–)5.1–6.2–7.4(–8.0) µm wide (s = 0.7, N = 18), septum narrow (1.0–)1.4–2.2–4.0(–6.0) µm (s = 0.6, N = 18).

Pycnidia ± common, immersed-protruding, darker than the upper surface,
Fig. 22. Known North American distribution of *Xanthoria montana*.

0.06–0.18 mm diameter. Conidia bacilliform, (2.8–)3.2–3.7–4.5(–5.0) µm long (s = 0.4, N = 18), c. 1 µm wide.

Chemistry—Parietin (major), fallacinal (major), emodin, teloschistin (major), parietinic acid. (Chemosyndrome A3).

Ecology—Corticolous, occasional collections on lignum. The corticolous collections are frequently made on the phorophyte trunks, but *X. montana* is not uncommon on twigs. The most important phorophyte genera are *Populus, Quercus,* and *Artemisia.* Other common substrates are *Picea* spp., *Robinia* spp., *Abies* spp., *Pseudotsuga* spp., *Salix* spp., and *Fraxinus* spp. *Xanthoria montana* grows in open, ± dry and nutrient rich habitats.

Distribution—Western montane to temperate areas of North America. Two collections made at a considerable distance from this distribution area were found in the material, one from Alaska (Portage Glacier) and one from Washington, D. C. (but see Discussion).

Discussion—*Xanthoria montana* is very similar to *X. hasseana* in gross morphology, but differs in several characters. Mainly, *X. montana* has significantly smaller, more cylindrical spores with narrow septa, thinner hymenium, hypothecium and exciple, and slightly narrower lobes. In addition, *X. montana* often seems to have a somewhat darker orange upper surface. The rhizines are frequently shorter than those of *X. hasseana,* and the rhizines on the thalline margin are often difficult to see as they are concealed under the apothecia, or may even be lacking on the thalline margin.
With respect to the occurrence of rhizines and the narrow spore septum, _X. montana_ is similar to _X. alfredii_ S. Kondratyuk & Poelt (_X. oxneri_ nom. nud.), which was recently described from Asia by Kondratyuk & Poelt (1997). According to the description as well as isotypes and material seen by me (C, GZU, LD, and UPS), _X. alfredii_ has a considerably larger thallus (up to at least 55 mm) and the lobes are broader, concave, and wrinkled and resembles the lobes in _X. parietina_. The report of _X. alfredii_ from the United States in Kondratyuk & Poelt (1997) refers to an unusually large and luxuriant specimen of _X. montana_. Still, the lobes of this large specimen are narrow and convex similar to _X. hasseana_, and clearly different from the broad, concave lobes of true _X. alfredii_.

_Xanthoria montana_ is one of several taxa that have been confused with _X. polycarpa_ in North America. The main reason is probably that they both have small and apotheciate thalli, and consequently key out as _X. polycarpa_ in most of the existing keys. They differ, however, in several important characters, e.g., the shape of conidia (bacilliform vs. ellipsoid) and morphology of attachment organs (rhizines vs. hapters). For a detailed discussion see _X. polycarpa_.

The single collection of _X. montana_ in Washington, D. C. (as "D. C., Georgetown, Oak Hill Cemetery. 18 Nov 1928 T. Naito") is problematic. The specimen clearly belongs to _X. montana_, and the substrate, smooth dry twigs, is typical for this species. It seems likely that the wrong label was put on the collection. Such mistakes frequently occur in the process of curating collections.


Xanthoria oregana Gyeln. (Figs. 14A & B, 23)

Thallus small-medium large, up to 30 mm, forming ± flattened rosettes, attached by lower parts of lobes and with rhizines. Lobes narrow-wide, 0.4–0.6–1.0 mm (s = 0.2, N = 5, n = 1), thin, ± plane-convex to somewhat inflated, horizontal as young to ± erect as mature, richly branched, tips narrow, ± pointed. Upper surface yellow to orange (to dark orange), wrinkled or smooth-shiny. Lower surface white, smooth to slightly wrinkled. Rhizines ± frequent, ± scattered, white to yellow, medium thick, short-long, pointed or somewhat frayed, free or attached. Soredia produced marginally-submarginally, blastidious from the somewhat crenulate margins or fine and powdery from the lower outer parts of the lobe (which may become almost helmet-shaped), greenish yellow to orange, c. 29–37–47 µm (s = 6, N = 7). Photobiont layer ± discontinuous and spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia very rare, diameter up to c. 3.2 mm (N = 2), concave-plane. Thalline margin c. 0.1 mm, smooth or soredious, rhizines not observed. Algal layer below exciple 50–75 µm. Exciple not visible from the outside, thickness below hymenium 25–38 µm, gelatinous, colourless, with somewhat elongated lumina. Hypothecium 25–38 µm, pale brown, irregular, cells with thin walls. Hymenium 70–80 µm. Paraphyses sparsely branched (0–2 times), c. 1.5–2 µm wide, tips c. 2–4 µm. Spores ellipsoid, 16.0–16.5–17.0 µm long (s = 0.7, N = 2), 7.6–8.1–8.7 µm wide (s = 0.6, N = 2), septum wide, 6.2–6.6–7.0 µm (s = 0.6, N = 2).

