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BIOSYSTEMATICS OF THE IONASPIS-HYMENELIA COMPLEX (LICHENIZED ASCOMYCOTINA) IN NORTH AMERICA: A STUDY AT THE GENERIC LEVEL

by

François M. Lutzoni

Thesis submitted to
the School of Graduate Studies and Research
in partial fulfillment of the requirements for the M. Sc.
degree in Biology

University of Ottawa/Université d'Ottawa

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ABSTRACT

Although modern lichen systematics is based exclusively on the mycobiont, the genera Ionaspis and Hymenelia were always distinguished uniquely by their different photobionts. Ionaspis was thought to be associated only with Trentepohlia, and Hymenelia only with Trebouxia. Despite the high degree of similarity between Ionaspis and Hymenelia, considerable heterogeneity was recognized within each genus. The aim of the present study was to circumscribe natural entities within the Ionaspis-Hymenelia complex and to assess the degree of similarity of these entities along with related genera, Eiglera and Aspicilia. Anatomical and morphological data were subjected to cluster, principal component and canonical variate analyses. Based on these analyses, a total of six species groups ("alba", epulotica, haematina, lacustris, melanocarpa, and odora) were recognized within the Ionaspis-Hymenelia complex; Eiglera and Aspicilia were maintained as distinct genera. To verify the degree of similarity among these groups and genera, as well as the possible occurrence of homoplasy, individuals from the six groups of the Ionaspis-Hymenelia complex, of Eiglera flavida, and of Aspicilia cinerea were subjected to electrophoresis. For the most part, the cluster analysis of the electrophoretic data concurred with that of the anatomical-morphological study, except to suggest that the odora group was more closely affiliated with the "alba" and lacustris groups, and that the genus Eiglera and the epulotica group each were more closely affiliated with the melanocarpa and haematina groups. Both the anatomical-morphological and electrophoretic

dendrograms were compared and fused using the canonical consensus analysis.

The specimens cited in the original description of the type species of Hymenelia (H. prevostii) were found to be associated with either one or the other photobiont. Those specimens which photobiont was Trentepohlia had no other character to justify their exclusion from Hymenelia. Therefore, the segregation of Ionaspis and Hymenelia based exclusively on the photobiont difference is nullified.

On the basis of anatomical-morphological data, electrophoretic data, and biogeographical factors, three genera are recognized within the Ionaspis-Hymenelia complex. As newly circumscribed genera based on North American species, Hymenelia includes the haematina, melanocarpa and epulotica species groups, and Ionaspis includes only the odora species group. A new genus is recognized, "Hymeneliella", which includes the lacustris and "alba" species groups.

The present study casts doubt on the status of Eiglera and Eigleraceae, taxa that previously were established primarily on the basis of the apical structure of their asci. Both the anatomical-morphological and electrophoretic studies revealed that Eiglera is very similar to Hymenelia, except for their different ascus apical structures. The high degree of similarity between Eiglera and Hymenelia suggests that differences in the apical structure of the ascus, as revealed by Lugol solution, may not necessarily reflect genetic differences relevant to the generic and family levels, and that Eiglera be classified within the Hymeneliaceae and perhaps

even subsumed in Hymenelia. This implies that taxa with different ascus apical structures could be classified within the same family or genus.

RÉSUMÉ

Même si la classification des lichens s'effectue maintenant exclusivement à partir des caractéristiques du mycobiote, le seul caractère diagnostique connu, pour distinguer les genres Ionaspis et Hymenelia, était leur différent photobiote. Trentepohlia était le photobiote associé au genre Ionaspis, et Trebouxia celui associé au genre Hymenelia. Malgré leur grande similarité, chacun des genres Ionaspis et Hymenelia était hétérogène. Le but de cette étude était de circonscrire, à l'intérieur du complexe Ionaspis-Hymenelia, des entités naturelles et de déterminer, tout en incluant les genres apparentés Eiglera et Aspicilia, leurs degrés de similarité. Des données anatomiques et morphologiques furent soumises à des analyses par groupement, en composantes principales, et discriminante multiple. Ainsi, six groupes d'espèces ("alba", epulotica, haematina, lacustris, melanocarpa, et odora) furent mis en évidence à l'intérieur du complexe Ionaspis-Hymenelia. Le statut des genres Eiglera et Aspicilia n'a pas été modifié dans le cadre de cette étude. Afin de vérifier le degré de similarité entre ces groupes d'espèces et genres, et de détecter la présence d'homoplasie, des individus de chacun des six groupes d'espèces du complexe Ionaspis-Hymenelia, d'Eiglera flavida et d'Aspicilia cinerea ont été étudiés par l'utilisation de l'électrophorèse. Les résultats de l'analyse par groupements des données électrophorétiques étaient, en majeure partie, en concordance avec ceux obtenus à partir des données anatomiques et morphologiques sauf pour les groupes odora, epulotica et le genre Eiglera. Ainsi le degré de similitude du groupe odora vis-à-vis les groupes "alba" et lacustris fut

accentué par l'étude électrophorétique de même pour le genre Eiglera et le groupe epulotica vis-à-vis l'ensemble formé par les groupes melanocarpa et haematina. Le dendrogramme obtenu à partir des données anatomiques et morphologiques fut comparé et fusionné au dendrogramme élaboré à partir des données électrophorétiques à l'aide d'une analyse canonique de consensus.

Les spécimens cités dans la description originale de l'espèce type du genre Hymenelia (H. prevostii) ont été trouvés en association avec l'un ou l'autre des photobiotes. Aucun autre caractère n'a été trouvé pour justifier l'exclusion, des spécimens dont le photobiote était Trentepohlia, du genre Hymenelia. La démarcation entre Ionaspis et Hymenelia, établie uniquement sur une différence photobiotique, n'est donc plus valable.

Sur la base des données anatomico-morphologiques, électrophorétiques et biogéographiques, trois genres sont reconnus au sein du complexe Ionaspis-Hymenelia. Tel que nouvellement défini pour l'Amérique du Nord, le genre Hymenelia comprend maintenant les groupes d'espèces haematina, melanocarpa et epulotica, tandis que le genre Ionaspis est restreint au groupe d'espèces odora. Un nouveau genre est reconnu, le genre "Hymeneliella". Il inclut les groupes d'espèces lacustris et "alba".

Cette étude soulève des doutes concernant le statut du genre Eiglera et de la famille Eigleraceae, taxons établis preque exclusivement sur la base de la structure apicale de l'asque. Exception faite de ce caractère, l'étude anatomico-morphologique et l'étude électrophorétique ont démontré une

très grande similarité entre Eiglera et Hymenelia. Ceci suggère que les différences au niveau de la structure apicale de l'asque, telles que révélés dans une solution Lugol, ne reflètent pas nécessairement une différence génomique propre au genre ou à la famille. Il serait donc possible de trouver sous une même famille ou un même genre des taxons dont l'asque n'aurait pas la même structure apicale.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

1. INTRODUCTION

1.1. DEFINITION OF LICHENS

Defining a lichen is a difficult task. Ultimately it depends on what type of symbiotic interrelationship between a mycobiont and photobiont should be excluded or included under that term. One of the best definitions of lichens appears in the Dictionary of the Fungi (Hawksworth et al., 1983): "a lichen is a stable self-supporting association of a mycobiont and a photobiont." However, this definition could apply to mycorrhizae as well. The segregation between mycorrhizae and lichens could be made by rephrasing this definition as follows: a lichen is a stable, self-supporting association of a fungus with green alga and/or cyanobacterium. Lichens are most often two-membered symbioses but can also be three- or four-membered.

Permanent symbiotic association between marine algae and fungi, in which the alga predominates and retains its normal outward appearance, has been the center of a debate since the beginning of this century (Hawksworth and Hill, 1984). The issue is whether or not such symbiosis should be regarded as a lichen. The term "mycophycobiosis" was chosen to distinguish these mutualist symbioses from lichens.

Lichens are a biological unit not a taxonomical unit. Therefore, the term "lichen" has to be considered the same way as is the term "mycorrhiza." In fact, these biological entities form "Group 6" (Table 1) of Cooke's classification of the symbiotic fungi (Cooke, 1977) and are called obligately mutualistic fungi (also obligately biotrophic fungi). Again, the limits of

Table 1. Symbiotic fungi divided into biological groups according to their degree of dependence and effect on their hosts (from Cooke, 1977)

		Degree of dependence	
		Facultatively symbiotic	Obligately symbiotic
Effect on host	Antagonistic	Group 1	Group 2
	Neutral	Group 3	Group 4
	Mutualistic	Group 5	Group 6

Cooke's (1977) biological groups are not clear-cut in nature. There are always some cases which overlap boundaries and give rise to paradoxical terms such as "biotrophic parasitism."

A final distinction has to be made regarding lichens. Under the rules of the International Code of Botanical Nomenclature (ICBN, Greuter 1988), the names given to lichens refer to the mycobiont; the alga can bear independent names. As a direct consequence, lichens are now completely integrated into the system of classification of fungi (Hawksworth et al., 1983). Since 1982, lichens have been listed intermixed with non-lichenized fungi in the Index of Fungi.

There are several reasons for this different nomenclatural approach. The mycobiont of lichens, contrary to the photobiont, is not found in a stable asymbiotic state in nature. Only five of 18 orders - the Graphidales, Gyalectales, Peltigerales, Pertusariales, and Teloschistales - are known to include exclusively lichenized species (Hawksworth & Hill, 1984). Several genera are known to have asymbiotic and symbiotic representatives. For example, in the genus Pezizella there are species which are lichen-forming, while others are parasitic, bryophilous, mycorrhiza-forming, or saprophytic. Of the 64,200 known fungi, one fifth are lichenized (Hawksworth & Hill, 1984). In most lichens, the mycobiont is the main constituent of the thallus, counting for 90-95% of the total biomass of the lichen, even though the photobiont is necessary for the ontogenesis of the thallus structure. The fungus provides water and minerals and produces the sexual and asexual reproductive structures. Furthermore, the photobionts of more than 90% of all lichens are drawn from only three genera: Trebouxia, Trentepohlia, and

Nostoc (Kendrick, 1985). Therefore the genetic diversity of lichens corresponds to the fungus and not to the photobiont.

1.2. GENUS CONCEPT IN LICHENIZED FUNGI

Much more work has been done on lichenized fungi at the generic level than at any higher taxonomic level. Nevertheless, until recently the generic concepts applied to lichenized fungi can be considered as pre-Darwinian, the classification of lichens being in many cases artifical and almost exclusively phenetic. One of the main goals of lichenologists is to achieve more homogeneous taxa and to define more natural generic groups.

The duality of lichens was another factor which has misled lichenologists and plant taxonomists for a long time. It was only after the work of Schwendener (1867) that the dual nature of lichens was appreciated. For example, Linnaeus (1753), classified lichens under "Algae." From Linnaean time to the middle of the 19th century, with the exception of Eschweiler (1824) and Fée (1824), who used ascospore characters, only gross morphological characters were used in classifying lichen species into genera.

The 1850's witnessed great changes in generic concepts, and the resulting controversies divided lichenologists into two bitterly opposed camps for many years (Hale, 1984). On one side, was the Italian-Silesian school with Massalongo and Körber as the leaders; and on the other side, the Nylanderian school, founded by Nylander. Contention between the two schools concerned the use of ascospores in establishing new genera. Nylander rejected the use of ascospores to delimit genera, and instead he

stressed internal structure of the thallus and pycnidial characters. He also used photobiotic characters in describing new genera, the use of which had been denied by Massalongo (1852). Massalongo (1853) listed the characters he used to define new genera in order of importance as follows: ascospores (color, septation, and number), asci and paraphyses, the hypothecium, exciple, and finally thallus characters (Hale, 1984).

Krempelhuber, who described the genus Hymenelia in 1852, definitely followed the Italian-Silesian genus concept. Th. Fries, seemed also, at least at first, to be more on the side of Massalongo. In his Genera Heterolichenum Europaea (1861), Th. Fries discussed generic concepts in general, and continued to accept a number of Körber-Massalongo genera. However, he progressively adopted Nylander's position, especially in his Lichenographia Scandinavica (1871-1874), in which he established the genus Ionaspis.

Müller Argoviensis (1862), in reviewing the characters used by the Körber-Massalongo school, rejected zeorine apothecia, evanescent margins, apothecial color, number and size of spores, and color of the hypothecium as good generic characters, but accepted spore septation and color, certain paraphysis differences, as well as thallus structure.

Over the past forty years, there has been considerable effort to make genera more homogeneous and, therefore, presumably monophyletic. The use of techniques such as electron microscopy and the chemistry of secondary substances has had a great impact on the classification of lichenized fungi. Many lichenologists have focused their attention on precise characters such as the conidia shape, the apical structure of the ascus as revealed with IKI solution, the presence on the ascospore of a diffuse epispore (halo), the

structure and anatomy of the upper and lower cortex, and the presence/absence of secondary substances. More taxonomical weight was attributed to these characters in the classification of lichens at the generic level. The result was the fragmentation of genera into a multitude of smaller homogeneous genera. For example, species of Parmelia in Zahlbruckner's Catalogus Lichenum Universalis (1922-1934) are now found under 20 genera (Hale, 1984; Hale & Fletcher, 1990) based on a series of thallus characters including the epicortical layers, cortex structure, as seen with scanning electron microscopes, lobe shape, distribution, as well as chemistry.

According to Hale (1984), the modern generic concept of crustose lichens is based on the following chief diagnostic characters: apothecial ontogeny, ascal structure, spore development, and paraphysis morphology. However, in some instances, there is no other possibility than to use less firmly established characters (e.g. thallus structure and ornamentation, chemistry, and phytogeography) to subdivide large, heterogeneous genera, into more biologically homogeneous groups. Hale (1984), also specified that in delimiting more natural genera, modern lichen taxonomists use several characters, none of which has overwhelming significance but taken together form a convincing case.

It should be stressed that during the last 10 years much emphasis has been placed on the apical structure of the ascus, especially its amyloid layers as revealed by Lugol's solution (IKI), in reorganizing crustose lichenized fungus classification at the genus and family level. The most prominent work is definitely that of Haffelner (1984) who, within the Lecideaceae s. lat.

and Lecanoraceae s. lat., established 35 new families based almost exclusively on the ascus apical structure of the respective type species. Paraphyses and ascospores, in a marginal way, were the only other structures used in his study. From his investigation, Haffelner (1984) established five principles, the third one being of crucial importance for his reorganisation of the classification;

> As a rule, different types of asci do not occur in the same genus (or family). Thus, the genus (or family) is usually defined by the type of ascus. This signifies that all species which do not have the same type of asci as the type species of a genus 'A' should be transferred to another genus 'B' with the same type of ascus.

It should be understood that Haffelner's (1984) third principle does not exclude the frequent case where two different genera share the same type of ascus apical structure. Nevertheless, even if the apical structure of the ascus is recognized by most lichenologists as part of the modern genus concept, the use of a single character in defining genera and families is precarious and, in principle, may be no more acceptable than older methods. Moreover, we have no indication whatsoever of the evolutionary and genomic significance of these structural variants.

Furthermore, it is important to mention that it is only recently that the genetics of lichens has been investigated (Ahmadjian et al., 1987; Armaleo & Clerc, 1990; Blum & Kashevarov, 1986, Culberson C. 1986; Culberson C. et al. 1988; Fashelt, 1989, 1988, 1986, 1985, 1980; Fahselt & Hageman, 1983; Hageman & Fahselt, 1984; Kilias 1987). There is a great need for such studies in lichenology. This will be the next step toward an evolutionary understanding of the lichenized fungi.

1.3. THE IONASPIS-HYMENELIA COMPLEX

Little is known about the lichenized fungi Ionaspis Th. Fries and Hymenelia Krempelhuber, especially in North America, where they have never been subjected to any systematic studies. The reasons for the absence of studies of these genera are mainly their cryptic characteristics and nature of their habitats. They are saxicolous crustose lichens, found mostly in arctic alpine regions, characterized by very small thalli, usually 2 to 3 cm in diameter and usually 0.2 to 0.3 mm thick, rarely exceeding 0.5 mm. The apothecia are minuscule and sunken in the thallus, approximately 0.3 mm in diameter, with extremes rarely exceeding 0.8 mm. The paraphyses and asci are embedded in a gelatinous matrix, making the observation and measurement of these structure very difficult. Some taxa are endolithic, others aquatic. Thus there are relatively few available collections of Ionaspis and Hymenelia in herbaria of the world.

The only monograph written on either genus was by Magnusson (1933) and dealt almost exclusively with the European representatives of the genus Ionaspis. Magnusson also included two species found in North America: Ionaspis lavata H. Magn. and I. ochromicra (Nyl.) Hue. The former is confined to the west coast of North America whereas the latter seems to have a wider range, since it was also reported from Europe (Santesson, 1984). Three new species in the lichen genus Ionaspis have been described recently, but none has yet been found in North America (Jørgensen & Santesson, 1989). Ionaspis fuegensis is from Argentina, I. granvina from Norway, and I. ventosa from Sweden.

Until recently (Jørgensen, 1989), the only taxonomic key to the species of Ionaspis was found in Magnusson's work (1933). This key was not always reliable for the following reasons: 1) it was primarily based on substrate characteristics (e.g., calcareous versus non-calcareous rocks); 2) most of the species described were based on one specimen; and 3) some confusing species were fragmented into several varieties and forms, based on environmentally modified characters such as the color of the thallus, and were not included in any keys (see taxonomical notes under "Hymenelia haematina", section 5.2.2.). The consequences of this ambiguity of the species concept within Ionaspis were confusion and misidentifications.

Nevertheless, Magnusson's work (1933) set the basis for understanding the genus Ionaspis. Prior to his work, Ionaspis consisted of nothing but a list of names as reported by Th. Fries (1871), with subsequent addition of taxa, more or less related to each other, by other lichenologists. The inclusion of non-related taxa in Ionaspis was mainly due to the few guidelines given by Th. Fries (1871) in his protologue of the genus. Any crustose lichen having an aspicilioid appearance and Trentepohlia as a photobiont could have been called Ionaspis.

Confusion was even greater for Hymenelia than for Ionaspis (see nomenclatural notes of section 5.1.2.). Although Hymenelia was established by Krempelhuber in 1852, Poelt and Vězda (1981) were the first to publish a key to the species of Hymenelia. However, this key was based exclusively on European material. As pointed out by Poelt and Vězda (1981), several unresolved problems remained at the genus and species level; but at least a starting point had been established.

Ionaspis and Hymenelia were also included in studies such as the detailed anatomical and morphological study of the genus Lecanora s. lat. by Eigler (1969), and the classification of the Lecanoraceae and Lecideaceae s. lat. by Haffelner (1984). These studies reveal the complexity of the taxonomic problem involved with Ionaspis and Hymenelia and related genera, without establishing any new classification within that complex. Recently Haffelner (1989) concluded that the Aspiciliaceae (including the genera Aspicilia, Megaspora, and Agrestia) form a natural unit. Therefore Hymenelia and Ionaspis are the only genera currently included in the family Hymeneliaceae.

The Ionaspis-Hymenelia complex involves two main problems. The first comes from the fact that the only known character to differentiate Ionaspis and Hymenelia was their different photobionts. By definition Ionaspis is associated with Trentepohlia whereas the photobiont of Hymenelia was believed to be Trebouxia exclusively.

Th. Fries (1871-74) consistently attempted to use photobiotic characters in his lichen classifications (Poelt, 1973a). One of his taxonomic rearrangements resulted in the establishment of the genus Ionaspis by segregating species from Aspicilia Massalongo having Trentepohlia instead of a trebouxioid photobiont. This was the only diagnostic character used. Presumably, this character was later accidentally transposed to differentiate Ionaspis from Hymenelia Krempelhuber. Since modern systematics of lichens is now based exclusively on the mycobiont, the distinction between Ionaspis and Hymenelia has been constantly questioned (Magnusson 1933, Eigler 1969, Ozenda and Clauzade 1970, Wirth 1980, Poelt and Vězda 1981,

Haffelner 1984, Clauzade and Roux 1985, Jørgensen 1989); Haffelner (1984) suggested that they at least ought to be included in the same family.

The second problem, the intergeneric similarity and intrageneric heterogeneity within the Ionaspis-Hymenelia complex, was revealed by more global systematic work such as that of Eigler (1969). By comparing Aspicilia, Ionaspis, and Hymenelia species, Eigler showed that some taxa of the Ionaspis-Hymenelia complex were more related to taxa of the other genus than to congeneric species. Some other taxa were so different from the rest of the species groups that it was hard to believe that they should stay within one or the other genus of this complex. The heterogeneity within this complex may be a result of the paucity of readily observable characters due to the restricted size of apothecia and the presence of a gelatinous hymenial matrix. Several taxa having small embedded apothecia and found in aquatic habitat, for instance, were almost automatically classified within Ionaspis or Hymenelia, depending on their photobiont.

The main goal of this study was to determine the interrelationships among the taxa within the Ionaspis-Hymenelia complex and their relation to the related genera Eiglera and Aspicilia. Basically, these four genera have one unique character in common: the immersed apothecia. The second goal of this study was to re-evaluate the importance of the photobiotic difference as a diagnostic character between Ionaspis and Hymenelia. Finally, based on an anatomical and morphological study coupled with an enzyme electrophoretic and a nomenclatural study, the third goal was to elaborate a new classification at the genus level of the hymenelioid lichens, including Eiglera, Ionaspis and Hymenelia. These three genera, in addition to having

sunken apothecia, share the following most apparent characteristics: small apothecia, thin thallus, and include aquatic and endolithic taxa.

2. METHODS

2.1 SYNOPSIS

An initial survey of the hymenelioid lichenized fungi and the type species, Aspicilia cinerea, was made using mainly anatomical and morphological characters. The purpose of this first step was to eliminate superfluous characters and to obtain a first perception of the phenetic patterns of variation of the Ionaspis-Hymenelia complex with regard to related genera Eiglera and Aspicilia. Individuals from each of the 8 clusters revealed in this first step were used in an electrophoretic study. The electrophoretic data were used to detect homoplasy in morphological and anatomical characters and to verify the degree of relatedness shown by numerical analysis based on the anatomical-morphological data. Dendrograms from the anatomical-morphological and the electrophoretic study were compared and fused using a canonical consensus analysis. This fusion led to a final dendrogram.

The recognition of natural generic entities was attempted by investigating more distant groups, i.e. 5 rather than 8 clusters, of the euclidean consensus dendrogram (Fig. 10). The five clusters were subjected to canonical variate analyses (CVA). Using the species groups found within

each of the 5 clusters (Fig. 10), the pairwise distances among these clusters, and the phenetic value of the diagnostic characters obtained with principal component analysis (PCA) and stepwise discriminant analysis, it was possible to determine to which taxonomic unit these 5 clusters belonged. Three of these 5 clusters correspond to taxa that are part of the Ionaspis-Hymenelia complex and, therefore, were subjected to further analyses (PCA and CVA) to determine the best characters that could be used to define these taxa. A nomenclatural study followed to determine the names that should be given to these three taxa found within the Ionaspis-Hymenelia complex.