Pycnidia rare to common, sometimes in groups, immersed-protruding, darker coloured than the upper surface to reddish, 0.1–0.2 mm diameter. Conidia variable within the pycnidium, ellipsoid to oblong ellipsoid to bacilliform, or irregular, (3.0–)3.4–3.6–3.8 (–4.0) µm long (s = 0.2, N = 7), c. 1–1.5 µm wide.

Chemistry—Parietin (major), fallacinal, emodin, teloschistin, and parietinic acid.
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Fig. 23. Known North American distribution of *Xanthoria oregana*.

(Chemosyndrome A; the concentration of teloschistin sometimes approaches A3).

Ecology—Corticolous, or occasionally on lignum, rock, or soil. When corticolous, *X. oregana* is about twice as common on the trunks of the phorophytes as on twigs. The most important phorophyte genus by far is *Quercus*, followed by *Artemisia* and *Populus*. Saxicolous collections are from various types of rock.

Distribution—Western coastal and montane areas in North America. The coastal localities lie within the mediterranean zonobiome (IV) and the montane localities lie within the arid-temperate zonobiome (VII).

Discussion—*Xanthoria oregana* is morphologically variable and difficult to characterize in a clear-cut and simple way. However, it is the only species in this treatment which has conidia with various shapes in the pycnidia (Fig. 3C). The morphological variation ranges from rather appressed yellow thalli with wrinkled lobes and marginal-submarginal soredia (corresponding to the type specimen) to orange thalli with semi-erect to erect, wrinkled-smooth lobes and soredia produced from almost helmet-shaped lobe apices. Lobe tips are often down-turned and apothecia are mostly lacking, or very sparse. In California *X. oregana* often grows together with *X. tenax* and in the montane parts of the distribution range it often grows with *X. montana*.

If pycnidia are lacking or the variation in conidial shape is less pronounced than usual, *X. oregana* may be difficult to separate from *X. fulva* and, sometimes, *X. ulophyllodes*. Compared to *X. fulva*, *X. oregana* mostly has a larger rosette-forming thallus with wider, longer and more wrinkled lobes. In contrast to *X. fulva*, *X. oregana* does not develop rounded "bird nests" with soredia at the lobe apices, and if the upper cortex persists it is helmet-shaped, rather than bent upwards. Compared to *X. ulophyllodes*, *X. oregana* has a thinner thallus with more wrinkled lobes, and not as
frequent soredia, which never becomes laminal.

According to Almborn (1963), X. oregana could be accommodated within the normal variation of X. candelaria. It must be remembered, however, that the concept of X. candelaria was considerably wider at that time. Xanthoria oregana can be separated from X. candelaria by having wider lobes, conidia with different shapes, and more frequently horizontal lobes.


11. Xanthoria parietina (L.) Th. Fr. (Figs. 13D, 24)


Thallus large, up to 100 mm, forming rosettes, sometimes coalescing, ± firmly
Fig. 24. Known North American distribution of *Xanthoria parietina*. A triangle denotes that the species is known from one locality only in the state, but the exact position is unknown.

attached with hapters. Lobes wide, 0.7–1.6–3.2 mm (s = 0.6, N = 30, n = 1), ± concave, often somewhat wrinkled, ± horizontal, sparsely branched, with rounded, wide apices. Upper surface yellow to light orange (to orange), ± smooth. Lower surface white, wrinkled. Hapters scattered-frequent, white, thick, short, pointed in early stages, attached with a terminal foot. Photobiont layer more or less continuous near the upper cortex. Medulla with hyphae in bundles, cells regular, elongate.

Apothecia almost always present, ± abundant, maximum diameter 1.1–2.6–8.0 mm (s = 1.3, N = 30, n = 1), concave-plane or folded, sometimes wavy. Thalline margin 0.07–0.12 mm, smooth to crenulate, with very short anchoring hapters. Algal layer below exciple 50–80–113 µm (s = 18, N = 30). Exciple often visible from the outside, thickness below hymenium 10–25–55 µm (s = 11, N = 30, n = 1), colourless, strongly gelatinous, cell walls thick, lumina elongate. Hypothecium 15–30–48 µm (s = 9, N = 30), pale brown, irregular, cell walls thin. Hymenium 53–73–90 µm (s = 9, N = 30, n = 1). Paraphyses sparsely branched (0–3 times), 1.5–3 µm wide, tips c. 4–7 µm, oil droplets sporadically observed. Spores ellipsoid, (12.0–)12.9–14.8–16.0 (–17.5) µm long (s = 0.7, N = 30), (5.0–)5.9–7.9–8.7(–10.0)µm wide (s = 0.6, N = 30), septum wide, (3.0–)3.8–6.2–7.9(–10.0) µm (s = 0.8, N = 30).

Pycnidia common, sometimes sparse, immersed or somewhat protruding, usually slightly darker pigmented than the upper surface, 0.07–0.17 µm diameter. Conidia ellipsoid to ± oblong ellipsoid, (2.5–)2.7–3.1–3.6(–4.0) µm long (s = 0.2, N = 29), c. 1–1.5 µm wide.
Chemistry—Parietin (major), fallacinal, emodin, teloschistin, and parietinic acid. (Chemosyndrome A).

Ecology—Corticolous and saxicolous, additional collections have been made on lignum, roof, mussel shells etc. More than one third of the corticolous collections lacked information about the phorophyte, but the most important phorophyte genera seem to be *Populus*, *Ulmus*, and *Salix*. Collections from the southern parts of the range are very frequently from twigs, e.g., of the Solanaceous shrub, *Lycium*. Along the Atlantic coast, *X. parietina* is very common on seashore rocks, as well as on anthrophogenous substrates, for example, walls, tombstones, and cement.

Distribution—Coastal regions along the Atlantic and the Pacific coasts, and also known from scattered localities along the Gulf of Mexico, in Louisiana and southeastern Texas. In the east it extends inland to the Great Lakes (Lake Ontario). The southern distribution range along the Californian and Texan coasts continues southwards into Mexico. – Widespread, also seen from Europe, Africa, Asia, Australia, America.

Nomenclatural note—Jørgensen et al. (1994) designated the Dillenian illustration (Dillenius 1741) cited by Linnaeus in Species plantarum 2 (1753) as lectotype and selected the corresponding specimen in the Dillenius herbarium (OXF) as epitype. This was done according to Art. 9.7 in the Tokyo Code (Greuter et al. 1994).

Discussion—Much has been written about *X. parietina*, especially about its variable morphology. All species in *Xanthoria* are known to be variable, but *X. parietina* seems to have attracted the most attention, probably because of its large and conspicuous thallus. Over a long period of time, many varieties and forms were described and named (see, e.g., Hillmann 1920). At the present time, however, most authors accept a reasonable amount of variation with regard to gross morphology, without necessarily assigning aberrant morphotypes any taxonomic rank. Still, very little is known about the mechanisms of the morphological plasticity. I found that specimens from the northeastern part of the range differed slightly from the specimens collected in the southern parts regarding thallus and lobe morphology. In addition, small differences in spore size could be detected. It was impossible, however, to establish with certainty whether the differences found were consequences of genetic differences between geographically separated populations, or simply a result of the thalli growing on different substrate types, i.e., bark and rock (eastern populations) vs. twigs (southern populations). Morphological variation may be a combination of these and other factors (Reyes et al. 1996). For further details of the morphological variation within *X. parietina* see the chapter Statistical and numerical treatment.

In Europe, *X. parietina* is a widespread and well-known species. The limited distribution range in North America has puzzled some authors (Degelius 1940, Hale 1955). Actually, the distribution pattern is similar to that of *X. polycarpa*, only much more restricted. Some reports of *X. parietina* from California have been regarded as probable misidentifications (Tucker & Jordan 1978), and consequently the species was thought to be restricted to northeastern North America (Noble 1982). However, some reports, both made earlier and later, have proven correct, e.g., Baltzo (1989). *Xanthoria*
parietina was recently reported as a probable recent arrival in western Canada (Goward et al. 1996). Because the scattered collections made in the northern part of the western distribution area are all from anthropogenous substrates, viz., planted trees in populated areas, it is commonly believed that X. parietina is introduced by man. Considering that X. parietina frequently grows on anthropogenous substrates in all other parts of its world distribution area as well, the possibility that the species has spread naturally from southern populations along the Pacific coast can not be ruled out. Habitats created by man could simply be the best suited sites for the early, primary establishment of X. parietina.

_Xanthoria parietina_ has been confused with several other species in North America, including _X. polycarpa, X. elegans, X. tenax_, and _X. fallax_. _Xanthoria parietina_ is recognized by having a rather large esorediate thallus, ± firmly (but not very tightly) attached with short hapters, wide and ± concave wrinkled lobes, and ellipsoid conidia.

Occasionally, collections of _Teloschistes chrysophthalmus_ (L.) Th.Fr. have been filed under _X. parietina_. The fact that they both have large and abundantly apotheciate thalli probably contributes to such mistakes. _Teloschistes chrysophthalmus_ has a fruticose growth form (but specimens may become flattened in the herbarium), prosoplechtenchymatic cortex, more or less frequent fibrils (cilia) on the thalline margin of the apothecia, and longer, bacilliform conidia.


Pennsylvania. Lancaster City, 1886, Eby (US).


12. Xanthoria polycarpa (Hoffm.) Th.Fr. ex Rieber (Figs. 14C, 25)


Thallus small, up to 25 mm, forming distinct to coalescing cushions, attached with wrinkles and hapters from the lower surface. Lobes narrow, 0.2-0.4-0.7 mm (s = 0.1, N = 30, n = 1), plane-convex, mostly horizontal, sometimes slightly raised, richly branched, with narrow apices. Upper surface yellow to light orange to bright orange, smooth, dull-shiny. Lower surface white, ± wrinkled. Hapters scattered, white, thin-thick, short, attached (free when young), often with small foot. Photobiont layer discontinuous and spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia frequent, mostly very abundant, maximum diameter 1.0–1.9–4.5 mm (s = 0.8, N = 30, n = 1), concave-plane or folded. Thalline margin 0.05–0.09–0.18 mm, smooth or sometimes crenulate. Algal layer below exciple 50–75–123 µm (s = 18, N = 30, n = 1). Exciple sometimes visible from the outside, thickness below hymenium 0–8–28 µm (s = 9, N = 30, n = 1), colourless, mostly consisting of not more than a few layers of hyphae, gelatinous, cell walls thick, lumina elongate. Hypothecium 18–33–50 µm (s = 10, N = 30, n = 1), pale brown, irregular, cell walls thin. Hymenium 43–68–90 µm (s = 10, N = 30, n = 1). Paraphyses sparsely branched (0–1(–2) times), 1.5–2 µm wide, tips c. 5–8 µm, occasionally with one to several oil droplets in the uppermost cells. Spores ellipsoid, (10.0–)11.3–15.0–(15.6) µm long (s = 1.0, N = 30) (4.0–)5.4–6.7–7.9(–9.0) µm wide (s = 0.6, N = 30), septum (2.0–)2.8–4.2–6.2 (–7.0) µm (s = 0.8, N = 30).
Pycnidia common, immersed in thallus, concolorous with the upper surface or slightly darker, 0.05–0.18 mm diameter. Conidia ellipsoid, (2.0–)2.2–2.5–2.9(–3.0) μm long (s = 0.2, N = 30), c. 1–1.5 μm wide.