2.2. HERBARIUM AND FIELD WORK

The herbarium specimens used in this study were gathered from the National Herbarium of Canada (CANL) or borrowed from the following herbaria: ASU, COLO, DUKE, H, LAM, M, MICH, MIN, NY, NYS, PH, QEF, QFA, TRTC, UC, UPS, US, WIS, and Claire Smith's personal herbarium (Holmgren & Keuken, 1981).

Field work was conducted during the fall of 1987 in the Mont Albert region (2 populations), and St-Jean-Port-Joli region (1 population) in the province of Québec. Two localities in the Ottawa region were visited during the spring and fall of 1988. The following Arctic localities were investigated during the months of July and August 1988: Iqaluit, Nettilling Lake and Amadjuak Lake, Southern Baffin Island; Southern Cornwallis Island; Coppermine; Cambridge Bay and Holman region on Victoria Island. A total of 154 populations was sampled in these Arctic sites. For each population, at

least three samples were collected. For 76 populations, five additional specimens were sampled for electrophoretic studies. For five taxa, approximately 40 samples were collected for exsiccatae (to be issued in Lichenes Canadenses Exsiccati). Standard ecological data, such as proximity to water, type of habitat (immersed in brook or river, wet or dry cliffs, in dry fellfield, on boulders in deciduous forest, rocky shores of lakes), approximate width of the water flow, general slope, and rock type (siliceous or calcareous); were recorded for each population. A 10% HCl solution applied directly on rock or rock powder was sometimes used to help determine the rock type (i.e., to reveal the presence of calcium carbonate).

Specimens collected during the summer of 1987 and 1988 were deposited in CANL. Complete sets of duplicates can be found in QFA and UPS.

2.3. SECONDARY SUBSTANCES AND PIGMENT CHARACTERIZATION

No secondary substances have ever been reported in the literature for Hymenelia (C. Culberson, 1969, 1970; C. Culberson, W. Culberson and Johnson, 1977). All past studies done on hymenelioid material found in CANL using TLC (thin layer chromatography) were negative. The same negative results were obtained in the present study using small fragments of old herbarium specimens. Some positive results were obtained when whole fresh thalli (excess material collected for electrophoretic study) were used. Spots were revealed but it was not possible to identify them. Most, however, seem to be pigments. Thus the use of TLC was discontinued. Instead, pigments were characterized by their color and their reaction to concentrated

HNO_3 and 10% KOH applied directly to dry, handmade sections and observed under a compound microscope.

2.4. ANATOMICAL AND MORPHOLOGICAL STUDY

All microscopic observations and measurements were made using a Leitz Dialux 20 EB compound microscope equipped with fluotar and phase contrast objectives or with a Wild-Leitz M-5 dissecting microscope. Color of the disk, thallus and apothecial pigment are reported using the U.S. National Bureau of Standards, Inter-Society Color Council (ISCC) Dictionary of Color Names (Kelly & Judd, 1976) using a chart of centroid colors (Kelly, 1965). For color determination of apothecial pigments, handmade sections were mounted in distilled water and observed under a compound microscope. A "daylight" filter and fluotar objectives were used for each determination.

Apothecia density was determined using a micro quadrat of 2.5 X 2.5 mm and a dissecting microscope. The quadrat was placed in areas of the thallus where the apothecia were the most abundant. Six observations were made whenever possible, and an average was calculated for each specimen. It is expressed in the keys and descriptions as 6.25 mm^2.

Minimum and maximum disk diameters of mature apothecia were measured using a dissecting microscope with an ocular micrometer at a 40 X magnification. The minimum and maximum widths of mature apothecial margins were measured using the same technique.

The identification of the photobiont was based on the intracellular orange pigment (characteristic of Trentepohlia), when present. If absent the photobiont was determined using polarized light (see page 73). For endolithic thalli, small rock fragments containing part of the thallus had to be dissolved in 20% HCl solution, to be able to see the photobiotic cells.

Ascospore measurements were made with an ocular micrometer at 400 X magnification. Length and width were recorded for a minimum of 5 ascospores per specimen. If considerable variation was observed, measurements were taken on as many ascospores as possible, to a maximum of 15 ascospores. All ascospore measurements were made from handmade sections mounted in distilled water. The minimum, maximum and average widths and lengths of ascospores were used for statistical analyses. Ascospores were drawn from each individual and the presence of a halo (diffuse epispore of ascospores) was determined by introducing China ink into the distilled water under the cover slip.

All apothecial anatomical observations and measurements were made on apothecia sectioned with a freezing microtome (set for 12 µm thick sections) and semipermenantly mounted in lactophenol-cotton blue solution (solution described in Duncan & James, 1970) for later comparisons. This procedure guards against possible variation due to different mounting media or different thickness of sections. For better comparisons, only radial longitudinal sections (i.e. the largest sections) of apothecia were used. Most information was recorded under 400 X magnification. Observation of the paraphyses was done under oil immersion at 1000 X magnification. Phase

contrast was also occasionally used for a better visualization of the paraphyses.

Hyphal tissues of apothecia were described using Korf's (1958) terminology (Fig. 1).

The apical structure of the ascus was studied by discarding the margins of the apothecia and, if possible, the thalline part under the apothecial tissues. This facilitated the spreading of the paraphyses and asci and as well reducing the presence of rock crystals which could break the cover-slip when the mounted material was squashed. This apothecial central piece was mounted directly in Lugol's solution and gently squashed with a dissecting needle by successive rotations to maximize the spreading. Observations of the reactions of hymenium and subhymenium to the Lugol's solution were recorded under 400 X, and the apical structure of the ascus under 1000 X magnification.

2.5. ELECTROPHORETIC STUDY

Fresh material was air-dried at the most 3 days after field sampling. It was frozen (-20 ° C) as soon as it arrived in Ottawa (i.e. within approximately 2 weeks in the case of specimens sent from the Arctic). When needed, the thalli were scraped off the rock. This was done under a dissecting microscope to avoid any contamination. In order to obtain enough lichen material, for some samples, material coming from different thalli on the same rock or nearby rocks had to be combined. This material was stored in 5 ml centrifuge tubes at -20 ° C until extraction.

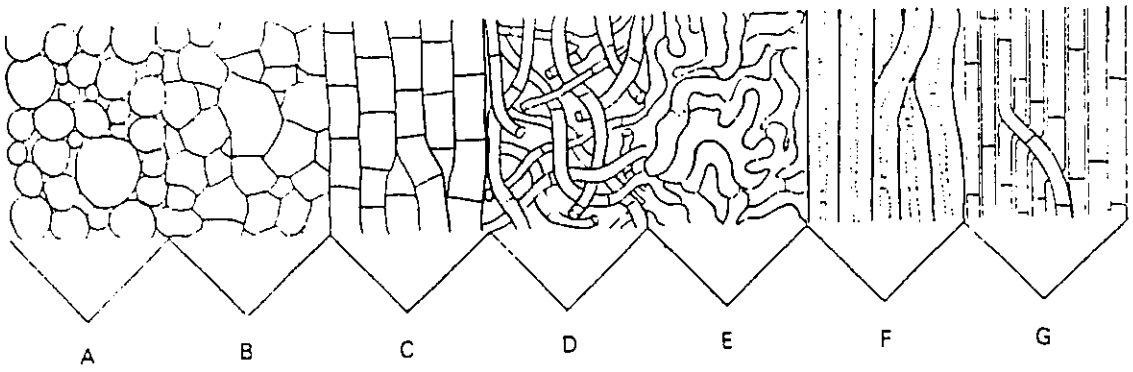


Figure 1. Hyphal tissue (textura) types (Korf, 1958). A) Textura globulosa, B) textura angularis, C) textura prismatica, D) textura intricata, E) textura epidermoidea, F) textura oblita, G) textura porrecta.

The quantity of lichen material could not be determined precisely since the sample contained rock crystals intermingled with lichenic material. A minimal volume (≈ 1ml) was estimated to contain enough enzyme for all taxa. The extraction was made using a mortar and pestle set in a pan of ice. Grinding was done for 15 seconds in liquid nitrogen. Ground sand and polyvinyl-polypyrrolidone (PVVP) was added as well as approximately 8 drops of cold 0.06 M phosphate buffer (pH 6.6) containing 1mM mercaptoethanol. Grinding was done using a mortar and pestle for 1 minute. The sludge was transferred to a cold glass tube and homogenized for 1 minute with a power-driven Teflon pestle while the tube containing the sludge was embedded in crushed ice. The homogenized sludge was returned to its initial cold centrifuge tube and stored at -40 ° C over night. The next morning the defrosted sludge, kept between 0 and 4 ° C, was centrifuged and wicks were inserted in the supernatant.

The activity of eighteen enzymes was tested in each of four gel systems, including a Tris - citric acid system at pH 8.8 (Gottlieb, 1981), a Tris - citric acid system at pH 8.3 (Gottlieb, 1981), a histidine - citric acid system at pH 6.5 (Warwick et al., 1984), and a histidine system at pH 5.7 (Warwick and Gottlieb, 1985). These included: diaphorase (DIA), esterase (EST), fumarase (FUM), glucose-6-phosphate dehydrogenase (G6PDH), glutamate dehydrogenase (GDH), glutamate-oxaloacetate transaminase (GOT), glyceraldehyde-3-phosphate dehydrogenase (G-3PD), glycerate-2-dehydrogenase (G2DH), hexokinase (HK), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), malic enzyme (ME), phosphoglucose isomerase (PGI), phosphoglucomutase (PGM), shikimate dehydrogenase

(SKDH), triose phosphate isomerase (TPI), xanthine dehydrogenase (XDH), and 6-phosphogluconate dehydrogenase (6-PGD).

Three enzymes could be scored reliably: a Tris - citric acid system at pH 8.3 was used with PGI, and a histidine system at pH 5.7 was used for IDH and 6-PGD. In the systematic survey of the 8 anatomical-morphological clusters (Fig. 4), 47 populations were studied: 18 populations from the haematina group, 20 from the epulotica group, 1 from the alba group, 2 from the lacustris group, 1 from the Aspicilia group, 1 from the melanocarpa group, 3 from the Eiglera group, and 1 from the lavata group. A total of 99 samples was selected and run on starch gels (Appendix A). Free-living Trentepohlia, often found side by side with lichenized fungi and where all stages of lichenization can be seen, was run simultaneously on the gels. This way enzyme activity of the photobiont could be detected and excluded from the numerical analyses.

Patterns were assessed by scoring the shared presence / absence of bands. An inter-gel comparison was made using standards. Interpretation of the bands as genetic loci was not possible for the following reasons: 1) samples were a mixture of monokaryotic and dikaryotic tissues, 2) often, nearby thalli had to be combined to obtain enough biomass, and 3) samples contained a multitude of apothecia within which the dikaryon may have been derived from different genetic parents.

2.6. CHOICE OF CHARACTERS AND NUMERICAL PROCEDURES

Initially, all characters used in previous studies on this complex (Magnusson, 1933, Eigler, 1969, Haffelner, 1984, Poelt & Vězda, 1981), as well as any additional character which had proven to be useful in other genera (Bellemère & Letrouit-Galinou, 1987; Brodo, 1984; Hale, 1984; Poelt, 1973b; Kärnefelt & Mattson, 1987) and that could be recorded in the Ionaspis-Hymenelia complex, were included (total of 92 characters) in a first survey of 20 individuals. These specimens were selected in order to cover, as much as possible, the whole range of variability of the characters within the hymenelioid lichens. Thirty-one variables were eliminated after this first step for one of the following reasons: 1) Absence of the structure to be measured, 2) no variability in the data, or 3) the impossibility of reliably describing a structure due to difficulties with its examination or to excessive variation within the same individual.

After this initial step, 61 characters remained. The scoring of these characters was extended to 94 individuals. Gower's (1971) similarity coefficient was used since this is appropriate for mixtures of quantitative and qualitative data. At this stage, cluster analyses, using single linkage (nearest neighbor), average linkage (UPGMA), furthest neighbor, and flexible sorting method (Lance and Williams, 1967), with α=0.625 and β=-0.25, were done using Agriculture Canada's CLUSTRIT (S075) program (Lefkovitch, 1981). Of these, the flexible sorting method was considered to be the most informative, since it produced dendrograms with the least chaining. All characters that were important to explain the clusters as revealed by the PCA and CVA were conserved. For PCA and CVA, PRINCOMP, STEPDISC, DIS CRIM and

CANDISC (SAS Institute Inc., 1985), respectively, have been used. Thus 35 characters (1-30, 32, 34, 36-38; Table 2) were kept for subsequent numerical analyses. Using these characters, the study was extended to almost 300 specimens. At this point the same numerical analyses, listed above, were done. Unweighted data were used throughout this study.

A dendrogram representing 196 specimens and based on the 35 characters mentioned above (Fig. 3) was the starting point of this study. Since the goal of this study was to work at the generic level, the first attempt was to break up the entire set of specimens into the most finely distinguishable partitions possible, so that in a second step, those small entities could be grouped into coarser partitions equivalent to generic rank. This first step was done by subjecting to CVA the different clusters suggested by partitions at different distances, and by investigating the characters revealed by CVA and PCA to find which characters are associated with these clusters. The lowest partition that could be made (i.e. when the probability of being greater than the Mahalanobis distance was 0.0001 for all pairwise distances, when less than 5 % of the items were reclassified by CVA, and when the individuals within each cluster still could be readily recognised macroscopically) corresponds to a vertical line passing through the anatomical-morphological dendrogram at the 1.1 distance (Fig. 3). This partition suggested six clusters. However, the genera Eiglera and Aspicilia were grouped together in one of these clusters, and a taxon that I have called "alba", which could not be placed in any known genus, was grouped with Hymenelia lacustris. In order to investigate these taxa separately in

subsequent studies, such as electrophoresis, these two clusters were subdivided into four, for a total of eight clusters.

Since the partition was at a supraspecific level in most cases, the individuals within each cluster were easily recognizable based on the study of the characters associated with each cluster, and misclassified specimens were readily identified. A reclassification could then be done, corresponding to the letters on the left of the dendrogram (Fig. 3). These reclassified clusters are those illustrated on the summarized dendrogram (Fig. 4) and are those submitted to the subsequent studies and analyses. The term "species group" was thereupon used to designate the reclassified clusters.

Characters included *a posteriori* in the descriptions of genera, but not used in the statistical analyses, were observed on at least 20 % of the total number of specimens investigated under each genus.

A pairwise comparison of the enzyme banding patterns was done for all species groups using Ochiai's (1957) coefficient of similarity:

$$S_{xy} = B_{xy} (B_x \cdot B_y)^{-1/2}$$

where B_x and B_y are the total number of bands found within the species group x and y, respectively, and B_{xy}, the number of bands shared by both groups. This method takes into consideration the number of bands shared with regard to the total number of bands for each groups; i.e., two species groups sharing 1 band, having repectively 1 and 4 bands in total will have a coefficient of similarity (S_{xy}=0.500) two times higher than two species groups sharing 1 band but having respectively 2 and 8 bands in total (S_{xy}=0.250). Also, groups having the same numbers of bands and having all of them in

common, will obtain a coefficient of similarity of 1.0 rather than 0.5 as with Jaccard coefficient of similarity.

From the resulting matrix of pairwise similarities, the inter-species groups distances were calculated (distance = complement of the coefficient of similarity) and a dendrogram produced using the single linkage (nearest neighbor) method. According to Abbott et al. (1985), this clustering method is considered to be appropriate above the species level, as it reveals the full diversity of clusters, chains, and outliers. In contrast with the anatomical-morphological study, there was no chaining in the dendrogram obtained with the single linkage method. Chaining is frequent with this method, because the algorithm of the single linkage clustering method is sequential, agglomerative, hierarchic, and based strictly on the degree of association between two objects at the time. The result is, that the presence of one or a few intermediates between two groups is sufficient for grouping them into one (Legendre & Legendre, 1984). High numbers of shared bands between two of the 8 species groups being rare, intermediates were also rare. Moreover, the proportion of pairwise similarities equal to zero being high (11/28, Table 6), differences among various cluster strategies would be minimal.

Using a canonical consensus analysis (Agriculture Canada S098 program; Lefkovitch, 1978), the dendrogram based on anatomical-morphological data was compared with that obtained from the electrophoretic data set, and combined to produce a third dendrogram.

2.7. DESCRIPTIONS

Characters included in the "characterization" part of the descriptions of genera, are the ones revealed by PCA and CVA to best explain the clusters. Measurements are usually given by five numbers [ex. (1.7-)**4.1 -<u>8.7</u>- 13.3**(-27.0)]. The numbers in parentheses are the most extreme measures recorded. The numbers in bold, but not underlined, are the lower and upper limit of the standard deviation applied on the average minimal measurement or applied on the overall average if minimum and maximum data were not recorded. The number in bold and underlined is the overall average. Descriptions of apothecia and pycnidia involve mature ascomata and conidiomata except when specified otherwise. The colors of disk, thallus and apothecial pigments were named according to the ISCC numbers and are written in parentheses.

Terminology used in this study to describe the internal parts of the apothecia are illustrated in Figure 2.

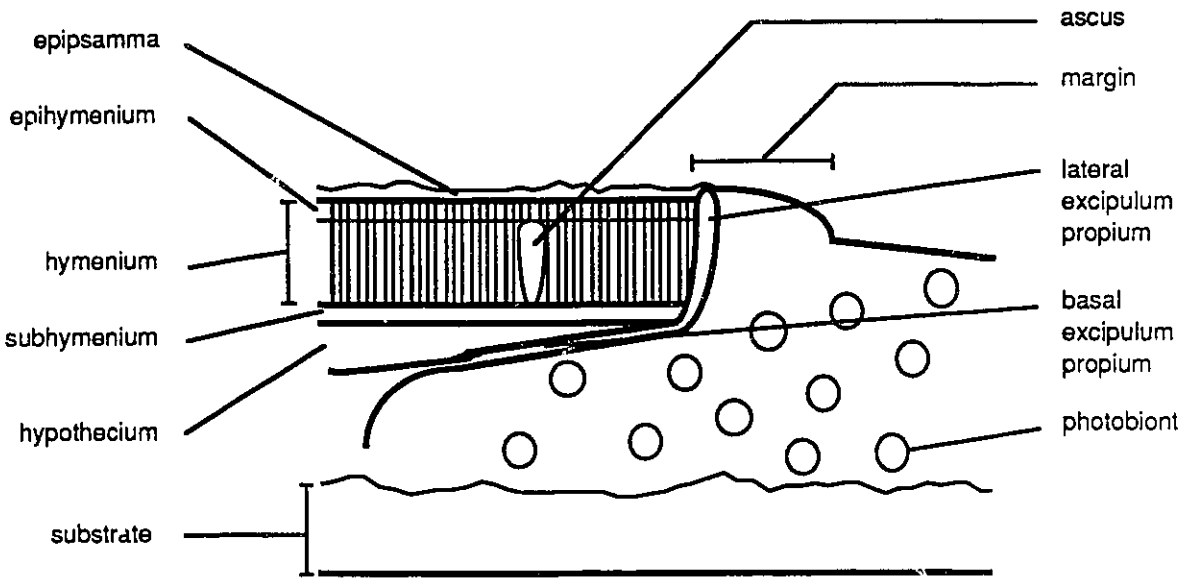


Figure 2. Schematic representation of a radial longitudinal section of an hymenelioid apothecia.

3. RESULTS

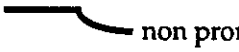
3.1. RECOGNITION OF SPECIES GROUPS WITHIN THE IONASPIS-HYMENELIA COMPLEX IN RELATION WITH EIGLERA AND ASPICILIA CINEREA

3.1.1. First numerical analysis of the anatomical-morphological data

A total of 61 characters was used to describe the genera and species. 58 characters are anatomical or morphological features of the taxa, two, the nature of the substrate and the habitat, are ecological descriptors, and a third describes the bioclimatic zones where the taxa are found. Of the 61 characters, 35 (1-30, 32, 34, 36-38; Table 2) were shown by the PCA or CVA to be potentially useful for generating clusters. The results are based exclusively on these 35 characters.

The flexible sorting method was optimal in producing dendrograms with the least chaining and, therefore, was used throughout the study to explore the anatomical-morphological phenetic pattern within the Ionaspis-Hymenelia complex, in relation with the related genera Eiglera and Aspicilia. From the dendrogram obtained from 196 specimens (Fig. 3) a synoptic dendrogram was built (Fig. 4), and eight clusters were retained (see methods section 2.6, page 21). Two of these clusters coincide with the genera Eiglera and Aspicilia, while the other six are part of the Ionaspis-Hymenelia complex. At this stage in this study, these six clusters are considered as species groups, with no taxonomic status.

Table 2. Annotated list of 61 characters used in the anatomical-morphological study. The numbers in the "matrix order" column correspond to the order of apparition in the matrix of the characters analyzed numerically. The variable descriptors are as following: (1) dichotomy, (2) alternative, (3) multistate unordered, and (4) multistate ordered of quantitative (Lefkovitch, 1981).

Matrix order	Variable descriptors	Characters	States
		Thallus	
		- color	chart of centroid colors (Kelly, 1965)
3	2	- type	1) endolithic, 2) epilithic
5	2	- photobiont	1) trebouxioid, 2) Trentepohlia
		Disk (mature apothecia)	
2	3	- color	chart of centroid colors (Kelly, 1965)
21	4	- minimum diameter	µm
22	4	- maximum diameter	µm
		Apothecia (mature)	
		- shape	1) circular, 2) subangular, 3) irregular, 4) elongate
		- margin shape (immature apothecia, dry, and epilithic thallus)	1)  non prominent, 2)  slightly prominent, 3)  prominent, 4)  very prominent and constricted at the base
4	3	- margin shape (mature apothecia, dry, and epilithic thallus)	1)  non prominent, 2)  slightly prominent, 3)  prominent, 4)  very prominent and constricted at the base

(continued on next page)

Table 2. (continued)

23	4	- margin minimum thickness	µm
24	4	- margin maximum thickness	µm
20	4	- average density (region of thallus having the greatest number of apothecia)	number of apothecia in 2.5 X 2.5 mm
6	3	- epihymenial color	chart of centroid colors (Kelly, 1965)
7	2	- black excipulum propium	1) continuous below the hymenial zone 2) only present in the margins
19	1	- epipsamma	1) present, 2) absent
		- hymenial color	chart of centroid colors (Kelly, 1965)
		- lateral excipulum propium color	chart of centroid colors (Kelly, 1965)
		- hypothecial excipulum propium color	chart of centroid colors (Kelly, 1965)
		- hymenial color minimum thickness	µm
		- hymenial color maximum thickness	µm
32	4	- hymenial height	µm
34	4	- subhymenial height	µm
36	4	- hypothecial height	µm
37	4	- minimum hymenial excipulum propium thickness	µm
38	4	- maximum hymenial excipulum propium thickness	µm
		- minimum hypothecial excipulum propium thickness	µm
		- maximum hypothecial excipulum propium thickness	µm
		- hypothecial textura (Korf, 1958; see Fig. 1)	1) globulosa, 2) angularis, 3) prismatica, 4) intricata, 5) epidermoidea, 6) oblita, 7) porrecta
		- lateral excipulum propium textura (Korf, 1958; see Fig. 1)	1) globulosa, 2) angularis, 3) prismatica, 4) intricata, 5) epidermoidea, 6) oblita, 7) porrecta

(continued on next page)

Table 2. (continued)

		- hypothecial excipulum propium textura (Korf, 1958; see Fig. 1)	1) globulosa, 2) angularis, 3) prismatica, 4) intricata, 5) epidermoidea, 6) oblita, 7) porrecta
10	3	- paraphysal ramification	1) simple, 2) ramified below the apex, 3) dichotomously ramified at the apex
11	3	- paraphysal constrictions	1) none, 2) slightly constricted, 3) submoniliform, 4) moniliform
12	2	- paraphyses shape 1	1) larger at the apex, 2) approximately the same width from top to bottom
		- paraphyses shape 2	1) straight, 2) undulate
		- paraphysal anastomosis	1) present, 2) absent
15	1	- hymenial pigment reaction to HNO_3	1) positive (color of reaction), 2) negative
16	1	- hymenial pigment reaction to KOH	1) positive (color of reaction), 2) negative
14	1	- hymenial reaction to Lugol's solution	1) positive, 2) negative
		- subhymenial reaction to Lugol's solution	1) positive, 2) negative
9	1	- tholus reaction to Lugol's solution	1) positive, 2) negative
		Ascospores	
25	4	- minimum length	µm
26	4	- maximum length	µm
29	4	- average length	µm
27	4	- minimum width	µm
28	4	- maximum width	µm
30	4	- average width	µm
8	1	- halo	1) present, 2) absent
13	3	- pattern in the ascus	1) uniseriate, 2) biseriate, 3) aseriate

(continued on next page)

Table 2. (continued)

		Pycnidia (part visible at the surface of the thallus)	
		- minimum diameter	µm
		- maximum diameter	µm
		- average diameter	µm
		Conidia	
		- minimum length	µm
		- maximum length	µm
		- average length	µm
		- minimum width	µm
		- maximum width	µm
		- average width	µm
		- shape	1) bacilliform, 2) rubanate, 3) elliptic, 4) filiform
		Ecological & phytogeographical data	
1	2	- substrate reaction to HCl	1) negative, 2) positive
18	3	- habitats	1) wet cliffs, 2) submerged or just above water in flowing water, 3) intermittent creek (dry at the moment of collection), 4) scree talus, 5) dry fellfield, 6) boulders in deciduous forests, 7) falls sprayed zone, 8) lake rocky shore
17	3	- bioclimatic zones	1) arctic, 2) boreal, 3) hemiboreal subzone, 4) temperate, 5) subtropical to tropical, 6) Appalachian Mountains, 7) Northwestern Cordillera, 8) Southern Rocky Mountains, 9) Sierra Nevada and American Coastal Mountains

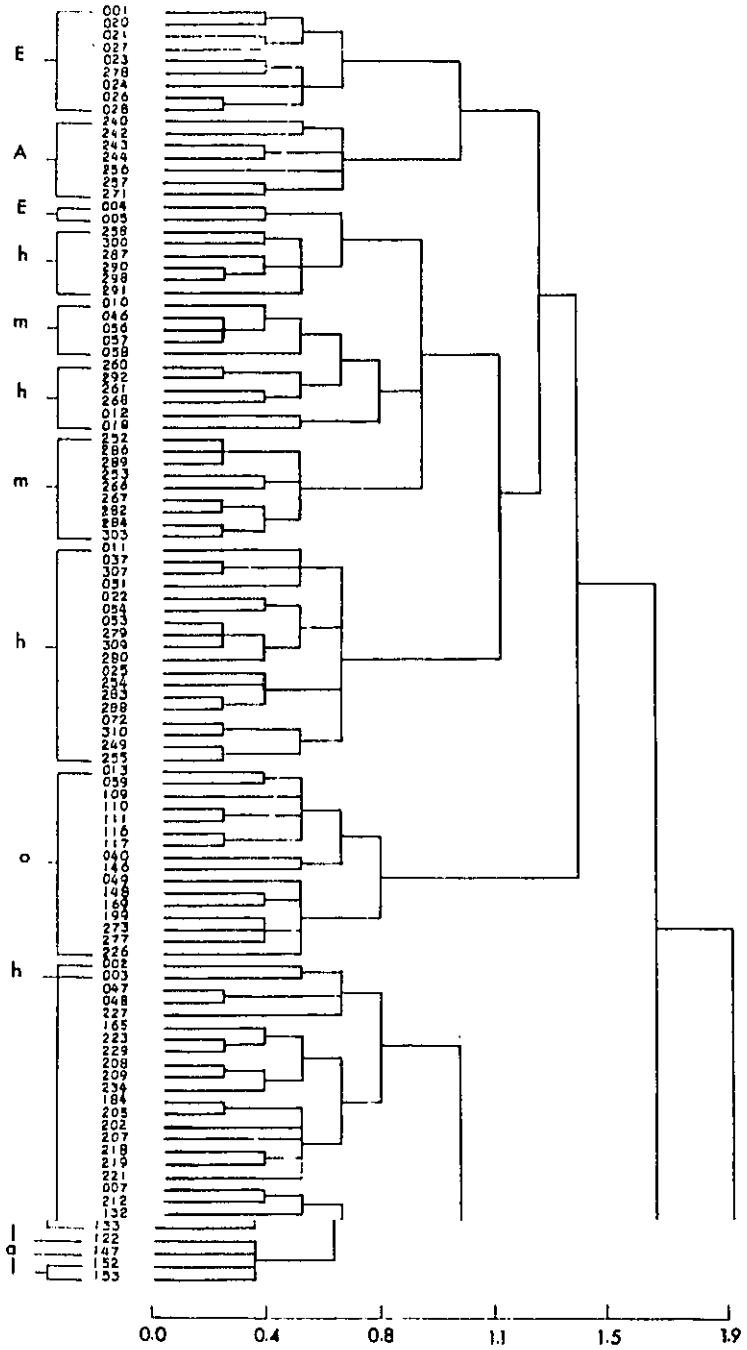


Figure 3. Dendrogram produced by the flexible sorting method, based on 35 characters (see table 2), and representing the pattern within the Ionaspis-Hymenelia complex in relation to the genera Eiglera and Aspicilia cinerea. The letters associated with the labels corresponds to the following species groups based on present study: E=Eiglera, A=Aspicilia cinerea, m=melanocarpa group, h=haematina group, o=odora group, e=epulotica group, l=lacustris group, and a=alba group. The number corresponds to the reference number for each individual in the anatomical and morphological study .

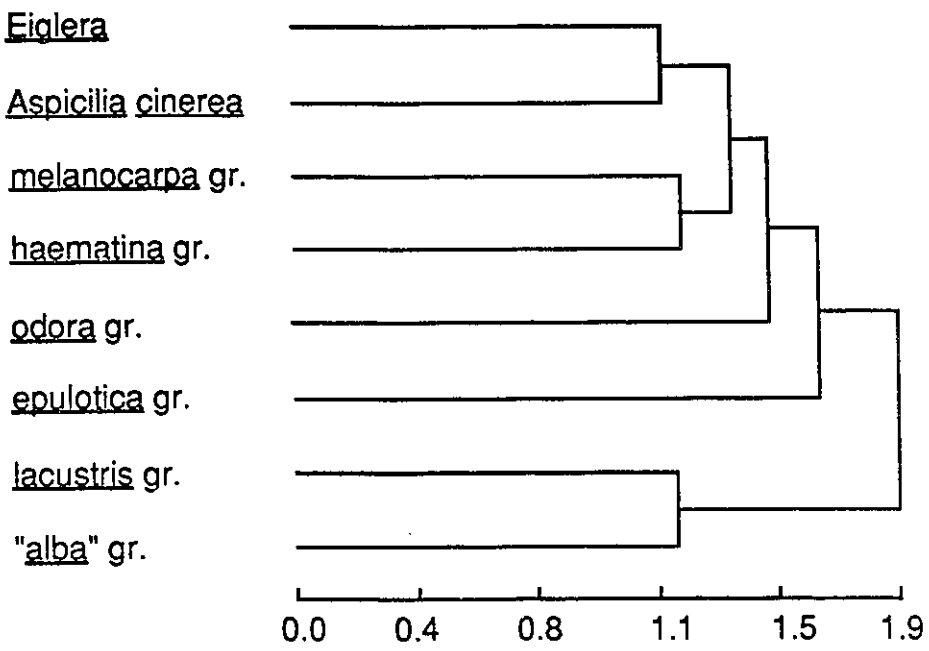


Figure 4. Intergroup distances based on anatomical and morphological data obtained from 196 specimens using the flexible sorting method.

The first two components of the PCA (Fig. 5) explain 30.6% of the total variation, the third 7.3%, while each of the 32 other components explains less than 5.8% of the variation. Except for the lacustris group, the clusters revealed by the flexible sorting method occupy more or less distinct regions of the PCA bidimensional projection. The characters corresponding with this pattern are listed in the second (PCA axis 1) and third column (PCA axis 2) of Table 3. With respect to these two dimensions, the main discontinuous variation among the specimens is provided by the second axis. All species groups with a bluish green epihymenial pigment, responsible for the black color of the apothecial disks and for the HNO_3 positive violaceous pink reaction, are found at the bottom part of the projection compared to the species groups having pale apothecia. The former (i.e., Eiglera, Aspicilia cinerea, melanocarpa and haematina groups) are recognizable by their solid symbol on Figure 5. Other characters, such as the thickness of the apothecial margin, the lateral excipulum proplum thickness, the thallus type, and ascus apical structure in Lugol's solution, contribute to this pattern (Table 3). The ascospore size, especially its width, the hymenium height, and the rock type are responsible for most of the variation along the first axis of the PCA.

In order to evaluate the 8 species groups revealed by the flexible sorting method, a canonical variate analysis using 16 quantitative variables (20-30, 32, 34, 36-38; Table 2) was done. The generalized distances among species groups were shown to be significant, the probability greater than Mahalanobis distance being 0.0001 for all pairwise distances except between the "alba" and lacustris groups, which was 0.0024.

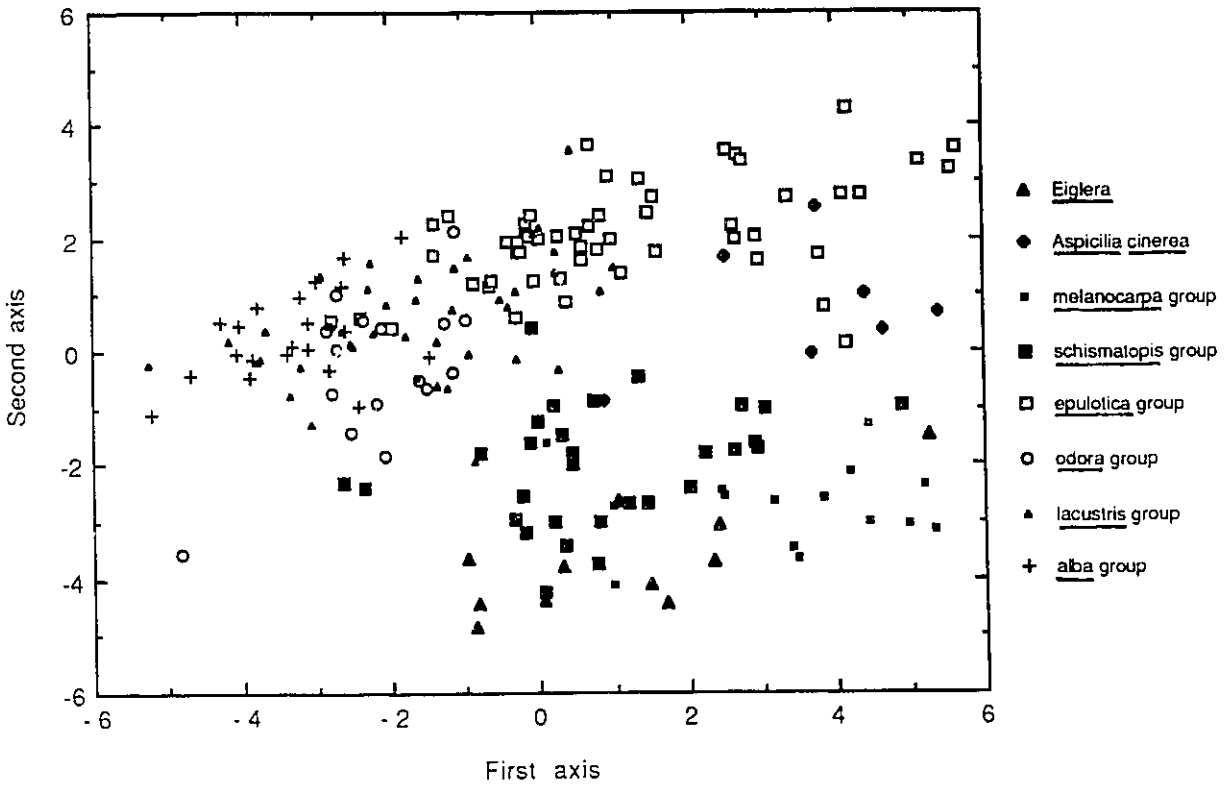


Figure 5. Projection of 196 specimens from the Ionaspis-Hymenelia complex and related genera onto principal component axes using 35 characters. The symbols indicate the clusters revealed by the flexible sorting method (see Fig. 3 and Fig. 4).

Table 3. List of characters, in decreasing order of importance, best explaining the distribution in multidimensional space of six species groups within the Ionaspis-Hymenelia complex as well as Eiglera and Aspicilia cinerea. Numbers following each character indicate the relative positions of the characters (as to their degree of concordance, in decreasing order of importance with the 8 species groups pattern) as revealed by PCA and stepwise discriminant analysis.

Characters	PCA axis 1	PCA axis 2	Stepwise discriminant analysis (prob. > F)
Ascospores dimensions	1-6		1, 2 (0.0001)
Apothecia margin thickness		4, 6	3, 6 (0.0001)
Hymenium height	7		5 (0.0001)
Lateral excipulum propium thickness		2, 3	9 (0.0074)
HNO_3 reaction of the ascoma pigment		1	
Thallus type (epi- or endolithic)		5	
Epihymenial color		7	
Ascus apical structure in Lugol's solution [1,3]		8	
Rock type	8		
Apothecial disk color			
Epipsamma presence/absence			
Ascospore halo [1,3]			
Phytogeography [2]			
Apothecial disk diameter			4 (0.0001)
Apothecia density			7 (0.0001)
subhymenium thickness			8 (0.0011)

1 Character considered useful at the generic level by Poelt (1973b) in previous studies for other genera

2 Character considered useful at the generic level by Hale (1984) in previous studies for other genera

3 Character considered useful at the generic level by Haffelner (1984) in previous studies for other genera

Of the 16 characters used, 9 were shown to be significant by a stepwise discriminant analysis to explain the 8 species groups (Table 3). Six of these characters coincide with the ones already found with PCA. The three additional characters were the apothecial disk diameter, the apothecial density, and the subhymenium thickness. Subsequently, it was found that some species groups could be characterized by the apothecial disk color, the presence or absence of an epipsamma, the presence or absence of halonate ascospores, and the phytogeography. Thus, these characters have been included in Table 3 even though they were not revealed by the numerical analyses.

Out of the 16 characters listed in Table 3, three have been used as diagnostic characters at the genus level in previous studies on other genera (Poelt, 1973b; Hale, 1984; Haffelner, 1984). These characters are: the ascus apical structure as revealed by Lugol's solution, halonate ascospores, and phytogeography. The first character relates to Eiglera. This genus is characterized by a unique ascus apical structure revealed by Lugol's solution (Fig. 6a). All the taxa included in the other seven species groups have an ascus apex which is IKI negative. The other two characters, the presence/absence of halonate ascospores and phytogeography, suggest that the alba and lacustris group, with halonate ascospores and mostly found in temperate and boreal regions, should be part of the same genus, but apart from the genera Ionaspis and Hymenelia, all with non-halonate ascospores and mostly found in Arctic-alpine regions. Some rare individuals of Hymenelia can have some halonate ascospores.

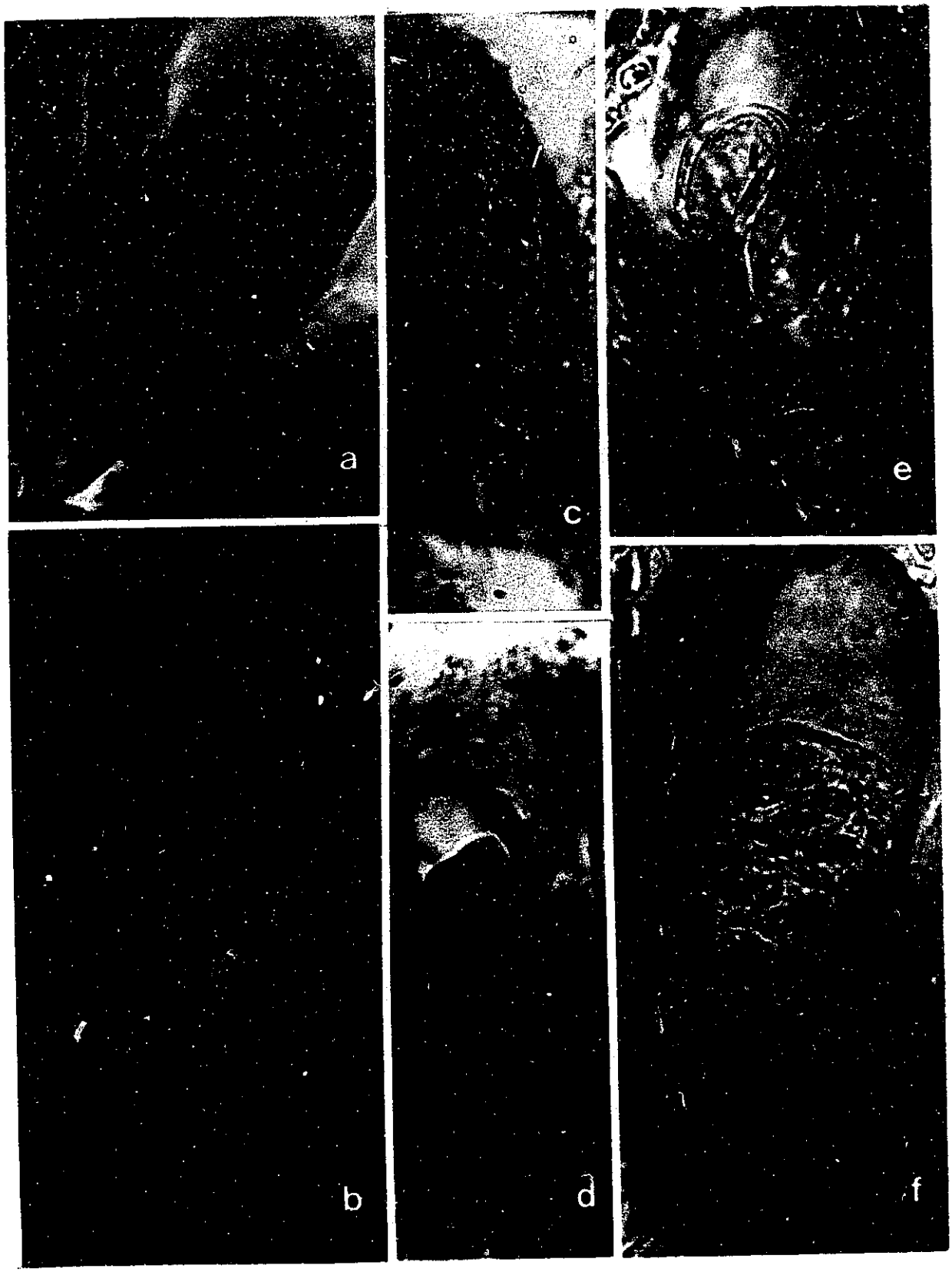


Figure 6. Apical structure of the ascus as revealed by Lugol's solution with a) Eiglera flavida (Lutzoni & Proulx no. 156 CANL; 1000 X), b) Hymenelia epulotica s. lat. (Lutzoni & Proulx no. 310 CANL; 1000 X), c) Ionaspis chrysophana (Du Rietz Gellivare, Suaeva 22.7.1922 UPS; 1000 x), d) Ionaspis lavata (Otto no. 3095 CANL; 1000 X), e) "Hymeneliella lacustris" (Brodo no. 5573 WIS; 1000 X), f) Aspicilia cinerea (Brodo no. 6030 CANL; 1000 X).

Using the canonical variate analysis, 27.6% of the specimens were considered "misclassified". This can be explained by the inclusion of species groups that have small distances (e.g. "alba"-lacustris groups; Fig. 3); therefore, which overlap with respect to the characters being used. The percentage drops to 5.5% when the dendrogram is considered at a higher level (Fig. 10) where only the three main clusters, excluding Eiglera and Aspicilia, are separated. This is perhaps not surprising since the protocol for this study was developed to solve classification problems at the genus level. Nevertheless, these 8 species groups are useful as a starting point. The North American species found in each species group of the Ionaspis-hymenelia complex are listed in Table 4.