Chemistry—Parietin (major), fallacinal, emodin, teloschistin, and parietinic acid. (Chemosyndrome A).

Ecology—Mainly corticolous with by far the most collections made on twigs, but also common on rock and lignum. Xanthoria polycarpa is one of two species in this study, the other species being X. fulva, with collections from an exceptionally large number of phorophyte genera. Corticolous specimens of X. polycarpa were collected most frequently on Picea, and almost invariably on the twigs. Other important phorophytes are Quercus spp., Abies spp., Pseudotsuga spp., Acer spp., and Pinus spp. The saxicolous collections are chiefly made on seashore rock, exposed to bird manure, by the Atlantic coast. The habitats where X. polycarpa occurs are generally open or semi-open, nutrient rich and more or less humid.

Distribution—Arctic, boreal, and western temperate regions. Scattered collections are made in the arctic. Judging from the frequency of collections there seems to be a tendency for X. polycarpa to prefer regions that are more or less oceanic (cfr. X. parietina). – Also seen from Europe.

Nomenclatural note—In the protologue of Lobaria polycarpa, Hoffmann (1796) included Ehrhart’s Pl. Crypt. Linn. 136. Because the specimen in GOET is likely to have been available to Hoffmann, it is selected here as the lectotype of X. polycarpa.

Discussion—In North America, the name X. polycarpa has commonly been used
for non-sorediate, richly apotheciate specimens of *Xanthoria* with ± small thalli. Thus, in herbarium collections, specimens of *X. hasseana*, *X. montana*, *X. polycarpa*, and *X. tenax*, and even *X. parietina*, are filed under “*X. polycarpa*”. For many recent American lichenologists, the confusion over *X. polycarpa* can probably be traced to the treatments of Rudolph (1955) or Hale (1969).

The name *X. ramulosa* has often been used for specimens with narrow lobes, viz., corresponding to *X. polycarpa* in the sense of European authors. This confusion probably arose already when Tuckerman (1882) first described “*Teloschistes ramulosus*” and it has persisted to the present time, for example in floristic treatments. Du Rietz (1922) erroneously reported presence of soredia for *X. ramulosa*. I have not with certainty been able to study the specimens on which Du Rietz based the report, but it may be a case of misidentification. Material from coastal California called *X. ramulosa* in the investigation by Rudolph (1955) corresponds to *X. hasseana* in the present treatment, and is actually morphologically almost identical with the type of *X. hasseana*. The material called *X. polycarpa* by Rudolph (1955) is more heterogeneous, and includes specimens from various taxa.

*Xanthoria polycarpa* is distinguished from *X. hasseana* and *X. montana* mainly by the lack of true rhizines on the lower surface and thalline margin and also by having ellipsoid conidia.

*Xanthoria polycarpa* is somewhat similar to *X. tenax* as well; both species have ellipsoid conidia and ± small thalli lacking rhizines. However, *X. tenax* has a flat, ± thick thallus with somewhat broader lobes that are closely attached to the substrate by the entire lower surface except for the outermost parts below the lobe apices.

The frequent occurrence of *X. polycarpa* on manured seashore rock along the Atlantic coast is interesting. In Europe, as it is throughout its entire range in North America, this species mainly occurs on twigs, and is only rarely collected on rock. In several of the European floras, *X. polycarpa* is not reported as growing on rocks, but Lyne (1921) for example noted that it occurs rarely on this substrate. The morph growing on seashore rock together with a specimen on lignum were described as *X. polycarpa* var. *maritima* by Lamb (1954). In the area, *X. polycarpa* grows on seashore rock as well as twigs of coniferous trees adjacent to the shore like *X. parietina* (although the latter usually prefers the trunks of the trees). I believe that the slight differences in thallus morphology are a consequence of the different texture and space provided by the substrates (twigs vs. rock). Thus, I prefer not to distinguish this form at any taxonomic rank. For further details regarding the intraspecific variation of *X. polycarpa* see the chapter Statistical and numerical treatment.

*Xanthoria alaskana* was described from Alaska a few years ago (Talbot et al. 1992) and was separated from *X. polycarpa* by having a bluish-grey colour and lesser abundance of apothecia. The type and additional material deposited in WIS that I have seen evidently belong to *X. polycarpa*, although the thalli are more or less pigment deficient and scrappy. Reports of more or less grey thalli in *X. polycarpa* are common (e.g., Hillmann 1922, Thomson 1984). The deficiency of yellow (anthraquinone)
pigments is usually thought to be a result of the thallus growing in shade (Hillmann 1922, Hill & Woolhouse 1966, Richardson 1967). In some cases, the greyish thallus may originally have been a living Physcia thallus, now being attacked by a Xanthoria, which primarily exhibits its yellow pigments on the apothecial disks and pycnidia (Ott 1987).