3.1.2. Electrophoresis

This part of the study is based on a very limited data set, and is used here only to verify and extend the anatomical-morphological study by comparing the results of the latter study with an entirely different way of measuring genomic variation, i.e., enzyme electrophoresis. Of the eighteen enzymes tested, only three (PGI, 6-PGD, and IDH) could be used reliably for the systematic survey of the 8 anatomical-morphological species groups (Fig. 7). The other fifteen enzymes could not be retained for one of the following reasons: 1) no activity was detected, 2) the activity was irregularly detected or at a low level, and 3) the resolution was not good enough, at any pH used, to enable the recording of the bands. The epulotica, odora and haematina groups, with 12, 10, and 13 enzyme bands, respectively, were the most variable (Table 5). At the other extreme, Aspicilia cinerea (2

Table 4. Taxa theoretically included in the 6 species groups of the Ionaspis-Hymenelia complex as suggested by the flexible sorting method.

haematina group	Ionaspis aigneri Zahlbr., I. annularis H. Magn., I. cyanocarpa (Anzi) Jatta, I. haematina (Körb.) Th. Fr., I. häyrenii Räs., I. heteromorpha (Krempelh.) Arn., I. melanocarpa (Krempelh.) Arn. v. crustosa H. Magn., I. ochraceella (Nyl.) H. Magn., I. reducta H. Magn., I. schismatopis (Nyl.) Hue, I. spitsbergensis H. Magn., Hymenelia sumatrana Zahlbr.
epulotica group	Ionaspis epulotica Th. Fr. var. arctica (Lynge) H. Magn., I. carnosula (Arn.) Arn., I. cyrtaspis Arn., I. epulotica (Ach.) Arn., I. ochromicra (Nyl.) Hue, Hymenelia prevostii (Fr. ex Duby) Krempelh., H. similis (Massal.) Poelt & Vězda
melanocarpa group	Ionaspis melanocarpa (Krempelh.) Arn.
lacustris group	Hymenelia lacustris (With.) Poelt & Vězda
"alba" group	"Hymeneliella alba" Lutzoni, ined.
odora group	Ionaspis alpina Zahlbr., I. lavata H. Magn., I. odora (Ach.) Th. Fr., I. sp. # 1

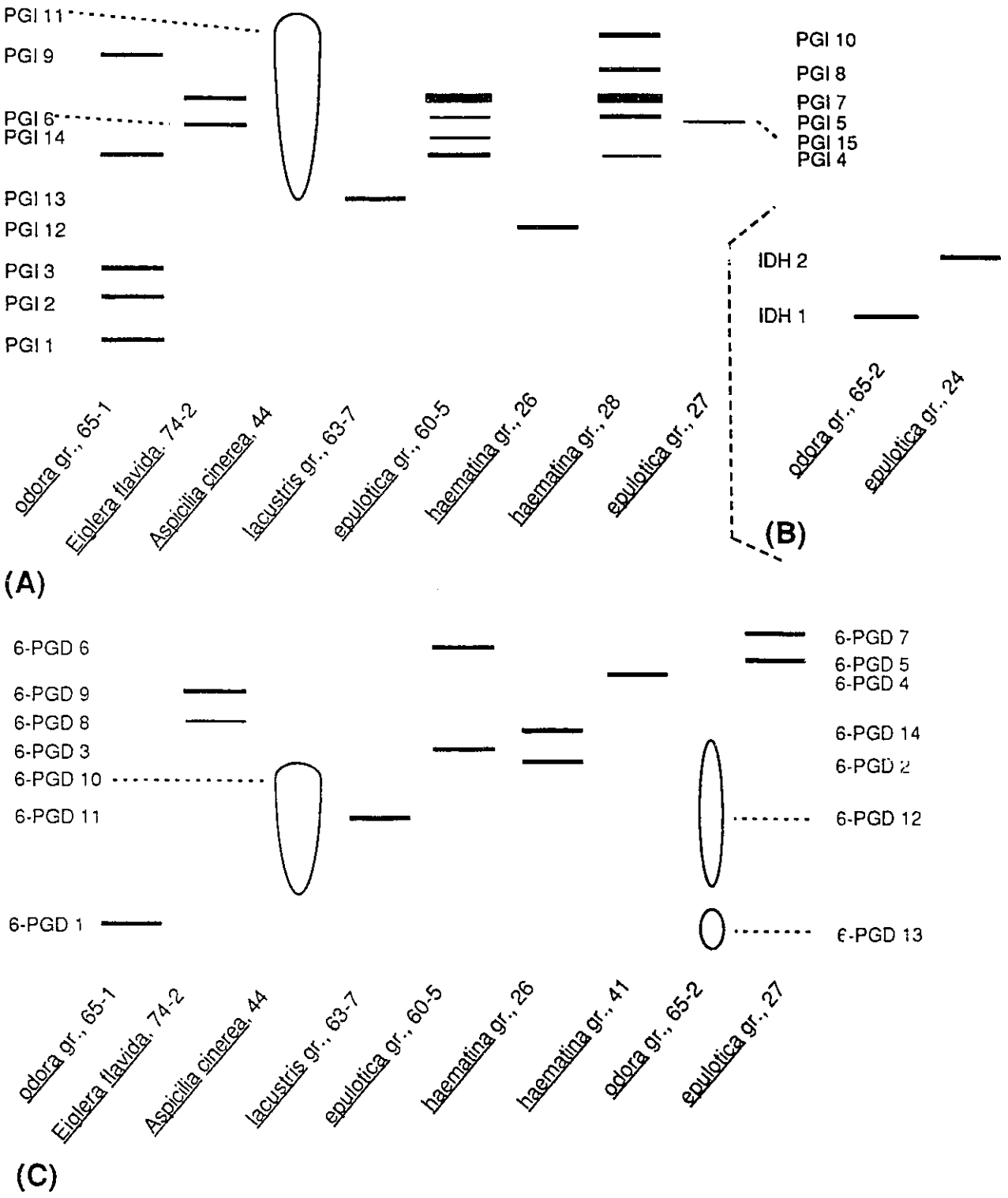


Figure 7. Identifications of electrophoretic bands obtained with (A) PGI, (B) IDH, and (C) 6-PGD, present in the Ionaspis-Hymenelia complex, Eiglera flavida, and Aspicilia cinerea.

Table 5. Number of shared enzymatic bands of IDH, PGI, and 6-PGD.

	1.	2.	3.	4.	5.	6.	7.	8.
1. Aspicilia cinerea	2	1	0	0	0	0	0	0
2. Eiglera flavida		8	0	1	4	1	3	5
3. alba group			6	4	0	6	0	0
4. lacustris group				8	2	4	2	3
5. epulotica group					12	1	3	7
6. odora group						10	0	2
7. melanocarpa group							4	4
8. haematina group								13

enzyme bands, with very poor resolution; no IDH activity has been recorded for this species) and the melanocarpa group (4 enzyme bands) were the least variable. Aspicilia cinerea was so different from the rest of the species groups that the conditions of the gels which gave the best resolution for the other groups were not so for A. cinerea. This tremendous difference between A. cinerea and the rest of the group might be the reason why no IDH activity was recorded for A. cinerea. Enzyme electrophoresis is not used to compare phylogenetically distant taxa, enzyme variations being too important to enable any comparison. Because the thallus of A. cinerea was much thicker than for any of the seven other species groups, sufficiant lichen material was always readily obtainable, and PGI as well as 6-PGD activity was much more intense than in any other species group. Nevertheless, these additional bands would emphasize even more the distinctness of A. cinerea when compared to the other species group. For endolithic lichens such as the melanocarpa group, the separation of the lichen material from the rock subtrate was very difficult, with the result that the lichen material, and consequently the enzymatic content in the sample, was often too low for enzymatic forms to be detected.

The highest absolute number of pairwise shared enzyme bands was between the epulotica and haematina groups (7), the alba and odora groups (6), as well as Eiglera flavida and the haematina group (5) (Table 5). The highest indices of similarity are found between the alba-odora pair (0.775), the alba-lacustris pair (0.577), the epulotica-haematina pair (0.560), the

melanocarpa-haematina pair (0.555), and the Eiglera flavida-melanocarpa pair (0.530), when considering the number of shared enzyme bands with the total number of enzyme bands found within the group pair (Table 6).

The pairwise intergroup similarities shown in Table 6 are summarized by the dendrogram in Figure 8. Three clusters were evident: 1) the Aspicilia cinerea , 2) the Eiglera flavida - melanocarpa - haematina- epulotica cluster, and 3) the lacustris - odora - "alba" cluster. On a genetic basis, Eiglera flavida is very closely related to the melanocarpa-haematina-epulotica group. This closeness was also evident in the anatomical-morphological study, as illustrated in Figure 3, where two specimens of the Eiglera group (Reference number 004, and 005) were misclassified into the haematina - melanocarpa cluster.

3.1.3. Canonical Consensus Analysis

The principal coordinate representations of the anatomical-morphological dendrogram and of the electrophoretic dendrogram (Fig. 9a, 9b) show that most similarities among the 8 species groups are concordant. The lacustris and "alba" groups were consistently shown to be very closely related and relatively far apart from most other species groups. This was seen in the first cluster analysis (Fig. 3) where some specimens from the lacustris group were classified with specimens of the "alba" group, and vice versa. The melanocarpa and haematina groups were also consistently very closely related but are related to a lesser extent to the epulotica and Eiglera groups. Aspicilia cinerea was definitely shown to be very distant from all the other groups

Table 6. Pairwise intergroup similarities based on electrophoretic data (IDH, PGI, and 6-PGD).

	1.	2.	3.	4.	5.	6.	7.	8.
1. Aspicilia cinerea	1.000	0.250	0.000	0.000	0.000	0.000	0.000	0.000
2. Eiglera flavida		1.000	0.000	0.125	0.408	0.112	0.530	0.490
3. alba group			1.000	0.577	0.000	0.775	0.000	0.000
4. lacustris group				1.000	0.204	0.365	0.354	0.294
5. epulotica group					1.000	0.091	0.433	0.560
6. odora group						1.000	0.000	0.175
7. melanocarpa group							1.000	0.555
8. haematina group								1.000

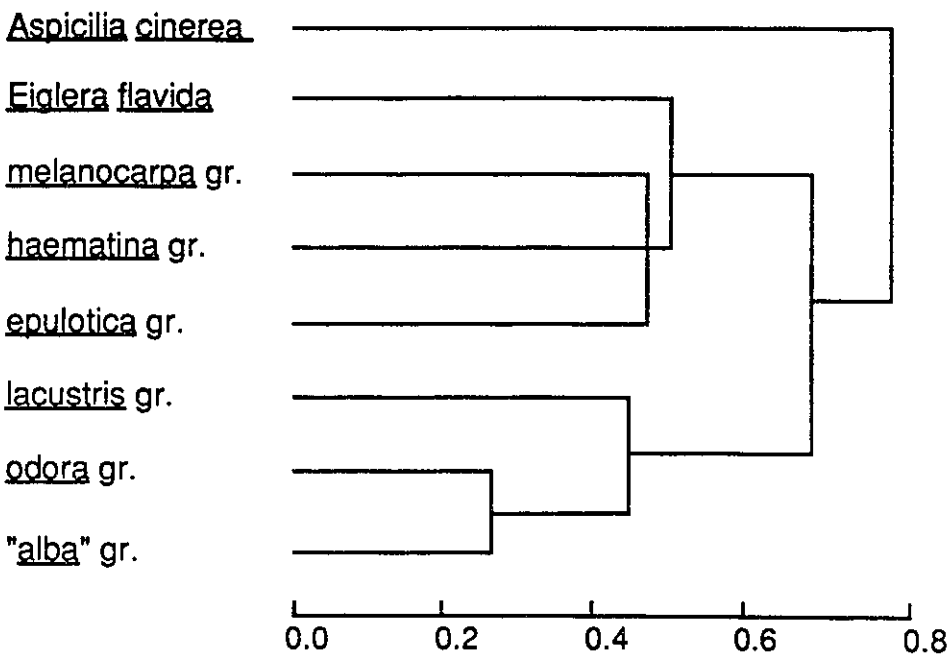


Figure 8. Intergroup distances based on electrophoretic data obtained with PGI, 6-PGD, and IDH using a single linkage (nearest neighbor) method.

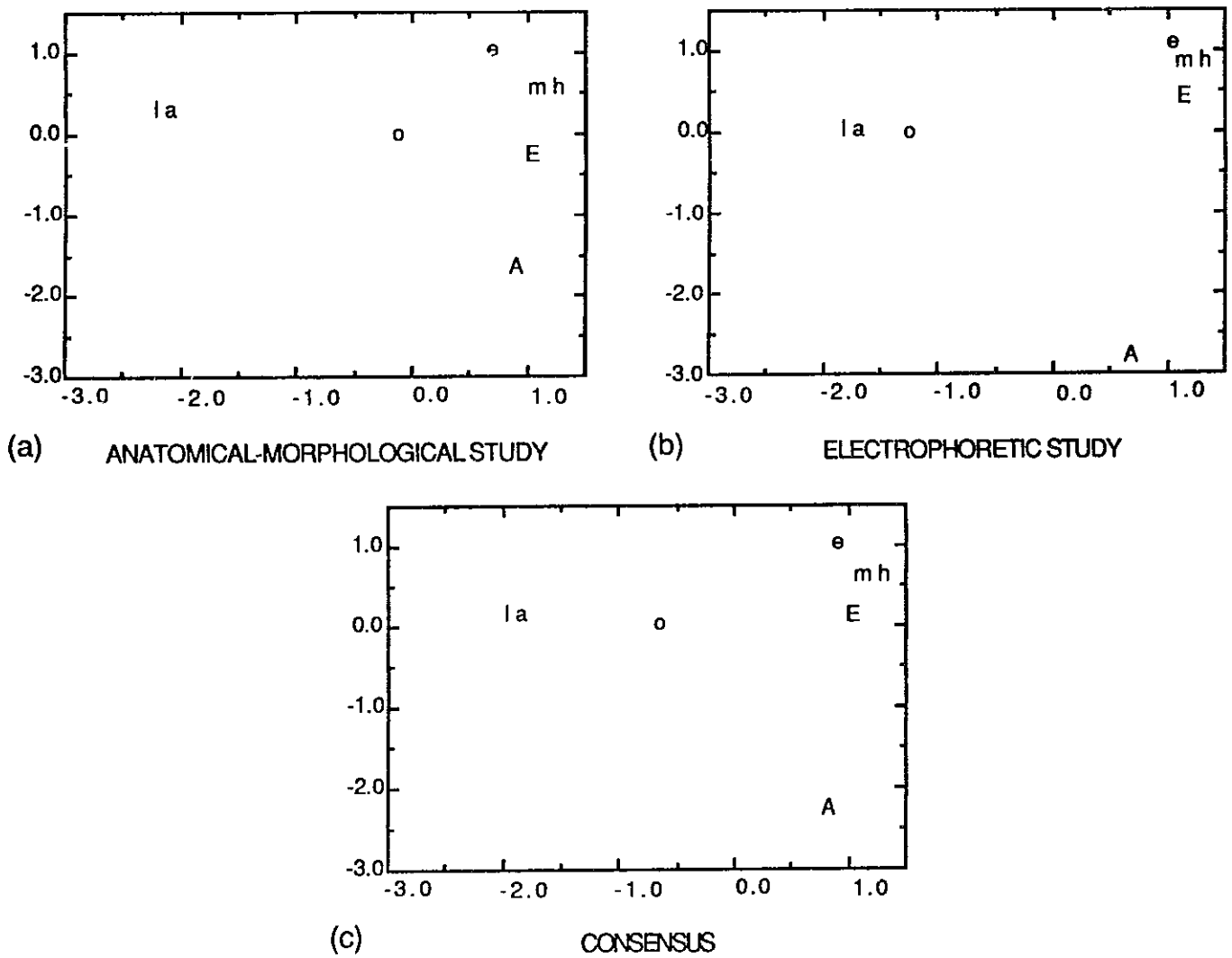


Figure 9. Principal coordinate representations of the dendrograms based on anatomical-morphological data (a) and on electrophoretic data (b) with the resulting principal coordinate consensus (c). The letters in the plots corresponds to the following species groups: E=Eiglera flavida, A=Asp:cilia cinerea, m=melanocarpa group, s=haematina group, o=odora group, e=epulotica group, l=lacustris group, and a=alba group. Ordinate = canonical axis 1, abscissa = canonical axis 2.

The principal coordinate representation of the anatomical-morphological dendrogram (Fig. 9 a), revealed a maximum of six groups: the distant (1) lacustris-alba, (2) Aspcilia cinerea and (3) odora groups; (4) the melanocarpa-haematina group with two less distinct group (5) the epulotica, and (6) the Eiglera species groups. The principal coordinate representation of the dendrogram based on electrophoretic data (Fig. 9 b) revealed three distinct groups: 1) the lacustris-alba-odora group, 2) the Aspicilia cinerea group, and 3) the epulotica-melanocarpa-haematina-Eiglera group.

The odora group was shown to be distinct on an anatomical and morphological basis but genetically more related to the lacustris-alba group. The epulotica group is genetically almost identical to the melanocarpa-haematina group but was set apart based on anatomical-morphological data. This is mainly due to the different epihymenial pigment involved. The increased distinctness of the Eiglera species group from the haematina-melanocarpa group, as revealed by the anatomical-morphological study when compared with the electrophoretic study, is due mainly to the unique ascus apical structure of Eiglera. Due to the scarcity of electrophoretic data, however, a more detailed genetic study of Eiglera in relation to the epulotica, melanocarpa, and haematina groups is needed before any modification on the existing classification of Eiglera should be made.

The fusion of both the anatomical-morphological and the electrophoretic dendrogram representations is shown by the principal coordinate consensus representation (Fig. 9c). It shows the existence of four main groups that essentially correspond to the three groups suggested by the

electrophoretic study (Fig. 9b), with the exception of the odora group, which remains distinct, as suggested by the anatomical-morphological study. Subsequently, a final dendrogram was derived from this pooled representation (Fig. 10).

3.2. RECOGNITION OF GENERA WITHIN THE IONASPIS-HYMENELIA COMPLEX

The second step in this study was to circumscribe natural generic entities among the eight species groups. The first fusion is at the euclidean distance 0.35, where eight groups combine to form six (Fig. 10). The six groups are: Aspicilia, Eiglera, melanocarpa-haematina, epulotica, odora, and lacustris-"alba". At this level of fusion, the epulotica group is distinct from the melanocarpa-haematina group, which is contrary to the results obtained in both the anatomical-morphological and the electrophoretic studies (Fig. 9). At the euclidean distance 0.44, four groups occur. Three of the four groups (lacustris-"alba", odora, and melanocarpa-haematina-epulotica) are part of the Ionaspis-Hymenelia complex. The fourth group comprises the genera Eiglera and Aspicilia.

The three main groups of the Ionaspis-Hymenelia complex should be considered as genera for the following main reasons: 1) the three groups of the Ionaspis-Hymenelia complex are morphologically, anatomically and genetically distinct, and 2) characters used at the generic level for other genera are also diagnostic characters for these groups (Table 3) It was found

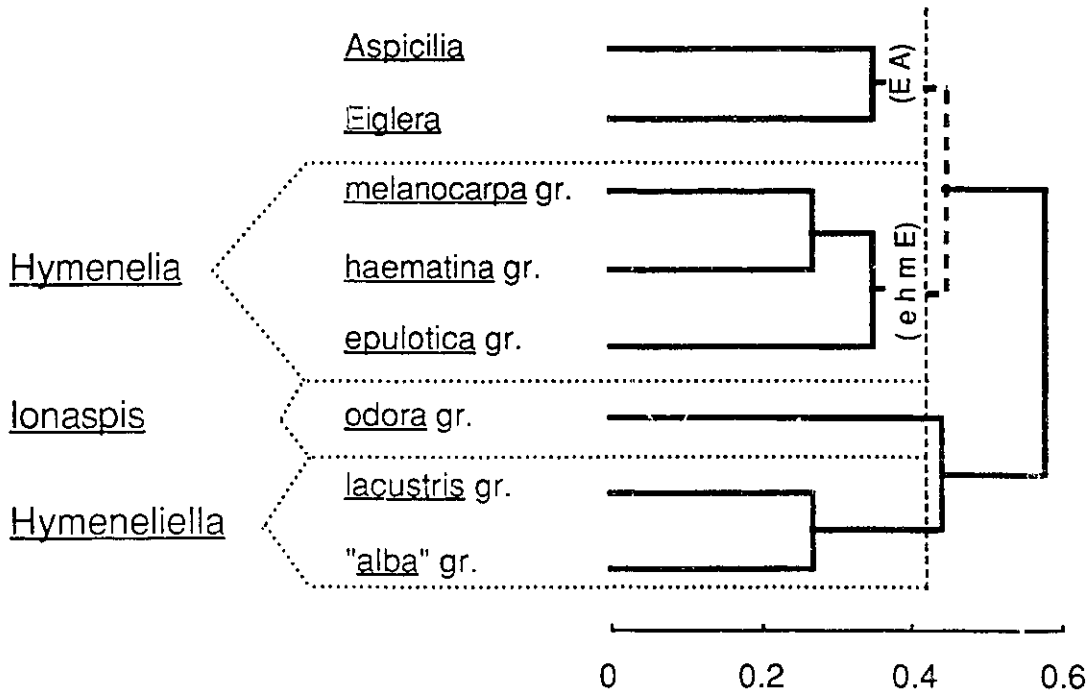


Figure 10. Euclidean consensus dendrogram based on the anatomical-morphological and the electrophoretic data sets. The letters in parentheses correspond to the following species groups: E=Eiglera flavida, A=Aspicilia cinerea, m=melanocarpa group, h=haematina group, e=epulotica group.

that two of the three groups in the complex have nomenclaturally valid names, and the third group requires a new name. The genus Hymenelia s. str., with H. prevostii (in the epulotica group) as its type, will now include the melanocarpa, haematina and epulotica groups. If Ionaspis chrysophana (the type species of the genus Ionaspis) is confirmed to be sufficiently related to the odora group so as to be included in the same genus, Ionaspis would then include I. chrysophana (=I. suaveolens auct), I. handelii, and the odora group. The former two species have an epihymenial KOH negative pigment compared to an epihymenial KOH positive violet reaction, a diagnostic character of the odora group. If I. chrysophana cannot be included in the same genus as the odora group, a new name will have to be given to the latter. Ionaspis chrysophana, and I. handelii, which are two species found exclusively in Europe, unfortunately, were not included in this study. Further work is therefore needed before any definitive decisions are made.

The lacustris and "alba" groups are included in a new genus to be called "Hymeneliella", no previous name being available. This name was selected mainly for practical purposes: to make it easy to relate the traditional combination "Hymenelia lacustris" to the new genus Hymeneliella, and to facilitate reorganizing herbarium material.

The position of Eiglera is problematic, as shown by the dotted lines of the dendrogram (Fig. 10). At the 0.44 distance (Fig. 10) Eiglera could have been grouped either with Aspicilia or with the melanocarpa-haematina-epulotica group because the element of the second canonical consensus coordinates (Table 7) corresponding to Eiglera was (-.0002) almost equal to

Table 7. Canonical consensus coordinates, scaled to unit norms, of the eight species groups.

Species groups	first coordinate	second coordinate	third coordinate	fourth coordinate	fifth coordinate	sixth coordinate	seventh coordinate
melanocarpa	0.1723	0.1003	-.1137	-.0162	0.0929	0.1935	0.0523
Eiglera	0.1665	-.0002	-.0236	-.1253	-.2447	-.0026	-.0015
haematina	0.1734	0.1004	-.0700	-.0952	0.1313	-.1765	-.0293
Aspicilia	0.1242	-.3846	0.0638	0.0224	0.0563	0.0044	0.0066
lacustris	-.3180	0.0148	0.0672	-.1106	0.0339	0.0627	-.1564
"alba"	-.3191	0.0148	0.0217	-.0337	0.0006	-.0402	0.1915
odora	-.1292	-.0094	-.1887	0.2129	-.0583	-.0371	-.0582
epulotica	0.1300	0.1639	0.2433	0.1458	-.0119	-.0042	-.0050
Squared lengths of coordinates							
	0.3395	0.1954	0.1222	0.1055	0.0936	0.0755	0.0682

zero (Lefkovitch, 1985). Eiglera was grouped with Aspicilia cinerea at the Euclidean distance of 0.44 (Fig. 10) since the element associated with Eiglera (-.0002), was negative as for Aspicilia, compared to the positive elements of the second canonical consensus coordinates for the melanocarpa, haematina and epulotica groups, and that it was shown that the epulotica group was genetically more closely related to the haematina-melanocarpa group than to Eiglera. Nevertheless, the results show that the genus Eiglera is barely distinct from the genus Hymenelia. This, if true, has serious implications with regard to the use of ascus structure alone, or as an overriding factor, for the classification of genera and even families (cf. Haffelner, 1984).

3.2.1. Second numerical analysis of the anatomical-morphological data

A second numerical analysis was done to find the diagnostic characters specific to Hymenelia, Ionaspis, and "Hymeneliella", the three genera of the Ionaspis-Hymenelia complex. To obtain a better representation of each genus, data were recorded for 57 other specimens and included in the subsequent numerical analyses. The reaction of the apex of the ascus to Lugol solution being constant among these three genera, this character was not used for this part, accounting for the total of 34 characters used for this PCA, instead of 35.