Thallus small–large, up to 35 mm, forming rosettes, sometimes coalescing. Lobes narrow to wide, 0.4–1.1 mm (s=0.2, N=20, n=1), plane-convex, horizontal, branched, apices occasionally ± concave. Upper surface yellow to ± bright orange, ± rough. Lower surface white, smooth-wrinkled. Haplers scattered, white, thick, very short and ± tightly anchoring the thallus. Soredia produced laminally, coloured as the upper cortex or lighter, initiated as small isidia, which later break up and become crater-like soralia, eventually coalescing and covering the central thallus parts. Photobiont layer more or less continuous, near the upper cortex. Medulla with hyphae in bundles, cells regular, elongate.

Apothecia very rare, found sparsely on a few thalli, maximum diameter 0.6–1.1–1.9 mm (s=0.4, N=6, n=1), slightly concave-plane or convex. Thalline margin 0.07–0.15 mm, smooth-crenulate. Algal layer below exciple 75–86–100 µm (s=10, N=4, n=1). Exciple mostly visible from the outside, thickness below hymenium 25–29–38 µm (s=6, N=4, n=1), gelatinous, colourless, cell walls thick, lumina elongate. Hypothecium 23–40–50 µm (s=12, N=4, n=1), colourless, irregular, cell walls thin. Hymenium 63–72–88 µm (s=11, N=4, n=1). Paraphyses mostly sparsely branched (1–3 times), c. 2 µm wide, tips 5–7 µm, rarely with small oil

Fig. 26. Known North American distribution of Xanthoria sorediata.
droplets. Spores ellipsoid, (11.0–)12.8–13.1–13.5–(15.0) µm long (s = 0.3, N = 4),
(5.5–)6.2–7.2–8.1–(9.0) µm wide (s = 0.9, N = 4), septum ± narrow, (2.0–)3.0–3.4–
4.0–(5.0) µm (s = 0.4, N = 4).

Pycnidia usually abundant, immersed in thallus, usually among the soralia,
somewhat darker than the upper surface, c. 0.07–0.13 mm diameter. Conidia ellipsoid,
(2.2–)2.6–2.9–3.0–(3.3) µm long (s = 0.1, N = 19), c. 1–1.5 µm wide.

Chemistry—Parietin (major), fallacinal, emodin, teloschistin, and parietinic acid.
(Chemosyndrome A).

Ecology—Usually saxicolous, but occasional collections have been made on
antlers and bark (Picea sp.). Of the saxicolous collections that have the type of rock
indicated on the label, the majority are made on calciferous rock, e.g., dolomite or
limestone. The habitats are mainly exposed and nutrient rich. Some collections (less
than 10%) grew on vertical, ± shaded rock faces.

Distribution—Widespread, mainly in the arctic-alpine and boreal regions. The
southern extensions follow the western mountain ranges, and are invariably from high
elevations. – Widespread.

Discussion—This treatment of X. sorediata should be regarded as tentative, as
material from only a few herbaria has been studied.

Of about 100 examined specimens, less than 10 were apotheciate. Mature spores
were found in only four specimens. The reason for the weak spore production is
unclear. It is a well-known fact, however, that sorediate as well as isidiate lichen taxa
seldom produce fruiting bodies, and when such structures are developed they are often
imperfect (e.g., Poelt 1970). The production of conidia, on the other hand, seems
normal, and pycnidia are usually common and easily found among the soralia.

Xanthoria sorediata was listed as a secondary species, although questionable, to X.
elegans in the paper introducing the species pair concept (Poelt 1970). In fact, some
morphological characters apart from the soredia separate X. elegans and X. sorediata,
e.g., general lobe morphology. The differences in secondary chemistry found by Arnold
& Poelt (1995) were not detected in my investigation. The ecology of X. sorediata is
similar to that of X. elegans, but tends to be more restricted, which is probably the
reason why X. sorediata is rarer although their main distribution areas completely
overlap. The morphology of the thallus and lobes varies in a similar way to that of
X. elegans. For example, when the lichen grows among bryophytes, especially in moist
conditions, the lobes tend to become more or less inflated and erect. It is sometimes
possible to observe this variation within one specimen, when parts of it grow directly
on rock, and other parts grow into a bryophyte cushion.

For a detailed discussion on the ontogeny of the soredia Giralt et al. (1993) can
be consulted.

Selected specimens examined. CANADA. ALBERTA. Banff Nat. Park, near upper Victoria
Glacier, 1950, Imshaug 6896 (LD). BRITISH COLUMBIA. Kutcho Creek valley, northern BC, 1979,
NEW BRUNSWICK. Albert Co., 1981, Gowan & Wallace 4724 (CANL). NEWFOUNDLAND.
14. *Xanthoria tenax* L. Lindblom spec. nov. (Figs. 14D, 27)

Thallus pusillus, orbicularis, impolitus, luteolus ad aurantiacus, esorediatus. Lobi appressi, non nisi sub apice corticati, rhizinae paucae, brevissimae. Apothecia frequentia praesertim in centro thalli. Sporae polaridiblastae, bacilliformes, (10.5-)12.9-14.3-15.7(-18.0)µm longae (4.5-)5.2-5.9-6.6(-8.0)µm crassae, septum (2.5-)3.6-4.6-5.6(-8.0)µm. Conidia ellipsoidea, (2.5-)2.7-2.8-2.9(-3.2)µm longa c. 1-1.5µm crassa.

Type: Mexico, “Estado de Baja California: ca 1 km W of route 1 in arroyo just N of Arroyo San Regis, 28°51’N 114°03’W, on Lycium.” 1990, Nash 29556, Nash : Lich Exs ASU 150 (ASU, holotype; GZU, H, LD, O, WIS, isotypes).

Etymology: *Tenax*, holding fast, tough.

Thallus small, 5-11-25 mm (s = 4, N = 16, n = 1), forming flat, appressed, ± distinct rosettes. Lobes narrow, 0.2-0.4-0.7 mm (s = 0.2, N = 15, n = 1), plane, thin-thick, horizontal, closely appressed to the substrate, sparsely branched, with rounded to fan-shaped tips. Upper surface yellow to orange, slightly-heavily pruinose. Lower surface attached to the substrate, lower cortex lacking, free, with a lower cortex near lobe apices, white, smooth. Hapters very rare, situated submarginally and near lobe apices, white, very short. Photobiont layer more or less continuous near the upper cortex.

Apothecia frequent, usually abundant, maximum diam. 1.1-1.5-2.7 mm (s = 0.5, N = 16, n = 1), slightly concave-plane, disk ± pruinose. Thalline margin 0.05-0.13 mm, smooth-crenulate. Algal layer below exciple 50-84-113 µm (s = 23, N = 16, n = 1). Exciple visible from the outside, thickness below hymenium 8-31-75 µm (s = 20, N = 12, n = 1), gelatinous, colourless, cells with thick walls and elongate lumina. Hypothecium 25-41-98 µm (s = 18, N = 16, n = 1), colourless to pale brown, irregular,
cell walls thin. Hymenium 60–78–95 µm (s = 10, N = 16, n = 1). Paraphyses ± sparsely branched (0–3 times), 1.5–2 µm wide, tips 4–6 µm. Spores narrow, cylindrical, (10.5–)11.2–14.3–16.8(–18.0) µm long (s = 1.4, N = 16), (4.5–)5.0–5.9–7.4(–8.0) µm wide (s = 0.7, N = 16), septum wide (2.5–)2.9–4.6–5.8(–8.0) µm (s = 1.0, N = 16).

Pycnidia common, immersed, slightly darker than the upper surface, 0.07–0.18 mm diam. Conidia ellipsoid, (2.5–)2.6–2.8–3.0(–3.2) µm long (s = 0.1, N = 15), c. 1–1.5 µm wide.

Chemistry—Parietin (major), fallacinal (major or not), emodin, teloschistin (major or not), and parietinic acid. (Chemosyndrome A and A3).

Ecology—Corticolous, mostly on twigs, and lignicolous. Known phorophytes include Quercus lobata, Q. douglasii, Lycium californicum, Ceanothus sp., Cupressus sp., Liquidambar sp., Salvia sp., and Tamarix sp. Usually, X. tenax grows on smooth substrates in open to semi-open, exposed habitats; mainly oak savannah and coastal shrub.

Distribution—The coast as well as valleys and foothills of California, the northernmost collections being from the Sacramento River valley. – Also seen from Mexico.

Discussion—Xanthoria tenax varies morphologically with regard to thallus thickness and pruinosity. Specimens collected on thin twigs, e.g., of Lycium or Ceanothus, are generally thinner and lighter yellow than specimens collected on, for example, lignum or bark of Quercus. This species probably corresponds to the taxon mentioned in Hale & Cole (1988, p. 130) growing on lower branches of oaks in the San Joaquin Valley.

Xanthoria tenax differs from all other species treated in this work by the almost entire lack of a lower cortex. Furthermore, it is the only species known in which both chemosyndromes A and A3 have been detected (cfr. Soechting 1997). The occurrence of two chemosyndromes could suggest that X. tenax should be split into two taxa. To date, however, I have not succeeded in finding any other characters supporting the recognition of two taxa based on the chemosyndromes.

The lack of a continuous lower cortex may suggest that X. tenax should not be accommodated in the genus Xanthoria in the present sense, but rather in Caloplaca.
Some species of Caloplaca in North America are similar to X. tenax in having a lower cortex only under the outermost lobe tips (Arup 1995a). Furthermore, X. tenax resembles taxa in the C. lobulata group in some aspects, e.g., the almost entire lack of a lower cortex and having ellipsoid conidia. Hapters, however, are unknown in the C. lobulata group (Steiner & Poelt 1982). The relationships of X. tenax and the taxa in the C. lobulata group remain to be examined. In any event, both Caloplaca and Xanthoria are currently being re-evaluated on genus level and so, even if I would describe X. tenax within Caloplaca, there is a distinct possibility that it would have to be recombined in a near future.

Some characters mentioned in the description of the South American taxon X. andina Rásänen (Rásänen 1939) correspond to X. tenax, e.g., the small appressed thallus and occurrence of pruina. Unfortunately, I have not had the opportunity to study the type of X. andina since it has not been available in herb. H during the time of my study. However, according to Söchting (in litt.) X. andina has an entirely different chemosyndrome, which is characterized by having fragilin as the major substance.