The first two components shown in Figure 11 obtained from PCA explain 30.8% of the total variation. The third component accounts for 8.3% whereas each of the 31 other components explains less than 6.5% of the variation. The three genera occupy more or less distinct regions of the bidimensional space. The most important characters responsible for the

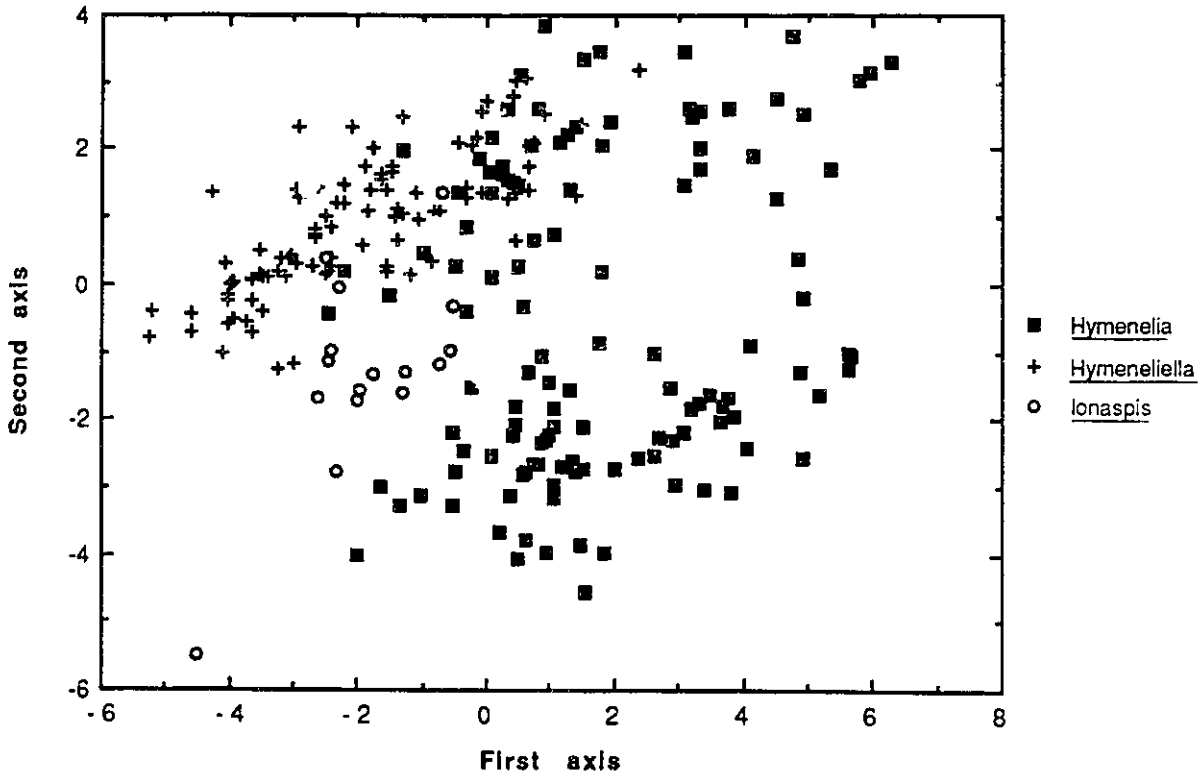


Figure 11. Projection of 235 specimens from the Ionaspis-Hymenelia complex onto principal component axis using 34 characters. The symbols indicate genera obtained with the euclidean consensus dendrogram.

distribution on the first axis are, in a decreasing order of importance, the ascospore width, the hymenium height, the nature of the rock, the subhymenium height, the disk diameter, and the ascospore length. On the second axis, it is mainly the HNO_3 reaction of the epihymenial pigment that is responsible for the distribution of the specimens.

In order to evaluate the 3 clusters corresponding to the 3 genera of the Ionaspis-Hymenelia complex, a CVA was done using 16 quantitative variables (20-30, 32, 34, 36-38; Table 2). The canonical distances between the genera were shown to be significant, the probability greater than Mahalanobis distance being 0.0001 for all pairwise distances. The lowest F-value obtained was between "Hymeneliella" and Ionaspis with 4.46 (using Hotelling's T-test, with 16 and 217 df), which is significant at the 0.01% level. The first axis of CVA alone represents 85.4% of the variation (Fig. 12). Contrary to the first CVA applied to 8 groups, the number of misclassified specimens is very low. Only 5.5% of the specimens (13/235) were considered misclassified. Twelve of the thirteen misclassified specimens were between Hymenelia and "Hymeneliella". This is mainly due to the fact that only quantitative data are used in the CVA and that these characters alone cannot separate the few extreme specimens. Several characters such as the distribution, the presence/absence of an epipsamma, the presence/absence of an halo surrounding the ascospores and the epihymenial pigments can justify the inclusion of these specimens in their respective genus.

Five characters were shown to be significant, for explaining these three genera, at levels lower than 0.5 % by a stepwise discriminant analysis. These are, in a decreasing order of importance, the ascospore width and

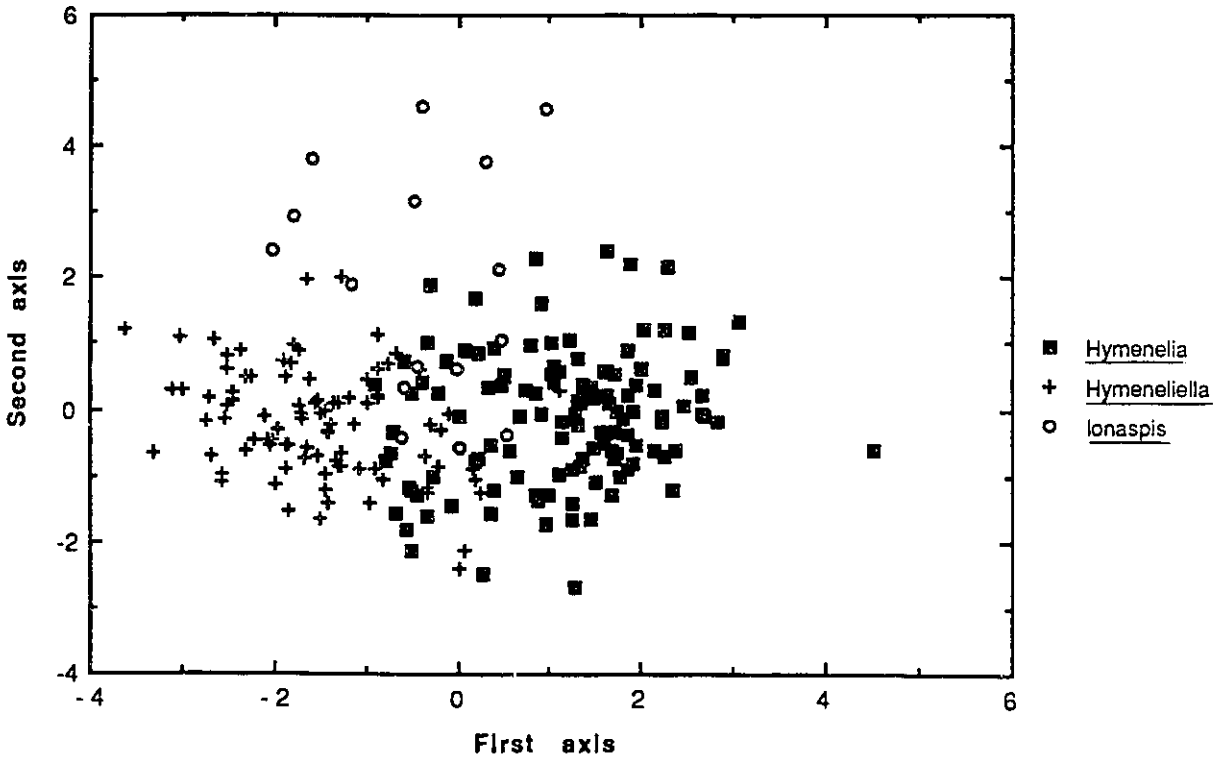


Figure 12. Canonical analysis of 235 specimens classified under 3 genera obtained with the euclidean consensus analysis, using 16 variables.

length, the subhymenium thickness, the average apothecia density, and the apothecia margin thickness.

3.2.2. Diagnostic comparison of hymenelioid genera and Aspicilia

The most readily observable diagnostic characters which differentiate the Ionaspis (odora group), Hymenelia, "Hymeneliella" and Aspicilia are the color of the apothecial disk and the following related characters: epihymenial color, HNO_3 reaction, KOH reaction, and the presence or absence of an epipsamma. Eiglera is readily distinguishable from these four genera by its unique ascus apical structure revealed by Lugol's solution. The apothecial disk color of Hymenelia, Ionaspis, Eiglera and Aspicilia is given by an epihymenial pigment, whereas for "Hymeneliella", the presence of a granular epipsamma is responsible for the rusty brown to yellowish brown color of the disk (Fig. 13i, Table 8). In the absence of an epipsamma as for "Hymeneliella alba", the disk is whitish, with no other hymenial pigment being present. The pigments found in Aspicilia, Eiglera, Hymenelia, and Ionaspis, are various. Ionaspis lavata and Ionaspis sp. # 1 are characterized by a yellowish to brownish pigment having HNO_3 positive orange and a KOH + violet reactions. Hymenelia species have an apothecial pinkish pigment or an apothecial bluish green to olive green pigment. The former is not visible in thin sections (≈15 µm), and is HNO_3 and KOH negative. The latter pigment has an HNO_3 positive violaceous pink reaction and is KOH negative as for the epihymenial pigment of Eiglera (Table 8). The dark olive brown to olive black pigment, responsible for the black color of the apothecial disk of Aspicilia, is HNO_3 + yellow-green and KOH + yellow to

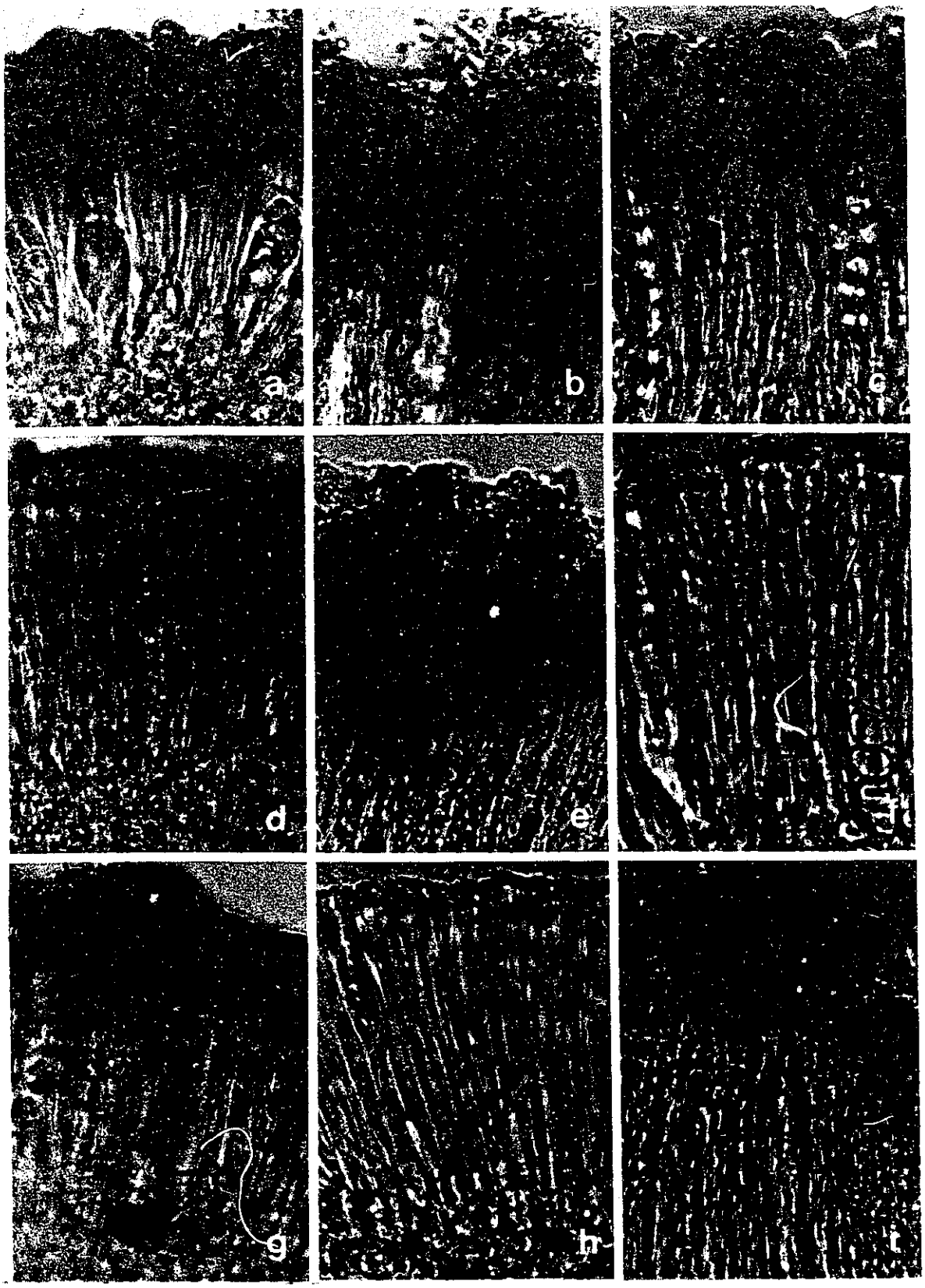


Figure 13. Unstained radial longitudinal sections in apothecia of hymenelioid lichens and Aspicilia showing hymenial coloration and epipsamma of the lacustris group; a) Eiglera flavida, b) Hymenelia melanocarpa, c) haematina group, d) odora group (Ionaspis lavata), e) Ionaspis chrysophana, f) epulotica group, g) Aspicilia cinerea, h) "alba" group, and i) lacustris group, (400 X).

Table 8. Diagnostic comparisons between hymenelioid lichens and related genus Aspicilia.

Diagnostic characters	Hymenelia	"Hymeneliella"	Ionaspis odora group (=Ionaspis lavata & I. sp. # 1)	Ionaspis chrysophana type species (Magnusson, 1933)	Eiglera	Aspicilia A. gibbosa group (Magnusson, 1939)
Thallus	epi- or endolithic	epilithic	epilithic	epilithic	epi- or endolithic	epilithic
epihymenium color	Bluish green, olive green or hyaline	hyaline	yellowish to brownish	emerald green or dark bluish green	green to bluish green, also olive brown	olive yellow or olive brown
apothecial HNO_3 reaction	+ violaceous pink or negative	negative	+ orange	negative (= + color unchanged)	+ violaceous pink	negative (= + pale yellow-green)
apothecial KOH reaction	negative	negative	+ violet	negative	negative	negative (= + deep yellow to olive-brown
Apothecial disk color	black or pinkish	rusty brown to yellowish brown or whitish	brownish or grayish to almost black	black	black	black
Epipsamma	absent	present	absent	absent	absent	absent
Ascus apex IKI reaction	negative	negative	negative	negative	+ blue	negative
Ascospores	not halonate rarely halonate	halonate	not halonate	not halonate	not halonate	not halonate
Ascospores width (µm)*	(4.9-)6.7 -9.0- 11.7 (-18.8)	(3.0-)4.9 -7.0- 9.8(-11.2)	(4.8-)6.9- 8.7 (-9.5)	6-8	(6.8-)7.7 -8.9- 10.2(-12.4)	(5-) 10-12 (-18)

(continued on next page)

* Measurements are usually given by five numbers [ex. (1.7-)4.1 -8.7- 13.3(-27.0)]. The numbers in parentheses are the most extreme measures recorded. The numbers in bold, but not underlined, are the lower and upper limit of the standard deviation applied on the average minimal measurement or applied on the overall average if minimum and maximum data were not recorded. The number in bold and underlined is the overall average.

Table 8. (continued)

Diagnostic characters	Hymenelia	"Hymeneliella"	Ionaspis odora group (=Ionaspis lavata & I. sp. # 1)	Ionaspis chrysophana type species (Magnusson, 1933)	Eiglera	Aspicilia A. gibbosa group (Magnusson, 1939)
Conidia length (µm)	(3.4-) 5.6- 7.7(-9.8)	(2.9-) 3.7 (-4.4)	(3.9-) 5.9- 8.2(-9.3)	---	4.8	(4-)15-17(-42)
Photobiont	Trentepohlia and Trebouxia	Trebouxia	Trentepohlia	Trentepohlia (*sensu* Th. Fries, 1871)	Trebouxioid	Trebouxioid
Substrate	siliceous or calcareous	siliceous	siliceous	siliceous	calcareous or siliceous	siliceous, rarely calcareous or lignicolous
Distribution	Arctic-alpine, rare in boreal zone and in Great Lakes region	Boreal-hemiboreal subzone, temperate, and Appalachian Mountains; rarely in Arctic	Arctic-alpine	boreal alpine	Arctic-alpine	widespread
Hymeneium height (µm)	(50-)85 -120- 150 (-210)	(45-)75 -95- 110 (-135)	(50-)60 -100- 130 (-160)	50-65	(39-) 72 -76- 79(-119)	(60-)100-115(-200)
Subhymenium height (µm)	(12-)25 -38- 51(-75)	(10-)16 -24- 31 (-50)	(12-)22 -42- 62(-82)	---	(7-)23 -27- 31(-48)	---
Apothecia density (no. of apo. /2.5 X 2.5 mm)	(1.7-)4.1 -8.7- 13.3 (-27.0)	(2.8-)7.3 -15.5- 23.7 (-42.0)	(10.5-) 14.3 -23.4- 32.5(-42.2)	---	5.3 -20.0- 66.0	---

olive-brown (considered HNO_3 negative or intensifying, and KOH + dull straw by Coppins in 1987).

Other important characters, such as consistently having halonate ascospores, the shortest conidia, no apothecial pigment except for the presence of an epipsamma in those individuals exposed to sun, differentiate "Hymeneliella" from the other hymenelioid genera and from Aspicilia (Table 8). Hymenelia also has several other characters which can help to distinguish it from "Hymeneliella" and Ionaspis; along with the widest ascospores, the highest hymenium, the lowest apothecia density, and an intermediate subhymenial height, Hymenelia is the only genus within the Ionaspis-Hymenelia complex having calcicolous species (see Table 8). Besides the fact that Aspicilia has thicker thalli, the gibbosa group is distinct from the hymenelioid lichens by having drastically longer conidia and, larger ascospores, by being widely distributed, and by producing secondary metabolites such as depsidones.

If it were not for the unique apical structure of its asci, revealed by Lugol solution, Eiglera would be classified within Hymenelia. Except for that character and its slightly lower hymenium, there is no obvious character that could be used to distinguish it from the rest of the hymenelioid lichens and Aspicilia (Table 8). However, during field work, I noticed that Eiglera flavida tolerates stronger water current than any other aquatic hymenelioid lichen in the Arctic, and seems to be restricted to these type of habitats. Neighbouring sympatry would therefore best characterize the distribution of Eiglera when compared to Ionaspis and Hymenelia. The habitat characteristics of E. homalomorpha, the only other species of the genus, are

needed in order to determine if this observation can be generalized for the genus as a whole. It is also important to note that Eiglera and Hymenelia are the only genera that have both endo- and epilithic thalli, which is further evidence for their close relationship.

From the description given by Magnusson (1933; Table 8), Ionaspis suaveolens auct. (= I. chrysophana) is best distinguished by its hymenial pigment. Even if the color of the pigment is similar to that found in Eiglera and some Hymenelia species, its reaction to KOH and HNO_3 are unique, being negative for both reagents. It is also the taxon having the lowest hymenium when compared to the rest of the hymenelioid lichens and to the Aspicilia gibbosa group. Based on these data alone it would be hazardous to determine to which genus or species group this taxon is most closely related. Once again, more data on this European species are needed before any definitive classification involving this species can be made.

The general distribution patterns of Ionaspis (= I. lavata and I. sp. # 1), Hymenelia and "Hymeneliella" in North America are also distinctive. "Hymeneliella" is by far the most meridional taxon, being reported mostly from the Appalachian-Great Lake region (Fig. 14). The most northern localities are Northwestern Alaska in the west and Iqaluit (Southern Baffin Island) in the east; "Hymeneliella" is rare in Iqaluit. The most southerly known population of "Hymeneliella" is from southern Oklahoma. Other populations are from northern Québec and the west coast.

Hymenelia, Ionaspis, and Eiglera are allopatric with regard to "Hymeneliella"; they are mostly Arctic-alpine taxa. Hymenelia has a typical Arctic-alpine circumpolar distribution. It is sympatric with Ionaspis and

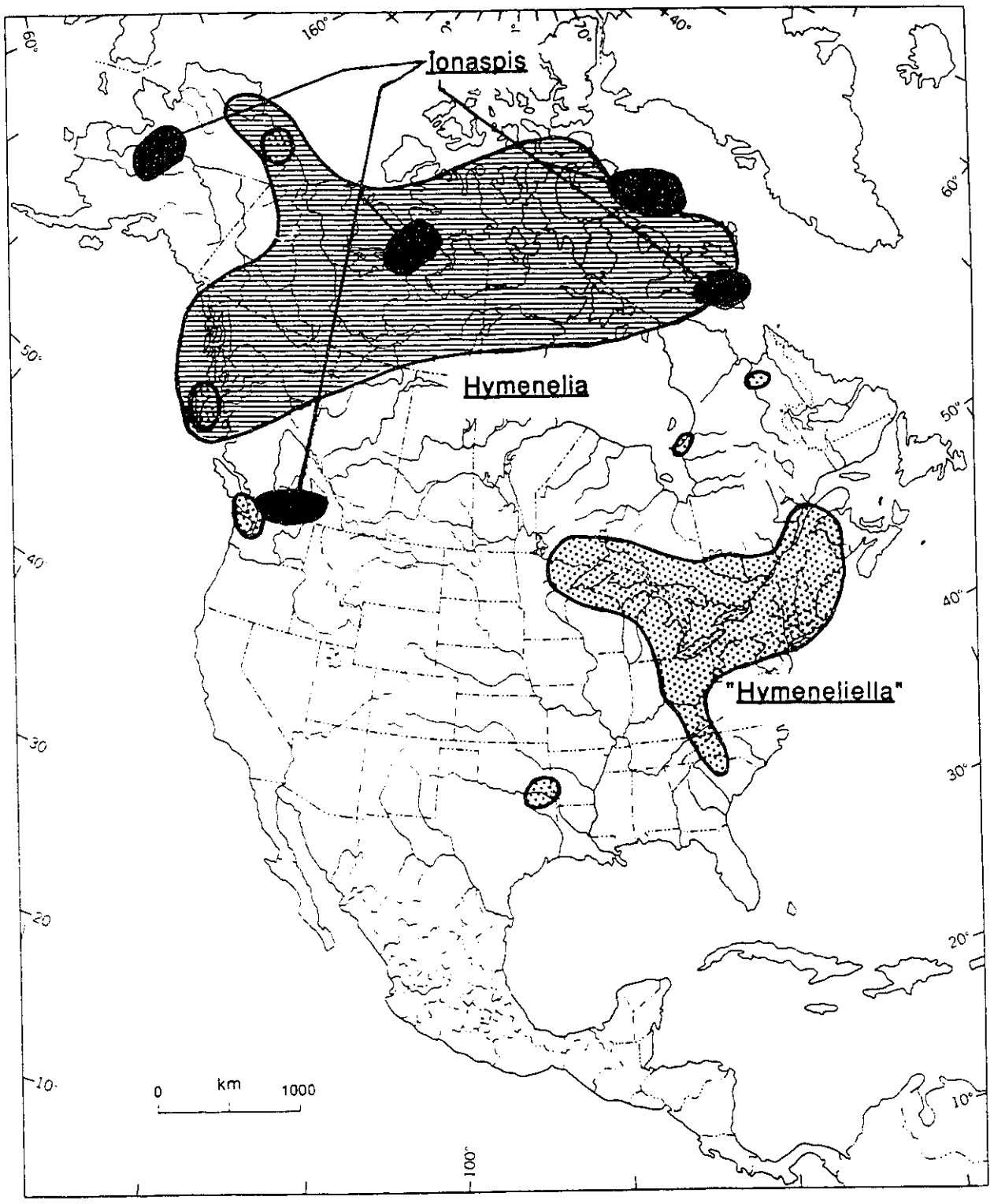


Figure 14. North American distribution of Hymenelia, "Hymeneliella", and Ionaspis.