15. **Xanthoria ulophyllodes** Rásänen


Thallus medium large, up to 32 mm, forming rosettes, frequently coalescing. Lobes narrow to medium wide, 0.3–0.9–1.4 mm (s = 0.06, N = 21, n = 1), ± plane, horizontal
or mostly slightly raised (showing the rhizines), branched, with rounded, wide tips. Upper surface yellowish orange to light orange to orange, smooth to shiny. Lower surface white, smooth to somewhat wrinkled. Rhizines very frequent, white-yellow, medium thick, short-long, pointed or somewhat frayed, free or attached. Soredia blastidious, produced marginally-submarginally, rare (on young thalli) to common, also laminal on well developed thalli, beginning as small holes in the upper cortex, gradually coalescing and covering large parts of the upper surface, ± irregular, with ± smooth surface, coloured as the upper surface or slightly lighter, c. 39–47–51 \( \mu m \) (s = 4, N = 9). Photobiont layer ± discontinuous and spread throughout the medulla. Medulla reticulate, with short irregular hyphae.

Apothecia rare, abundant on some thalli, maximum diameter. 1.0–1.8–2.7 mm (s = 0.5, N = 21), (slightly concave-)plane-convex, disk sometimes wavy. Thalline margin 0.05–0.13 mm, ± smooth, often with soredia, usually with vertical or ventral, white-yellow, pointed rhizines. Algal layer below exciple 50–77–125 \( \mu m \) (s = 24, N = 1, n = 10). Exciple not visible from the outside, thickness below hymenium 20–45–75 \( \mu m \) (s = 15, N = 20), gelatinous, colourless, cell walls thick, lumina elongate. Hypothecium 28–40–68 \( \mu m \) (s = 10, N = 20, n = 1), pale brown, irregular, cell walls thin. Hymenium 50–69–80 \( \mu m \) (s = 7, N = 20). Paraphyses sparsely branched (0–2 times), 1.5–2.5 \( \mu m \) wide, tips c. 4–7 \( \mu m \). Spores ellipsoid, (12.5–)13.8–15.0–16.3(–18.0) \( \mu m \) long (s = 0.7, N = 16), (6.0–)6.8–7.3–7.9(–10.0) \( \mu m \) wide (s = 0.3, N = 16), septum ± wide, (2.5–) 3.3–3.9–5.2(–6.0) \( \mu m \) (s = 0.5, N = 16).

Pycnidia common, immersed in thallus or slightly protruding, darker than thallus, 0.10–0.13 \( \mu m \) diameter. Conidia bacilliform, sometimes almost oblong ellipsoid,
Fig. 29. A. *X. borealis*, 1943, Santesson 3481 (UPS holotype); B. *X. mendozae*, 1987, Rosentreter 4683 (GZU); C. *X. falax*, 1993, Lindblom L143 (LD); D. *X. ulophylloides*, 1974, Thomson 18320 (H); E. *X. hasseana*, 1976, Wetmore 26497 (MIN); F. *X. montana*, 1993, Lindblom L273 (LD). Bar = 2 mm.
L. LINDBLOM: The genus Xanthoria in North America

(2.5–)2.9–3.2–3.6(–4.0) µm long (s = 0.1, N = 19), c. 1 µm wide.

Chemistry—Parietin (major), fallacinal (major), emodin, teloschistin (major), and parietinic acid. (Chemosyndrome A3).

Ecology—Mainly corticolous on the trunks of trees, occasionally on rock, lignum, and twigs. The most important phorophytes are *Populus* spp., *Quercus* spp., and *Ulmus* spp. Other substrates include *Fraxinus* spp., *Tilia* spp., and *Acer* spp. The saxicolous specimens occurred on various kinds of rock, but rock type was not indicated on the labels of most collections. *Xanthoria ulophyllodes* seems to have a habitat similar to that of *X. fallax*, being found in open to semi-open, dry to somewhat moist, and nutrient rich sites.

Distribution—Mainly a north temperate species with eastern extensions and scattered western extensions. *Xanthoria ulophyllodes* does not reach north of zonobiome VIII. Also seen from Europe, Asia (Himalaya).

Discussion—The soredia of *X. ulophyllodes* are basically produced from the lobe margins. Small (young) thalli have very sparse soredia, but on mature thalli they are usually quite common. On large and luxuriant thalli soredia may dominate large parts and also occur laminally. The laminal soralia are initiated as small distinct holes in the cortex. Soredia are produced in an eruptive way and eventually the laminal soralia coalesce to cover large parts of the thallus. Thus, *X. ulophyllodes* is the only North American species that regularly can have soredia on the upper surface of the lobes (apart from the isidia breaking up into soredia of *X. sorediata*).

Poelt & Petutschning (1992a) distinguished two varieties of *X. ulophyllodes*, var. *ulophyllodes* (which should correspond to the taxon on North America) and var. *subsorediosa* (which should occur in Asia). From the description in Poelt & Petutschning (1992a) it can be understood that *X. ulophyllodes* var. *subsorediosa* needs to be further investigated.

*Xanthoria ulophyllodes* is most similar to *X. fallax*. These species are primarily distinguished by the morphology of the soralia and soredia but several other characters support the separation (see the latter species and the chapter Statistical and numerical treatment). The distribution areas overlap, although *X. ulophyllodes* generally seems to be rarer than *X. fallax*. Additionally, *X. ulophyllodes* is more rarely found with apothecia. It was difficult to find mature apothecia to carry out studies of apothecial characters and spore measurements in this treatment. Furthermore, apothecia that superficially appeared healthy and mature often turned out to contain few, undeveloped spores. Most apothecia studied were found in collections from Minnesota, which is not surprising considering the fact that more than half of the number of collections were collected in that particular state.