Eiglera, but Ionaspis might have a different geographical origin than Hymenelia. Out of the five species included in Ionaspis, only I. odora is Arctic circumpolar. Ionaspis sp. # 1 is known only from three localities, two on Baffin Island and one in Coppermine. Ionaspis lavata is confined to the Northwestern Cordillera, I. chrysophana appears to be strictly Eurasian, whereas the only known report of I. alpina is from China. This suggests that the odora group (excluding I. chrysophana) might have originated in the Pacific basin. This is the most poorly collected taxon of the three genera of the Ionaspis-Hymenelia complex in North America. Collections from several different localities are needed before any reasonable speculations regarding the phytogeographic origin of Ionaspis can be made.

3.3. ANATOMY AND MORPHOLOGY OF HYMENELIOID LICHENS

A general description of hymenelioid thalli is given in section 1.3, along with a short description of apothecia and a discussion on paraphyses. The variation in the distribution and in the following diagnostic characters among hymenelioid genera and Aspicilia are treated in section 3.2.2: presence / absence of endo- or epilithic thalli, color of apothecial disk and related characters, ascus apical structure, ascospore characteristics, conidium length, substrate, hymenium and subhymenium height, and apothecial density. This information is summarized in Table 8.

Additional information about anatomical and morphological variation can be found in "Taxonomical notes", which is found under most species in the preliminary treatment of the North American species (section

5.2). Magnusson's (1933) calcicolous and non-calcicolous species concept is discussed under Hymenelia haematina, in addition to paraphyses shapes, and some thallus and apothecial characteristics (pages 119-126).

3.3.1. Thallus morphology

In this study, most thallus characters were found to be unimportant at the genus level. Thallus thickness and areolation were not recorded in this study because their variation in Ionaspis *s. l.* correlates with the proximity of the thalli to streams (Magnusson, 1933).

According to Schneider (1979) the most informative thallus characters are: 1) the texture of the cortex, 2) the arrangement of the algae, 3) the manner of attachment, and 4) the nature of the structure of attachment. The third character is uniform in crustose lichens and the fourth character is absent. The extremely thin thalli of hymenelioid lichens make Schneider's second character unobservable. Finally, the cortex was found to be very variable within species groups due to their wide ecological amplitude (aquatic to xeric habitats) and to the drastically different forms that individuals can have (epilithic to endolithic). Within the haematina group, the epi- and endolithic thalli variation correlates with the habitat (page 122, last paragraph). The presence of both epi- and endolithic thalli was observed only in 2 of the 5 genera included in this study (Eiglera and Hymenelia) and agrees with the strong anatomical-morphological and electrophoretic similarities shown between these two genera.

The thallus color was found to be very variable within the same species (see species descriptions, section 5.2). This variation in color is

related to the proximity of the thallus to water, the nature of the rock, and whether or not it is found in shade or full sun.

Nevertheless, some generalities on color and thickness of thalli can be made. The thalli of Ionaspis (= I. lavata and I. sp. # 1) and Hymenelia often have pinkish or yellowish tints. Eiglera flavida has brownish-yellow thalli with a texture resembling dried mud. "Hymeneliella lacustris" usually has rusty brown thalli and those of "H. alba" are greyish-green. Aspicilia usually has much thicker thalli than any other hymenelioid genus. The thickest thalli were observed on Ionaspis lavata and "Hymeneliella lacustris".

3.3.2. Photobiont difference

In this study (section 3.4), the difference in photobiont was shown to be an unimportant variable at the genus level. However, Eiglera and the odora group are consistently associated with Trebouxia and Trentepohlia, respectively, in North America. Hymenelia can be found with one or the other photobiont, whereas "Hymeneliella" is mostly associated with Trebouxia. Some specimens of "Hymeneliella lacustris" are associated with two photobionts (Trebouxia and probably Trentepohlia) forming a three-membered symbiosis.

An introduction and discussion on the problem of the photobiont association in the Ionaspis-Hymenelia complex is found on page 8 and in section 4.1 (page 78). A more detailed description of the problem, in relation to Ionaspis epulotica and Hymenelia prevostii, is found in section 3.4 (page 73) and section 4.3 (page 87).

3.3.3. Apothecial anatomy

The ascocarp organization of hymenelioid lichens and Aspicilia is called cryptolecanorine (Haffelner 1989). The thicknesses of three apothecial tissues, namely, the hymenium, hypothecium, and subhymenium, were significant in discriminating among the different hymenelioid genera. However, their discriminating value was low in differentiating the hymenelioid genera. These tissues have a wide range of variation, and demonstrate substantial overlapping. These characters are much more promising at the species level. Eiglera is distinctive in having the narrowest hymenium. "Hymeneliella" and Eiglera have the narrowest subhymenium, but there is a lot of overlap with the other genera (see Table 8).

3.3.3.1. Non acetone-soluble pigments

Five apothecial pigments have been identified within the Ionaspis-Hymenelia complex (including Ionaspis chrysophana) and Aspicilia (see Table 8). The color of the disk is provided by the presence of a pigment found mostly in the epihymenium, except in "Hymeneliella" whose rusty brown to yellow-black disk color is due to the presence of an epipsamma, and in the epulotica group whose pinkish disk color comes from a pigment seemingly in the hypothecium. The only pigment shared among the genera considered here is bluish green to olive green in color. It is responsible for the black color of the apothecial disks of Eiglera and Hymenelia. It is HNO_3 + violaceous pink and KOH negative. This pigment corresponds to Bachmann's (1890) Lecidea green "pigment type". As reported by Coppins (1987), some of these non acetone-soluble pigments may be represented by

more than one substance. The Lecidea green pigment seems to be one of the most widespread non acetone-soluble pigments. Coppins (1987), reports the presence of this pigment in 18 genera, including Eiglera flavida and Ionaspis heteromorpha (synonym of I. haematina in this study).

Hymenelia is the only genus studied here that includes species with different pigments (this might also be true for Ionaspis). Hymenelia haematina and H. melanocarpa have a pigment of the Lecidea green type, whereas the other species have pinkish disks. This latter pigment is very diffuse in the hypothecium and is both HNO_3 and KOH negative. This pigment was not reported by Coppins (1987). The pinkish appearance of the disk might just be due to the absence of the Lecidea green pigment. In other words, the pink pigment might be present in all members of Hymenelia, but hidden by the Lecidea green pigment in H. haematina and H. melanocarpa. This pink apothecial pigment is also present in thallus of most black fruited and pale fruited species of Hymenelia.

Ionaspis (I. lavata and I. sp. # 1) has an HNO_3 + orange and KOH + violet pigment, which gives a brownish or grayish to almost black color to the disk. In thin sections, the pigment is yellowish to brownish. This pigment best fits what Coppins (1987) reported as Thalloidimia green, under which he included I. odora (here called I. suaveolens). However, he described the pigment as being dull greenish, KOH + violet, C + violet, and N + red or red purple. This might mean that I. lavata and I. sp. # 1 have a pigment different from that of I. suaveolens. In future studies, special attention should be given to this character on European specimens of I. suaveolens, along with I. chrysophana (syn. I. suaveolens auct.) and I. lavata.

Coppins (1987) reported the presence of an Aspicilia green pigment in both Aspicilia and I. suaveolens auct. (here called I. chrysophana). Aspicilia pigment (as observed here on A. cinerea, A. caesiocinerea, A. candida, and A. verrucigera) is olive yellow or olive brown, with an HNO_3 negative (also interpreted as "+ slight change in color, becoming pale yellow-green") and KOH + deep yellow to olive brown reaction, corresponding to the Aspicilia green pigment described by Coppins (1987). However, specimens of I. chrysophana observed here were emerald green or dark bluish in color (see Fig. 13e) and had HNO_3 negative (also interpreted as "+ color unchanged") and KOH negative reactions. Aspicilia and I. chrysophana are considered here to have different pigments rather than the same. The term Aspicilia green should be restricted to the olivaceous pigment typical of Aspicilia.

Coppins (1983) indicated that the nature of acetone insoluble pigments and their location (especially within apothecia) are of prime importance in the delimitation of species within many lichen genera. The epihymenial pigments were determined here to be important diagnostic characters at the species or genus level for hymenelioid lichens. As discussed by Coppins in 1983, little is known about the structure and biogenesis of these pigments; unfortunately this is still the case. This type of information would be invaluable for the evaluation of their taxonomic significance. More information on non acetone-soluble pigments is summarized in Table 8, illustrated in Figure 13, and discussed on pages 82-85.

3.3.3.2. Epipsamma

Poelt (1973b) defined the epipsamma as being a granular excretum over the paraphyses. This term is used here in the same sense as Poelt and pinpoints the non-refringent, rusty brown, granular layer located at the surface of the epihymenium and on the apothecial margin of some "Hymeneliella"species. The apothecia of "Hymeneliella alba" are usually completely devoid of an epipsamma and contain no pigment, hence the apothecial disks are whitish in color. When present in "H. alba", the epipsamma is very thin and is located almost exclusively on the margin of the apothecia, as compared to "H. lacustris" whose apothecia are usually uniformly covered with an epipsamma. The production of an epipsamma in "Hymeneliella" seems to be related to the degree of exposure to the sun. The more exposed the thallus is to the sun, the thicker the epipsamma would be. "Hymeneliella lacustris" is an heliophilous species, whereas "H. alba" is sciaphilous. Individuals of "H. alba" that are growing along forest margins, or in forest openings, are the ones with an epipsamma on their apothecial margin, and sometimes with a thinner layer covering the disk.

3.3.3.3. Ascus structure

Eiglera has the most distinctive ascus apical structure of all hymenelioid lichens and Aspicilia. It is the only genus studied here with an IKI + blue tholus. The ascus wall is hyaline with an external IKI + brown apical cap (Fig. 6a). Even though the apical structure of Hymenelia is not quite as spectacular, it is still very distinctive. Hymenelia has long and narrow asci with parallel sides, often containing uniseriate, spherical

ascospores. Finally, Ionaspis chrysophana and I. lavata have similar asci, as do "Hymeneliella lacustris" and Aspicilia cinerea (Fig. 6). Variation in the ascus apical structure is discussed on page 85.

3.3.3.4. Ascospores

Within the Ionaspis-Hymenelia complex the ascospores are simple, hyaline, spherical to ellipsoidal, and eight per ascus. Their width is more useful than their length to discriminate among the different species and genera. In some instances, the ascospores have a compact or diffuse epispore (a "halo"). Halonate ascospores are observed consistently only in "Hymeneliella". This outer layer of the ascospore wall is dense compared to the typical halo of ascospores of Rhizocarpon for instance. After being released by the ascus, the spores of "Hymeneliella" have a tendency to remain agglomerated. When the ascospores are separated from one another they often lose their halo. This type of halo is similar to Porpidia (Brodo, pers. comm.). Halonate ascospores are rarely seen in Hymenelia and they do not "behave" in the same way as in "Hymeneliella". In Hymenelia, the halo is dense, but the ascospores do not remain agglomerated when they are released; only a few isolated ascospores with such a halo might be seen on a microscope slide. Halo formation in ascospores has been regarded in many groups as a character with at least generic value (Poelt 1973b). It should be noted, however, that in some cases the halo can be seen only at certain stages of maturity. Along with phytogeography, conidia length, and the presence of an epipsamma, halonate ascospores were used to establish the new genus "Hymeneliella".

3.3.3.5. Paraphyses

The paraphyses of hymenelioid lichens are imbedded in a gelatinous matrix which makes their observation difficult. Their shape can be very variable within the same section. The use of paraphyses is therefore hazardous within the Ionaspis-Hymenelia complex, as concluded by Magnusson (1933) for Ionaspis. The paraphyses of hymenelioid lichens are often bifid and swollen at the apex (last two to four cells). These terminal cells are consequently subspherical to spherical, yielding a paraphysis shape referred to as submoniliform. If more than two apical cells are spherical, the paraphyses are called moniliform (Magnusson, 1933). Moniliform paraphyses are frequently observed in Hymenelia melanocarpa and were observed in other species of Hymenelia, but their presence was not as consistent in those other species. In no instance were the apical ramifications numerous enough to use the term epithecium rather than epihymenium. The lower part of the paraphyses can be simple (Eiglera flavida) or slightly divided (Hymenelia epulotica) and they have a tendency to be slightly constricted at the septa.

The length of the paraphysal cells is not uniform. At the apex, they are usually shorter and are progressively longer towards the base. The septa can be quite difficult to observe, but septate paraphyses are always present. Often non-septate paraphyses are encountered among the septate paraphyses. Paraphysal anastomoses are always present within hymenelioid lichens. The frequency of anastomosis might be significant, but could not be reliably recorded in this study. Most paraphyses are slightly undulated except for the straight paraphyses of Eiglera flavida. None of the paraphysal characters

(paraphysal ramifications, constrictions, and shape; see Table 2) used for the numerical analyses were shown to be diagnostic at the genus level.

3.3.4. Conidia

Conidia are mostly bacilliform in hymenelioid lichens, but can also be filiform, as in Ionaspis lavata. The taxonomic value of conidia shape is of the most use at the species level within the hymenelioid lichens. The length of conidia, however, is diagnostic at the genus level. "Hymeneliella" has the shortest conidia and Aspicilia has the longest conidia, with almost no overlap with the other genera included here. According to Poelt (1973b), the shape and length of conidia can be of importance at the family or genus levels, or only at the species level in genera that have a great range of variation..

3.4. THE PHOTOBIONT DIFFERENCE BETWEEN IONASPIS EPULOTICA AND HYMENELIA PREVOSTII

The distinction between trebouxioid algae and Trentepohlia can be difficult to make with old material, especially endolithic thalli. The cells of the photobiont are interspersed among rock crystals, their pigments are degraded, and their cell walls are hardly visible. In the present study, a new readily observable character was found to discriminate efficiently Trentepohlia from Trebouxia, as found in old herbarium specimens. Unlike Trebouxia, the cell walls of Trentepohlia are refringent in polarized light (Fig. 15). This was found to be true of free living Trentepohlia as well as Trentepohlia seen in a number of lichens, including Ionaspis, Hymenelia, and Racodium.

Six specimens were studied (Table 9), that is, the lectotype of Ionaspis epulotica and five specimens mentioned in the protologue of Urceolaria prevostii Duby. The cell walls of the photobiont of Gyalecta epulotica (lectotype), two specimens of Mougeot and Nestler exsiccatae, and Urceolaria prevostii collected by Prost were all found to be refringent. The two other specimens were found to be associated with Trebouxia, as was the material seen by Krempelhuber (not included in Table 9; Bayern, berchtesgadener Alpen, Watzmann, 5500-8000', 1855, no. 3468; 5, Herbarium Krempelhuberi) and identified as H. prevostii f. rosea. This implies that the distinction between Ionaspis epulotica and Hymenelia prevostii based on a difference in photobionts no longer holds, if no other diagnostic characters are found.

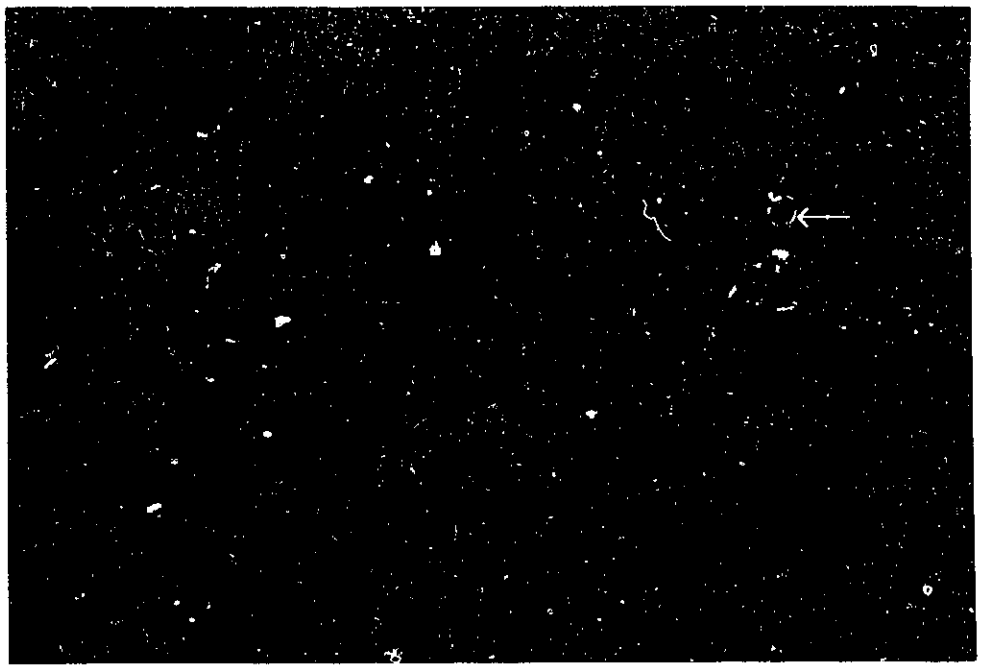


Figure 15. Longitudinal radial section in apothecia of Ionaspis lavata stained with lactophenol cotton blue subjected to polarized light (800 X). The arrow points to the refringent cell wall of Trentepohlia individual cell.

Table 9. Comparison of type material of Ionaspis epulotica var. epulotica and Hymenelia prevostii.

characters	Gyalecta epulotica (H-ACH) Angliae Lectotype	Biatora prevostii (M) Mou. and Nes. exs. 848	Gyalecta prevostii (UPS) Galliae Lectotype Le Prévost no. 197	Gyalecta prevostii (UPS) Galliae Mougeot	Biatora prevostii (CANL) Mou. and Nes. exs. 848	Urceolaria prevostii (M) Lozère Prost
Photobiont	Trentepohlia	Trentep.	Trebouxia	Trebouxia	Trentep.	Trentep.
Apothecia disk color	31 pale y. pink	52 light orange	52 light orange	52 light orange	73 pale orange yellow	54 brownish orange
Average apothecia density (n/6.25mm^2)	26.3	11.3	14.0	10.7	7.0	15.7
Apothecia disposition	agglomerate	agglom. or not	agglom. or not	agglom. or not	agglom. or not	agglom. or not
Apothecia shape	round	subangular to irregular	irregular to elongate	irregular to elongate	round to subangular	irregular to elongate
Apothecia disk diameter (µm)	85.8-147.0	168.7-265.1	120.5-241.0	120.5-241.0	241.0-361.5	120.5-192.8
Apothecia margin thickness (µm)	24.5-49.0	36.2-48.2	24.1-48.5	24.1-36.2	48.2-72.3	36.1-48.2
Ascospore length (µm)	(12.8-)14.8 (-16.0)	15.2	(12.5-)14.9 (-18.8)	(15.0-)16.0 (-17.5)	(12.5-)15.0	(13.8-)14.4
ascospore width (µm)	(6.5-)8.7 - 11.2(-13.4)	(10.0-)11.4 (-12.5)	10.2	10.6(-12.5)	10.4	12.0
Ascospore shape	subspherical to elipsoid	idem	idem	idem	idem	idem
Ascospore epispore	not halonate	idem	idem	idem	idem	idem
Ascospore disposition in ascus	uniseriate	idem	idem	idem	—	idem

(continued on next page)

Table 9. (continued)

Hymenium thickness (µm)	108	95	175	250	----	175
Subhymenium thickness (µm)	48	----	75	50	----	88
Excipulum propium thickness (µm)	36	38	30	112	---	---
Paraphyses ramification	from the base to the apex	idem	idem	idem	----	idem
Paraphyses constriction	slightly constricted	slightly constricted	slightly constricted	not constricted	----	slightly constricted
Paraphyses shape	about the same width from top to bottom	idem	idem	idem	----	idem
Paraphyses degree of fusion	highly anastomosed	idem	idem	idem	idem	idem

4. DISCUSSION & CONCLUSION

4.1. PHOTOBIONT DIFFERENCES, INTERGENERIC SIMILARITIES, AND INTRAGENERIC HETEROGENEITY OF THE IONASPIS-HYMENELIA COMPLEX

As noted previously, modern systematics of lichens is based exclusively on the mycobiont. However, the only character cited in the literature that distinguishes Ionaspis from Hymenelia is the photobiont. It was believed that Hymenelia is associated exclusively with Trebouxia, whereas the photobiont of Ionaspis is Trentepohlia.

The second problem associated with the Ionaspis-Hymenelia complex is that some taxa are much more similar to taxa of the other genus than to congeneric taxa. Ionaspis epulotica (Ach.) Blomb. & Forss. var. epulotica and Hymenelia prevostii (Duby) Krempelhuber (the type species of Hymenelia) reflects perfectly these two problems.

Prior to any discussion on these two problems, the identity of Hymenelia prevostii must be established. As shown in table 9, specimens cited in the protologue of Urceolaria prevostii by Duby (1830) were found with one or the other photobiont. Duby did not specify the photobiont since the new species was recognized on the basis of other characteristics, and did not specify a type. A lectotypification is therefore necessary, and is crucial since the selection of a specimen associated with Trentepohlia would eliminate the only known character to separate the two genera as they were circumscribed previous to this study.

The specimen identified by Fries as Gyalecta prevostii and collected by Le Prévost in "Galliae" (no. 197; UPS!) is here designated as the lectotype of Hymenelia prevostii. This lectotypification is justified by the fact that Le Prévost was the first to collect this taxon, and it was he who sent specimen(s) to Elias Fries for identification. Fries judged that this material represented a new species and named it after Le Prévost as Gyalecta prevostii. The specimen selected here is associated with Trebouxia (table 9). The specimens cited in the protologue that are associated with Trentepohlia can therefore be considered as misidentifications. Based on their photobiont they could be named as Gyalecta epulotica Achar. (see also the nomenclatural discussion on p. 99-100).

Even though H. prevostii and I. epulotica s. str. had been classified in different genera, they are among the most closely related species of the whole Ionaspis-Hymenelia complex and, in fact, probably are conspecific (see Jørgensen, 1989; Magnusson, 1933; Mougeot & Nestler, exs. no. 848). Jørgensen (1989) noted that I. epulotica s. str. may be confused with Hymenelia prevostii, and that the only character distinguishing them is the same one used at the genus level, i.e. the photobiont difference. This strong similarity between I. epulotica and H. prevostii, two endolithic species with pinkish apothecial disks, was noted from the beginning by Mougeot and Nestler. On their exsiccatae no. 848 of Biatora prevostii Fries in Litt., one can read "Affinis Gyalectæ epuloticæ Achar." Fröberg (1989) detected a different hymenial iodine reaction between Hymenelia prevostii (hymenium 0.3% I + blue) and Ionaspis epulotica (hymenium 0.3% I + red-brown). However, in the next sentence he implies that this is not an important character because

he states that Ionaspis and Hymenelia are probably congeneric since the only character separating them is their photobiont being trentepohlioid or trebouxioid respectively.

In the present study the IKI reaction of the hymenium was not retained as a reliable character. This character was found to be difficult to interpret since intermediate reactions were seen, where only some part(s) of the hymenium reacted. Also, most species had both positive and negative reactions. Finally, this character was never shown to be important in the explanation of the clusters. In the specific case involving H. prevostii and I. epulotica, a verification of the hymenial reaction to IKI should be done since Fröberg's observations seem to have been based on only one specimen for each species. This verification should include H. similis as well. The latter, is a European species, more or less endolithic, with slightly larger ascospores than H. prevostii (Poelt & Vězda, 1979). Hymenelia prevostii and H. similis are found in the same couplet of Poelt & Vězda's (1979) key to the genus Hymenelia.

Magnusson (1933) compared I. epulotica var. patellula (Arnold) Magnusson (= I. epulotica var. epulotica) with H. prevostii (Duby) Krempelhuber. Based on the stratification, the aggregation pattern, and size of the algae, and the hyphal cell shape, Magnusson concluded that these taxa should be considered as different species and should be kept in different genera. However, in his discussion of the thallus of Ionaspis, he considered Ionaspis prevostii sensu Bachmann (1892, 1919), to be a synonym of I. epulotica var. patellula (Arnold) Magnusson. Moreover, I. prevostii was not a new combination set by Bachmann, as believed by Magnusson (1933), but

dates from Arnold (1884), under which name he included f. rosea (Krempelhuber) Arnold. The combination Ionaspis prevostii Arnold, was illegitimate (ICBN) because Hymenelia prevostii is the type species of an older genus, Hymenelia, and the name of the genus must follow the type species when reclassified (Art. 52.1). The earliest legitimate generic name is the one which survives (Art. 57.1). Since Hymenelia (Krempelhuber, 1852) was described before Ionaspis (Th. Fries, 1871), the former has priority. Nevertheless, this last discussion by Magnusson implies that Ionaspis epulotica and Hymenelia prevostii are confuseable, if not conspecific. Other combinations have been made according to this last implication: Biatora epulotica var. prevostii Hepp (1857: no. 273); Lecidea epulotica var. prevostii Nylander(1861: 189); Lecanora epulotica var. prevostii Leighton (1871: 212).

In comparing type material of H. prevostii associated with trebouxioid algae or Trentepohlia with the lectotype of I. epulotica var. epulotica, no characters used in modern systematics of lichens were found to suggest any distinction between these taxa at the genus or at the species level (see Table 9). These results show at the very least that I. epulotica and H. prevostii are too closely related to be maintained in different genera. Therefore, Ionaspis epulotica has to be included in Hymenelia since Hymenelia is the oldest name and H. prevostii is the type species of Hymenelia (see also nomenclatural notes under Hymenelia, p. 98). Whether or not these two species ought to be considered as part of one species or not is still to be determined. This would necessitate a study of more material included under H. prevostii, I. epulotica var. epulotica, and H. similis as well.

4.2. RELATEDNESS AMONG THE HYMENELIOID GENERA

The numerical analyses coupled to nomenclatural considerations showed, in agreement with Eigler (1969), that some species groups are more similar to other genera than to the other species groups within the same genus and that some species groups had to be separated from the genus in which, hitherto, they were included.

The characteristics of the epihymenial pigments were revealed to be efficient generic discriminant characters within the hymenelioid lichenized fungi. However, as predicted by Jørgensen (1989), the genetic significance of such characters is not uniform among the different genera. As opposed to the peculiar pigment characteristic of the odora group, the apothecial disk pigments in Hymenelia sensu nov. [black (ex. haematina group) and pinkish (ex. epulotica group) apothecia] do not correlate significantly with other characters. Thus, there is no solid basis to recognise two subgeneric entities within Hymenelia, i.e. one with black apothecia and one with pinkish apothecia. The apothecial pigment difference between the epulotica and haematina groups seems to be the result of a recent genetic divergence, and may involve only a few genes. It is rare to find a population of the haematina group, without finding representatives of the epulotica group at the same place. The only case known is the disjunct population of the epulotica group ("Hymenelia epulotica ssp. meridionalis) found in the Great Lakes region. No Hymenelia sensu nov. with black apothecia was found in that locality.

In the case of a heterozygous ascus, half the ascospores would carry gene(s) responsible for black apothecia and half would carry the homologous gene(s) responsible for pinkish apothecia. In fact, thalli growing intermixed from the epulotica and the haematina groups are frequently observed (Fig. 16). The growth of thalli can be so intermixed that it can give the impression that the same thallus has both pinkish and black apothecia, as mentioned by Lynge (1926). In his discussion under Ionaspis schismatopis, Lynge notes that the colour of the disk changes from pale pinkish to purely black. As mentioned by Magnusson (1933), there was no transition seen between these two types of apothecia, and one taxon does not produce both pinkish and black apothecia.

By comparing the anatomical-morphological results with the electrophoretic results, no homoplasy was detected; i.e. none of the groups shown to be similar based on anatomical and morphological data were shown to be different on an enzymatic basis. Most of the intergroup similarity tendencies resulting from the anatomical and morphological study were enhanced by the electrophoretic study. The anatomical-morphological study tended to slightly set apart the epulotica, odora and Eiglera groups from the melanocarpa-haematina group, compared to the electrophoretic study which tended to show a strong relationship with this group (Fig. 9 a, 9 b). However, when comparing previous classifications of the hymenelioid lichens with the present classification, homoplasy was detected for the epulotica and odora groups. Magnusson (1933) thought that

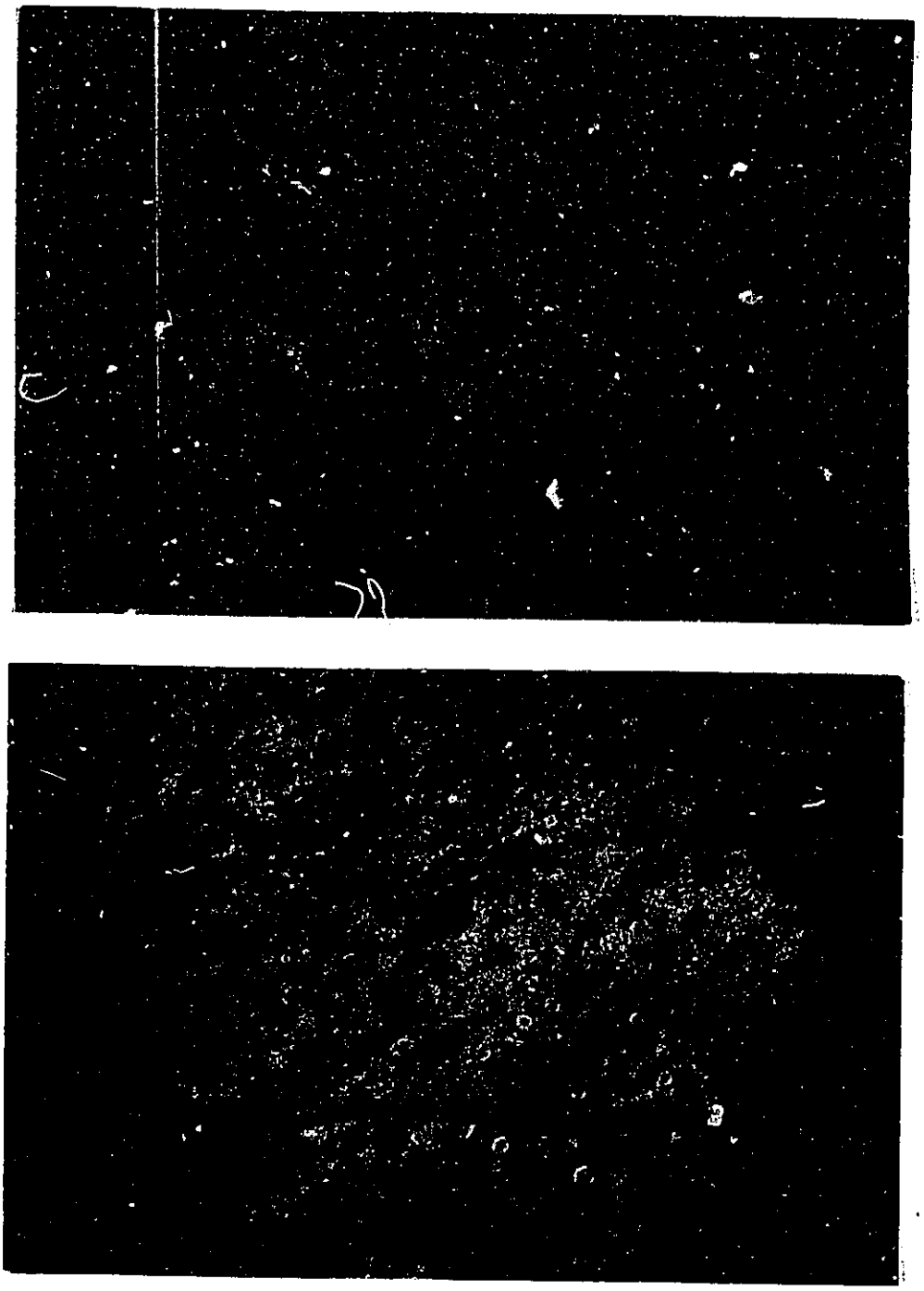


Figure 16. Intermixed thalli of the epulotica (pale apothecia) and haematina groups (black apothecia).

the odora group was more related to the epulotica group. He included these two species groups under the section Pallescentes of Ionaspis. The results of the present study show that the odora group is very distinct on an anatomical and morphological basis from all the groups previously classified within Ionaspis. Genetically, it seems to be more related to what was previously called Hymenelia lacustris than to the epulotica group. This strongly suggests that Magnusson's sections Pallescentes and Coerulescentes within Ionaspis were artificial since the melanocarpa and haematina groups of the section Coerulescentes are almost genetically identical to the epulotica group of the section Pallescentes (Fig. 9).

The high similarity of Eiglera to the melanocarpa-haematina group, shown by both data sets, raises important questions about the weight given to the apical structure of asci by Haffelner (1984) for natural classification purposes at the genus and family level. Haffelner segregated Aspicilia flavida (Hepp) Rehm from the genus Aspicilia to form a new genus called Eiglera and a new family called Eigleraceae. Haffelner's decision (1984) to establish a new genus and family was based mainly on one of the five principles he developed:

> "as a rule, different types of asci do not occur in the same genus (or family). Thus, the genus (or family) is usually defined by the type of ascus. This signifies that all species which do not have the same type of asci as the type species of a genus 'A' should be transferred to another genus 'B' with the same type of ascus."

If we accept this rule and the resulting separation of Eiglera from Hymenelia by Haffelner and try to remain consistent with that rule when

considering the other species groups of the hymenelioid lichens, it is difficult to believe in the rank that would be given to the lacustris-alba, odora and Aspicilia cinerea groups (Fig. 9 c). In fact the distance between Eiglera and the haematina-melanocarpa group is just slightly higher than between the epulotica group and the haematina-melanocarpa group. The epulotica group was definitely shown to belong to the same genus as the melanocarpa-haematina group. It seems that the peculiar apical structure of the ascus of Eiglera has the same genetic weight as does the apothecial pigment difference of the epulotica group when compared to the haematina-melanocarpa group.

Concerning the question raised by Haffelner (1984) as to whether or not it is justified to combine Hymenelia and Aspicilia in one family, the results from the present study suggest, in agreement with more recent work by Haffelner (1989), that they should be at least in different families, in conformity with the status given to Eiglera by Haffelner (1984).

The rigid use of the principle cited above might explain why Haffelner (1984) was not able to clarify the family Hymeneliaceae Körber, using solely the apical structure of the ascus. The present results suggest that the third principle developed by Haffelner (1984: 255) should be amended, that is, "when no other stable characters correlate with the ascus apical structure, this last character alone should not be used to make classification rearrangements at the family level." The question is still open at the generic level. However, the present results suggest that the same amendment would hold at the genus level. For the moment it is preferable to maintain the status of Eiglera as given by Haffelner (1984) since the understanding, on

a genetic basis, of the apical structure as a diagnostic character for natural classification at the genus and family level is still in its early stages.

4.3. CLASSIFICATION OF THE HYMENELIOID LICHENS

With time, the delimitation of Hymenelia has become more and more confused with respect to Ionaspis. The present misunderstanding of Hymenelia derived directly from the introduction of the genus Ionaspis by Th. Fries (1871). Ionaspis was established to accommodate all Aspicilia species with Trentepohlia, with no reference being made to the older genus Hymenelia. Fries apparently did not realize that Hymenelia already included many similar species associated with Trentepohlia. Hymenelia, as established by Krempelhuber (1852), included almost all taxa found under Ionaspis as understood by Magnusson (1933); see the nomenclatural notes for the genus Hymenelia on page 98. The transfer of most Hymenelia taxa to Ionaspis came from the use of a readily observable character, at least with fresh material, i.e., the photobiont difference. This choice of character by Fries had a great impact on lichenologists since this character was easy to use in a group (the Ionaspis-Hymenelia complex) where diagnostic morphological characters are non existent at the genus level. When fresh, Trentepohlia is orange, whereas Trebouxia is green. Since most subspecific taxa included under H. prevostii by Krempelhuber (1852) are associated with Trentepohlia, all taxa except H. coerulea (associated with trebouxioid alga)

and H. prevostii α rosea (*forma typica* of the species *sensu* Krempelhuber) were transferred to Ionaspis and have been considered as such since then.

Originally, the photobiont difference was used to separate Ionaspis from Aspiciiia (Th. Fries, 1871). It was only afterwards that this distinction was transposed to the Ionaspis-Hymenelia complex. The reasons for this transposition are not clear. Krempelhuber (1852, last paragraph of his paper), gave ineluctable clues to the nature of the photobiont found in Hymenelia prevostii sensu lato by referring to the typical color of fresh Trentepohlia. He described the alga as being golden yellow in moist, shady locations, the alga probably being more prolific and more apparent in such a habitat. He does not, however, specify if this applies to all infraspecific taxa included in H. prevostii. He also notes that this color fades away after relatively long storage and then turns green. Yet in the same paper, as he describes the various infraspecific taxa found within H. prevostii, including f. rosea (the forma typica, sensu Krempelhuber 1852), he consistently describes the alga as being green in color. Presumably, these descriptions were based on herbarium specimens. Another reason for the association of Trebouxia with Hymenelia by lichenologists might be related to the fact that in Zahlbruckner's classification (1907, 1926) of the lichenized fungi, Hymenelia was considered to be a synonym of Lecanora Acharius section 1. Aspicilia Stizenberger. Species of this section are well known to be associated with trebouxioid algae. This classification was followed very strictly by lichenologists for 50 years following the 1907 edition (Santesson, personal communication; Hale, 1984). Therefore, lichenologists might have thought that Hymenelia also had Trebouxia as a photobiont since all taxa of Hymenelia as described by Krempelhuber for a long time were called

Aspicilia. Finally, another reason might be related to the fact that two different types of photobiont (Trentepohlia and a trebouxioid algae) are associated with the original material of H. prevostii sensu stricto. After the establishment of Ionaspis, specimens with trebouxioid algae were automatically identified as Hymenelia as, by definition, I. epulotica could not be associated with photobionts other than Trentepohlia.

The most efficient way to solve the Ionaspis-Hymenelia complex classification problem would be to reintroduce into Hymenelia the taxa that were included in Krempelhuber's (1852) protologue of Hymenelia and are now called Ionaspis. This reorganization would immediately solve part of the problem by clarifying the delimitation of Hymenelia. Progressively, as was done with Eiglera and will be done with the lacustris group, taxa will be separated from Hymenelia to be included in more related genera or to form new genera. This would inevitably lead to a more homogeneous genus Hymenelia clearly distinguishable from Ionaspis. The latter will gain homogeneity from this reorganization as well.

The reclassification suggested by the present study of North American species groups classified under Hymenelia and Ionaspis, in relation to Eiglera and Aspicilia, is summarized in Figure 17. All species groups previously classified under Ionaspis, except for the odora group, are reclassified under Hymenelia. Ionaspis, with Aspicilia chrysophana as its type, would now include I. alpina, I. chrysophana (previously I. suaveolens auct.), I. fuscoclavata, I. handelii, I. lavata, I. sp. # 1, and I. suaveolens (previously I. odora). This will be valid as long as I. chrysophana will be considered sufficiently related to the odora group (= I. lavata and I. sp. # 1)

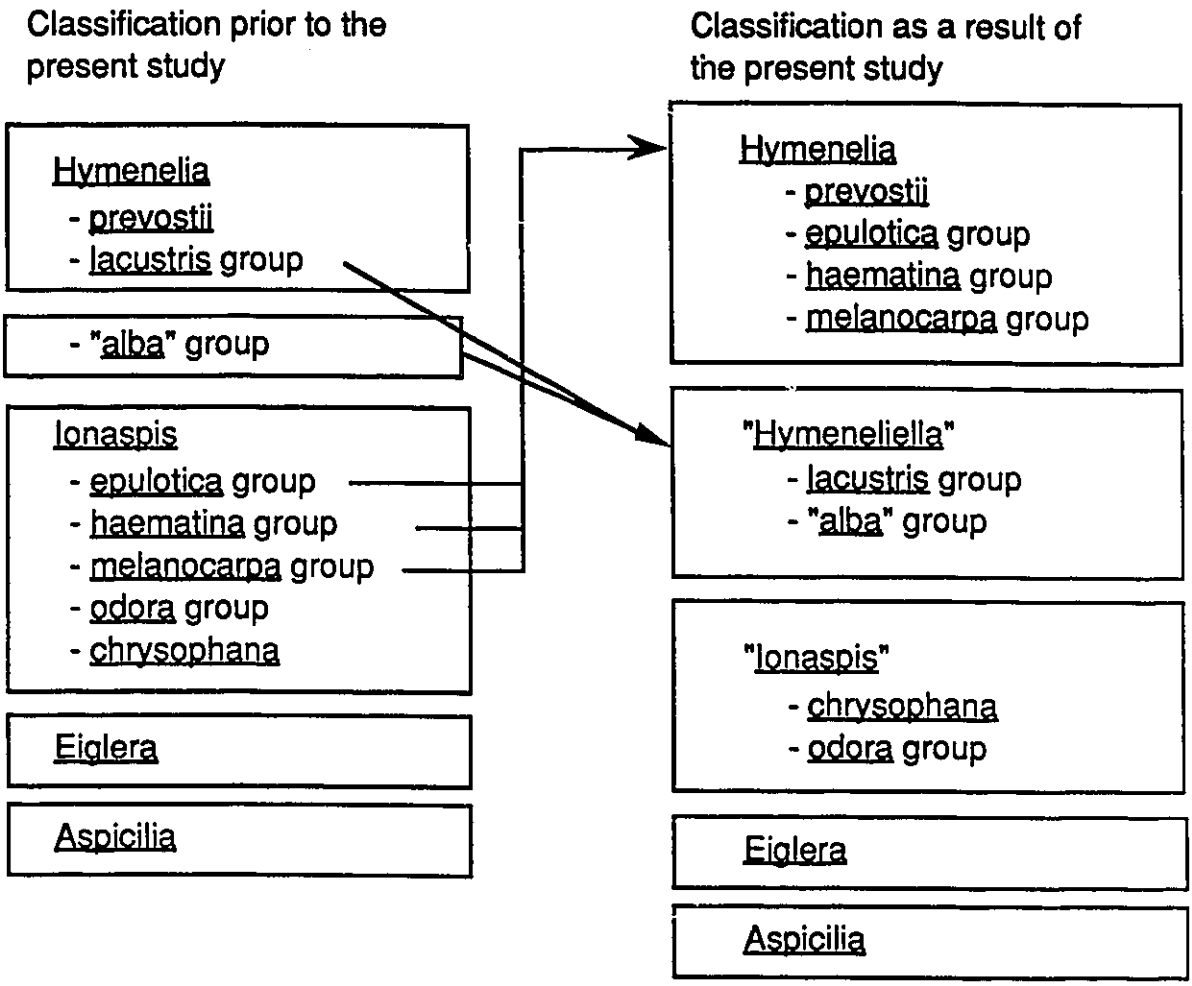


Figure 17. Schematic summary of the rearrangements in the classification of the hymenelioid lichenized fungi as suggested by anatomical-morphological and electrophoretic data.

to be included under the same genus name and that future work does not reveal a stronger affiliation of the chrysophana group of species (i.e., I. chrysophana, I. handelii, I. fuscoclavata) to another older genus. In the latter case the name Ionaspis would have to be synonymized.

According to Jørgensen (1989) some forms of Ionaspis suaveolens auct. (= I. chrysophana) are difficult to distinguish from I. cyanocarpa (now included in Hymenelia). In those cases the epihymenial pigment has to be tested with KOH and HNO_3. Usually, the thallus of I. chrysophana is more areolate, and the apothecia are without a bluish tinge in the black exciple (Jørgensen, 1989). If ever I. chrysophana, the type of the genus, has to be classified within Hymenelia, Ionaspis Th. Fries (1871) would become a synonym of the older name Hymenelia Krempelhuber (1852), and a new genus would have to be established for the odora group. The relatedness between I. suaveolens auct. and I. odora (= I. suaveolens) seems to result from a nomenclatural confusion (see nomenclatural notes, section 5.1.4) and from superficial similarities. Magnusson (1933), explains that specimens of I. odora with dark blackish olive apothecial disks and dark thallus were often called "suaveolens" or chrysophana. This strongly suggests that the inclusion of I. chrysophana and I. suaveolens might be artificial. Nevertheless, until more evidence is gathered, it is preferable to maintain these two species in the same genus.

The genus Hymenelia typified by Urceolaria prevostii Duby, will now consist mostly of species that were previously called Ionaspis (Fig. 17). The lacustris group would be separated from the genus Hymenelia to form a new genus called "Hymeneliella", typified by Lichen lacustris With. This

new genus would also include a new taxon called the "alba" group, which could not be accomodated in any known genera. Hymenelia ceracea is also part of this new genus "Hymeneliella" (see Poelt & Vězda, 1981). Finally, the genera Eiglera and Aspicilia are not to be changed for the moment. However, the classification of Eiglera by Haffelner (1984) in its own family, definitely needs to be reexamined in relation to the Hymeneliaceae.