EXAMINED EXSICCATES OF NORTH AMERICAN MATERIAL

This chapter comprises a list of the exsiccates that I have seen. The exsiccates included in the list were listed in Lynge (1915, 1939) or Sayre (1969). I have also included Anderson's "Lichens of western N. Am." , Baker's "Pacific Slope Lichens", Brodo's "Lichenes Canadenses Exsiccati", Nash's "Lich. Exs. ASU", and University of California's "Lichens of Oregon". Of these, "Lichens of Oregon" is listed in Brodo & Hawksworth (1978). Sayre (1969) mentioned "Pacific Slope Lichens", but she did not state clearly whether it should be considered an exsiccate or not. Macoun's "Canadian Lichens" was listed in Lynge (1915, 1939) and Sayre (1969), but I have excluded it for several reasons (see Culberson 1959, Brodo & Hawksworth 1978).

The number of each exsiccate is followed by the name under which it was issued, the herbaria in which I have seen it, and finally my determination of the specimen seen. Herbarium is indicated only once, regardless if more than one specimen was seen.

Anderson: Lich. western N. Am.
18. Gasparinina sorediata (COLO, O), X. sorediata
37. Xanthoria candelaria (COLO), X. fulva

Baker: Pacific Slope Lichens
719. Theloschistes lychnes f. laciniosa (NY, US, WIS), X. hasseana
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148. Xanthoria candelaria (COLO, GZU, H, LD, STU, UBC, US, WIS), X. candelaria
223. Xanthoria cfr. papillifera (COLO, GZU, H, LD, STU, UBC, WIS), X. elegans
224. Xanthoria parietina (COLO, GZU, H, LD, O, STU, UBC, WIS), X. parietina

Clements & Clements: Cryptogamae Formationum Coloradensium
109. Theloschistes polycarpus (NY, US), X. montana
521. Theloschistes lychneus (COLO, US), X. oregana
522. Theloschistes parietinus, var. (COLO, NY, US), X. montana

6. Theloschistes parietinus (H, US, WIS), X. parietina
7. Theloschistes polycarpus (C, US), X. fulva
99. Theloschistes concolor (a correction label was sent out: Theloschistes polycarpus) (WIS), X. hasseana
342. Theloschistes polycarpus (C, COLO, H, US, WIS), X. hasseana

20. Theloschistes parietinus (COLO, H, US), X. parietina
21. Theloschistes lychneus (COLO, H, US), X. fulva
95. Placodium elegans (LD), X. elegans

Farlow Herb.: Reliquiae Tuckermanianae
92. Theloschistes parietinus var. polycarpus (BP, C, LD, NY, O, US, WIS), X. hasseana

8. Xanthoria polycarpa (C, COLO (with X. fallax), LD (with X. fallax), WIS), X. montana
124. Xanthoria fallax (COLO, H, LD), X. ulophyllodes
125. Xanthoria sorediata (COLO, LD), X. sorediata

Hasse: Lich. Exs. ex Herb. Hasse, relict (by Plitt)
123. Xanthoria lychnea laciniosa (COLO), X. hasseana
124. Xanthoria lychnea polycarpa (COLO, O), X. hasseana
125. Xanthoria lychnea pygmaea (COLO), X. candelaria
181. Caloplaca elegans (O), X. elegans

Howe: Lich. Novae Angliae
24. Theloschistes parietinus (H), X. parietina
42. Theloschistes lychneus (COLO, H), X. fulva

2969. Xanthoria ramulosa (C, COLO, H, LD, O), X. hasseana
3920. Xanthoria fallax (GZU, H, LD, US), X. fallax

151. Theloschistes parietinus (COLO, H, O, US), X. parietina
158. Theloschistes lychneus (COLO, H, US), X. fulva
246. Placodium elegans (O), X. elegans
263. Theloschistes polycarpus (C, COLO, O), X. polycarpa

Merrill: Lich. Exs. (2nd ser.)
117. Caloplaca elegans (UBC), X. elegans
133. Xanthoria parietina (COLO, UBC, US, WIS), X. parietina
Nash: Lich. Exs. ASU
199. X. cf. polycarpa (LD, O, STU), X. montana

12. Xanthoria parietina (a correction label was sent out: X. fallax) (COLO, LD, US), X. fulva
62. Xanthoria fallax (LD), X. fallax

Univ. of California: Lichens of Oregon [=California Fungi]
1324. Xanthoria candelaria (COLO, H, NY, UPS), X. fulva
1325. Xanthoria polycarpa (H, NY, PC, UPS, WIS), X. polycarpa

198. Xanthoria candelaria (H, LD, US), X. fulva

Weber: Lich. Exs. COLO
151. Xanthoria polycarpa (C, COLO, GZU, H, LD, O, STU, US, WIS), X. montana
188. Xanthoria polycarpa (C, COLO, GZU, H, LD, O, STU, US, WIS), X. polycarpa
354. Xanthoria fallax s. latiss. (COLO, GZU, H, LD, STU, US), X. fulva
679. Xanthoria candelaria (COLO, H, LD, NY, STU, WIS), X. candelaria

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