The conclusions drawn here have several advantages: 1) both names, Hymenelia and Ionaspis, are conserved, 2) the original circumscription of Hymenelia , i.e. sensu Krempelhuber (1852), is reestablished, and 3) the infrageneric heterogeneity and intergeneric similarity problems in the Ionaspis-Hymenelia complex can be resolved by the recognition of three natural genera, i.e. Ionaspis, Hymenelia, and "Hymeneliella". These three genera would constitute the family Hymeneliaceae.

4.4. FUTURE WORK

Future studies need to be done on a worldwide basis so that a global classification can be developed. At the genus level, research should be directed towards two main goals: 1) determination of the genetic affiliation of Ionaspis chrysophana and related species, as well as I. suaveolens *s. str.*, to the other species groups found within the Hymeneliaceae, and 2) investigation of the evolutionary and genetic meaning of the apical structure of the ascus as revealed in Lugol's solution. This second line of research would determine what weight should be given to this character for

systematic uses and to reevaluate the establishment by Haffelner (1984) of Eiglera and Eigleraceae with regard to the closely related genus Hymenelia.

At the species level most of the work is yet to be done. A better definition of the species limits is essential. This will be achieved by testing the keys produced here and by gathering as many diagnostic data as possible at the species level. More data should be gathered for each subgeneric taxon and subjected to numerical analyses in order to locate the gaps between the different populations.

5. TAXONOMY

5.1. TAXONOMIC TREATMENT OF NORTH AMERICAN HYMENELIOID GENERA, INCLUDING ASPICILIA

5.1.1. Key to the hymenelioid lichen genera of North America, including Aspicilia

1 Ascus apex IKI + blue.....Eiglera
- Ascus apex IKI -.....2

2 Epihymenium olive green to olive brown, remaining this color in HNO_3.....Aspicilia
- Epihymenium hyaline or with pigments different from above.....3

3 Apothecial pigment HNO_3 + orange, KOH + violet.....
.....Ionaspis (odora species group)
- Apothecial pigment HNO_3 - or + violaceous pink, KOH -.....4

4 Ascospores halonate; disk brownish or whitish, brownish coloration given by an epipsamma; on siliceous rocks; in boreal-hemiboreal subzone, temperate, and Appalachian Mountains.....
....."Hymeneliella"
- Ascospores not halonate; disk pinkish or black, coloration given by pigment of the epihymenium and hymenium; on siliceous or calcareous rock; Arctic-alpine, with one population (H. epulotica ssp. meridionalis) in the Great Lakes region.....Hymenelia

5.1.2. The genus Hymenelia

Hymenelia Krempelhuber, A. V. 1852. Flora 35: 17-26.

= Pinacisca Massalongo, Neagenea Lich. 5 (1854). Type species: P. similis Massal.

= Manzonia Garovaglio, Mem. Mat. Fis. Soc. Ital. Sci. Mondena, Pt. Mem. Fis. ser. 2.2: 3, page 97 (1866). Type species: M. cantiana Garov. = Hymenelia prevostii γ caerulescens Krempelhuber, Flora 35: 17-26 (1852).

= partly Ionaspis Th. Fr. Lichenographia Scandinavica (1871).

TYPE SPECIES: Hymenelia prevostii (Duby) Krempelhuber, Flora 35: 17-26 (1852) ≡ Gyalecta prevostii (Duby) Fries, Lichenographia Europaea reformata 197 (1831). ≡ H. prevostii (Duby) Krempelhuber α rosea Krempelhuber, Flora 35: 17-26 (1852).

BASIONYM: Urceolaria prevostii Duby, Aug. Pyrami de Candolle Botanicon gallicum 671 (1830). Lectotype, here designated: Galliae, Le Prévost 197 sub Gyalecta prevostii (UPS!).

Characterization: Apothecial density **4.1 -8.7- 13.3** / 6.25 mm^2, the disk is black or pinkish and devoid of an epipsamma. The epihymenium is bluish green, olive green or hyaline; when not hyaline, the epihymenium is HNO_3+ violaceous pink, and KOH negative. The hymenium is **85 -120- 150** µm high, and subhymenium **25 -38- 51** µm high. The ascus tip is IKI negative. The ascospores lack a halo and are **6.7 -9.0- 11.7** µm wide. The

conidia are 5.6- 7.7 µm long. Found on siliceous or calcareous rocks in Arctic-alpine regions, with rare intrusion in the boreal zone and one population in the Great Lakes region.

Description: Thallus color very variable: from light gray to pale yellow, or grayish yellowish brown to orange yellow (31, 32, 69, 70, 73, 76, 79, 80, 89, 92, 93, 265); epilithic, or endolithic when growing on calcareous rocks; rimose and/or rimose-areolate when epilithic. Photobiont Trentepohlia or trebouxioid algae.

Apothecia circular to irregular, density (1.7-)4.1 -8.7- 13.3(-27.0) /6.25 mm^2. Disk black, or pale yellowish if old herbarium specimen, pinkish if recently collected; (0.07-)0.10 -0.25- 0.46(-0.72) mm diameter. Margins not prominent to slightly prominent when young, becoming slightly prominent to prominent, rarely becoming very prominent and constricted at the base (excluding endolithic individuals); (0-)30 -80- 150(-290) µm thick.

Apothecial anatomical characters: Epihymenium bluish green (161, 165, 166), or olive green to brownish black, olive black, or blackish green (65, 96, 114, 128, 146, 147, 151, 152), or hyaline; HNO_3 + violaceous pink or negative, KOH negative. Hymenium color the same as epihymenium; color thickness (30.0) -45.8- 59.6(-76.5) µm. Hymenium (50.0-)85.6 -118.3- 151.0(-212.5) µm high; IKI + blue or negative; HNO_3 + violaceous pink or negative, KOH negative. Subhymenium hyaline; (12.5-)25.0 -38.1- 51.2(-75.0) µm high; IKI + blue or negative; HNO_3 and KOH negative. Hypothecium hyaline; 0.0 -28.3- 58.5(-225.0) µm high; HNO_3 and KOH negative; textura globulosa, or angularis, or epidermoidea (Fig. 1). Lateral excipulum propium hyaline to reddish black (24), dark olive brown (96) dark grayish olive (111), blackish

green (152), very dark bluish green (166), or bluish black (193); (0.0-)31.6 -64.5- 97.4(-225.0) µm thick; HNO_3 violaceous pink or negative, KOH negative; textura extremely variable. Basal excipulum propium hyaline to grayish yellowish brown (80), dark grayish olive (111), very dark green (147), or hyaline or olive black (114), or very dark bluish green (166), or dark grayish brown to brownish black (62, 65); (0.0-)10.9 -17.5- 24.1(-30.6) µm thick; HNO_3 + violaceous pink or negative, KOH negative; textura very variable. Excipular dark color continuous or discontinuous. Epipsamma absent, color of the disk given by pigments in the ascoma.

Paraphyses undulated; dichotomously ramified at the apex, usually with ramification below the apex, rarely ramified only below the apex; anastomosed; not constricted to moniliform; the same thickness from top to bottom, or larger at the apex. Ascus tip IKI negative. Ascospores (7.5-)9.7 - 13.7- 18.5(-25.0) X (4.9-)6.7 -9.0- 11.7(-13.8) µm; simple, hyaline, not halonate, rarely halonate; uniseriate or aseriate.

Pycnidia: buried in thallus; (25-)45 -90- 140(-220) µm diameter, same color as disks; conidia bacilliform, (3.4-) 5.6- 7.7(-9.8) X 1.0(-2.0) µm.

Habitat: Mainly submerged in small creeks, rivers, or growing in the spray zone of falls. Also growing in intermittent creeks, on wet cliffs bordering rivers or on rocky shores of lakes. Some species, however, can be found in extremely dry habitats such as the summit of small hills blown by strong wind, on calcareous rock only. When found in habitats associated with wet areas, colonizes siliceous or calcareous rocks.

Distribution: Arctic-alpine, extending south to the Southern Rocky Mountains, with an intrusion into the boreal zone (Fig. 14). One population, H. epulotica ssp. meridionalis, is found in the temperate zone in the Great Lakes Region.

Species included: Hymenelia prevostii (Fr. ex Duby) Krempelh., H. similis (Massal.) Poelt & Vězda, Ionaspis aigneri Zahlbr., I. annularis H. Magn., I. arctica Lynge, I. carnosula (Arn.) Arn., I. cyanocarpa (Anzi) Jatta, I. cyrtaspis Arn., I. epulotica (Ach.) Arn., I. haematina (Körb.) Th. Fr., I. häyrenii Räs., I. heteromorpha (Krempelh.) Arn., I. melanocarpa (Krempelh.) Arn., I. ochraceella (Nyl.) H. Magn., I. ochromicra (Nyl.) Hue, I. reducta H. Magn., I. schismatopis (Nyl.) Hue, I. spitsbergensis H. Magn., I. sumatrana Zahlbr.

Nomenclatural notes: Eigler (1969: 155) erroneously cited H. caerulea as the type species of Hymenelia. Hymenelia prevostii (Duby) Krempelh. has to be the type species of the genus since in the protologue var. (α) rosea was clearly stated to be "forma typica" by Krempelhuber (1852). The establishment of Hymenelia by Krempelhuber (1852) was based on H. prevostii alone. Hymenelia prevostii sensu Krempelhuber (1852) was mainly an endolithic lichen, with very polymorphic thallus and apothecia. These characters along with anatomical characteristics distinguished this taxa from Lecidea Acharius, Gyalecta Acharius, Biatora Fries, and Thelotrema Acharius.

Krempelhuber's concept of Hymenelia prevostii was quite broad since he included four main infraspecific entities under that name all of which are now treated at the species level: 1) α rosea, which he chose as the typical form of the species, and which is very similar to Ionaspis epulotica

(Acharius) Blomberg and Forssell var. epulotica; 2) β melanocarpa a. punctata, which correponds to Magnusson's (1933) epilithic Ionaspis section Cærulescentes and to Hymenelia haematina in this treatement; 3) β melanocarpa b. lecanorina, corresponds to what is called I. melanocarpa (Krempelhuber) Arnold; and 4) γ caerulescens, which is now called Hymenelia coerulea (De Candolle) Massalongo. The protologue for the genus Hymenelia, therefore, included almost all the taxa which were, until now, included in the genus Ionaspis, and contained taxa mostly associated with Trentepohlia, except for H. coerulea & H. prevostii. Krempelhuber (1852) did not consider the photobiont difference as a diagnostic character for this genus.

In the same paper, Krempelhuber stated that it was Fries (1831: 197), using Le Prévost's specimens, who first published this species under Gyalecta prevostii. However, this species was validly published by Duby in 1830 under the name Urceolaria prevostii where Le Prévost's specimens (and others) were cited. The latter name is considered here to be the basionym of H. prevostii (Duby) Krempelhuber, in agreement with Cannon et al. (1985), and Santesson (1984). Poelt and Vězda (1981) and Farr et al. (1979), considered Gyalecta prevostii Fries (1831) as the basionym, whereas Haffelner (1984) considered Lecidea prevostii Schaerer (1833) as the basionym. There was a previous name for U. prevostii Duby, that is, Biatora prevostii Fries, found on the label of Mougeot and Nestler exs. no. 848 and cited by Duby (1830). Yet it was never validly published, as noted by Duby himself. No diagnosis was found for B. prevostii Fries on the label of the exsiccatae nor in any accepted printed matter (ICBN, Art. 29). The latter name is a nomen nudum under ICBN Art. 32.

In UPS, a specimen with the label "Gyalecta prevostii L. E. p. 197, Gallia. Prévost", was assigned the status of holotype. It cannot be a "holotype", since Duby (1830) notes three localities in the protologue of Urceolaria prevostii: "Ad rupes calcarias Jurassi (Cl. Moug.and Nestl.), Rothomagi (cl. Le Prévost), Mimatis (cl. Prost). -Moug. and Nestl. vog. n. 848. Biatora Prevostii Fries ined. ex cl. Le Prévost in litt. (v. s.)." No published lectotypification ever seems to have been made. This specimen is designated here as the lectotype of Hymenelia prevostii (see table 9 and page 79).

Duby's collection is mainly in STR, but some specimens can be found in UPS (Hawksworth, 1974). It was not possible to see any material from the former herbarium, but six specimens cited by Duby in the protologue of U. prevostii were studied. Three of them are Mougeot and Nestler, Stirpes Cryptogamae, exs. 848, (CANL, M, UPS); two others are from UPS "Gyalecta prevostii L. E. p. 197, Galliae, Prévost"; "Gyalecta prevostii L. E. p. 1907, Ad rupes calcarea, Galliae, Mougeot"; and the sixth specimen is from M "Urceolaria prevostii Duby, Lozère, Prost." It was found that one of the packets of the exsiccata (UPS) was not Hymenelia prevostii but Petractis clausa (Hoffm.) Krempelhuber.

5.1.3. The genus "Hymeneliella"

"Hymeneliella Lutzoni"

TYPE SPECIES: "Hymeneliella" lacustris (With.) Lutzoni

BASIONYM: Lichen lacustris With., A Botan. arrang. Brit. Plants. edit. 3, vol. IV, p. 21 tb. XXXI (1796). Type: BM (not seen)

Characterization: Apothecial density 7.3 -15.5- 23.7 / 6.25 mm2, the disk is rusty brown to yellowish brown or whitish. The coloration of the disk, other than white, is due to the presence of a pigmented, granular epipsamma. The epihymenium is hyaline, HNO_3 negative, and KOH negative. The hymenium is 75 -95- 110 µm high and subhymenium 16 -24- 31 µm high. The ascus tip is IKI negative. The ascospores are halonate and 4.9 -7.0- 9.3 µm wide. The conidia are 3.7 µm long. Found on siliceous rocks in Boreal-hemiboreal subzone, temperate, and Appalachian Mountains, with rare extensions into the Arctic.

Description: Thallus light to strong brown (55, 57), or brownish gray (64), or pale to moderate orange yellow (70, 71, 73), or light to deep yellowish brown (74-77, 79, 80), or yellowish white to grayish yellow (90, 92, 93), or light olive gray (112); epilithic; rimose and/or rimose-areolate. Photobiont Trebouxia; rarely trentepohlioid, i.e. with refringent cell wall but agglomerated into a sphere below the apothecia. These spherical structures, formed by what is here believed to be trentepohlioid algae, were observed on Hymeneliella lacustris collected on the Canadian west coast only.

Apothecia circular to irregular, (2.8-)**7.3 -15.5- 23.7**(-42.0) /6.25 mm^2. Disk grayish reddish orange (39), or strong to moderate reddish brown (40, 41, 43), or light to deep orange (50-54), or light grayish brown to deep brown (55-63), or pale to dark orange yellow (69, 72, 73), or light grayish to deep yellowish brown (75, 76, 79, 81), or white to yellowish gray (92, 93, 263, 264); (0.03-)**0.06 -0.19- 0.39**(-0.73) mm diameter. Margins not prominent to slightly prominent when young, becoming slightly prominent to prominent; (0-)**10 - 60- 130**(-270) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 negative, KOH negative. Hymenium hyaline; (45.0-)**75.8 -93.6- 111.4**(-135.0) µm high; rarely IKI + blue; HNO_3 negative, KOH negative. Subhymenium hyaline; (10.0-)**16.5 -24.2- 31.9**(-50.0) µm high; IKI + blue or negative; HNO_3 and KOH negative. Hypothecium hyaline; (0.0-)**10.2 -37.1- 64.0**(-122.5) µm high; HNO_3 and KOH negative; mostly textura globulosa, or angularis. Lateral excipulum propium hyaline or vivid to deep orange or orange yellow (48, 51, 66, 68, 69), or strong brown to brownish black (55, 59, 65), or strong to deep yellowish brown (74, 75), or vivid yellow (82), or light olive brown (94) ; (0.0-)**20.3 -47.2- 76.8**(-125.0) µm thick; HNO_3 and KOH negative; textura prismatica, or epidermoidea. Basal excipulum propium mostly hyaline; (0.0-)**12.2 -23.4- 23.4**(-37.5) µm thick; HNO_3 and KOH negative; textura mostly prismatica, or oblita. Granular epipsamma present or not, responsible for the color of the disk when not whitish.

Paraphyses simple, or dichotomously ramified at the apex, sometimes with ramification below the apex, rarely ramified only below the apex; anastomosed; slightly constricted, submoniliform, or moniliform;

generally larger at the apex. Ascus tip IKI negative. Ascospores (8.0-)10.3 - 13.7- 17.4(-21.6) X (3.0-)4.9 -7.0- 9.3(-11.2) µm; simple, hyaline, halonate (character sometimes difficult to see); uniseriate or aseriate.

Pycnidia: buried in the thallus; (40-)60(-70) µm diameter, same color as disks; conidia bacilliform, (2.9-) 3.7 (-4.4) X 1.0 µm.

Habitat: Submerged in small creeks, rivers, or growing in the sprayed zone of falls. Found on rocky shores of lakes or on boulders in opening of the forest. Also growing on small boulders in deciduous forest. Colonizes siliceous rocks.

Distribution: Boreal-hemiboreal subzone, temperate, and Appalachian Mountains (Fig. 14). One record from the Sierra Nevada and American Coastal Mountains zone, and rare extension into the Arctic zone.

Species included: "Hymeneliella alba Lutzoni ined.", Hymenelia lacustris (With.) Poelt & Vězda (including Hymenelia ceracea collected by Gowan in Fundy National Park, CANL)

5.1.4. THE GENUS IONASPIS (the following description includes only the odora group, i.e., Ionaspis lavata and I. sp. # 1)

Ionaspis (Th. Fries) Lutzoni

Fries, Th. 1871. Lichenographia Scandinavica. Uppsala, p. 273.

TYPE SPECIES: I. chrysophana (Körb.) Th. Fr. in B. Stein, designated by Clements & Shear (1931).

BASIONYM: Aspicilia chrysophana Körber, Systema Lichenum Germaniae (159-160: 1855). Type: "An Felsen im Hochgebirge. Ward am Basalt der kleinen Schneegrube 1853 von mir entdeckt, woselbst sie gar nicht selten zu sein scheint." L (not seen).

Characterization: Apothecial density **14.3 -23.4- 32.5** / 6.25 mm^2, the disk is brownish or grayish to almost black and devoid of an epipsamma. The epihymenium is yellowish to brownish, HNO_3 + orange and KOH + violet. The hymenium is **60 -96.3- 130** µm high and subhymenium **22 -42- 62** µm high. The ascus tip is IKI negative. The ascospores are devoided of an halo and are **6.9- 8.7** µm wide. The conidia are **5.9- 8.2** µm long. Found on siliceous rocks in Arctic-alpine regions.

Description: Thallus pinkish white (9), or pale yellowish pink (31), or yellowish white to dark grayish yellow (91, 92); epilithic; rimose and/or rimose-areolate when epilithic. Photobiont Trentepohlia.

Apothecia subangular or irregular, (10.5-)**14.3 -23.4- 32.5**(-42.2) /6.25 mm^2. Disk light to dark grayish reddish brown (45-47), or light to dark brown (57, 59), or light grayish brown to brownish gray (60, 61, 63, 64), or grayish yellowish brown (80), or dark gray (266); (0.07-)**0.09 -0.26- 0.52**(-0.67) mm diameter. Margins not prominent to slightly prominent when young, remaining this way or becoming slightly prominent or prominent; (0-) **60-130**(-220) µm thick.

Apothecial anatomical characters: Epihymenium light to orange yellow (70, 72), or light to strong yellowish brown (74, 76) or light grayish yellowish brown (79), or grayish to dark yellow (88, 90), or dark grayish olive (111), or

hyaline; HNO_3 + orange, KOH + violet. Hymenium color same as epihymenium; (50.0-)62.6 -96.3- 130.0(-162.5) µm high; IKI negative; HNO_3 + orange, KOH + violet. Subhymenium hyaline; (12.5-)22.2 -41.9- 61.6(-82.5) µm high; IKI + blue or negative; HNO_3 and KOH negative. Hypothecium hyaline or pale yellowish brown; (0.0-)16.6 -41.5- 66.4(-90.0) µm high; HNO_3 and KOH negative; textura angularis, or prismatica. Lateral excipulum propium hyaline or light yellowish brown (76); (0.0-)10.3 -49.4- 99.7(-150.0) µm thick; HNO_3 + orange, KOH + violet; textura prismatica. Basal excipulum propium light to grayish yellowish brown (76, 80); (0.0-) 7.5- 17.1(-20.0) µm thick; HNO_3 + orange, KOH + violet; textura prismatica. Epipsamma absent.

Paraphyses dichotomously ramified at the apex, sometimes with ramification below the apex, rarely simple; anastomosed; slightly constricted, rarely submoniliform; generally larger at the apex. Ascus tip IKI negative. Ascospores (8.5-)9.3 -11.6- 14.4(-16.2) X (4.8-) 6.9- 8.7(-9.5) µm; simple, hyaline, not halonate; mostly aseriate.

Pycnidia: buried in thallus; (25-)50- 80(-100) µm diameter, same color as disks; conidia bacilliform or filiform, (3.9-) 5.9- 8.2(-9.3) X 1.0 µm.

Habitat: Submerged in small creeks. Colonizes siliceous rocks.

Distribution: Arctic-alpine; regarding the alpine zone, until now found only in the Northwestern Cordillera (Fig 14).

Species included (non North American species included): Ionaspis alpina Zahlbr., I. chrysophana (Körber) Fries, I. fuscoclavata Eitn., I. handelii Zahlbr., I. lavata H. Magn., I. sp. # 1, I. suaveolens (Fr.) Th. Fr. in B. Stein (?).

Nomenclatural notes: The genus Ionaspis was established by Th. Fries in 1871. His description of the genus is very short and is found under Aspicilia as follows: "*-E speciebus antea Aspiciliis adscriptis permultæ (v. c.* chrysophana *Körb.,* rhodopis *Sommerf.,* odora *Ach.,* suaveolens *Ach.,* hæmatina *Körb.,* cyanocarpa *Anzi,* epulotica *Arn. exs. 41 et 164,* cinereorufescens *b* heteromorpha *Krmplh. cet.) ob gonidia concatenata sunt excludendæ; ex his novum genus,* Ionaspis *Th. Fr., est condendum.*" The chainlike alga cited by Th. Fries is Trentepohlia, and it is the only diagnostic character. Fröberg (1989) and Santesson (1984) concluded that this description did not fulfill the requirements of the International Code of Botanical Nomenclature (ICBN; Greuter, 1988) in order to be accepted as validly published. Santesson's conclusion (personal communication) was based on the ICBN Article 13.1(d), stipulating that "for nomenclatural purposes names given to lichens shall be considered as applying to their fungal component." However, since at the end of the 19th century, characters of the photobiont were considered as good as any other characters for lichen classification, Fries' description of Ionaspis should be regarded as validly published, in agreement with Cannon et al. (1985), Jørgensen (1989), and Santesson (verb. comm., 1989), unless it is decided that Article 13.1(d) is retroactive to that time.

No type species was designated by Th. Fries (1871) for the genus Ionaspis. Eigler (1969) erroneously proposed I. ceracea (Arnold in Krempelh.) Jatta as the type for Ionaspis. This species is not part of the original description. Recently, Haffelner (1984) chose I. epulotica (Acharius) Th. Fr. as the lectotype. However, I. chrysophana (Körb.) Stein had already been

chosen as the lectotype of Ionaspis by Clements and Shear in 1931. This lectotypification was overlooked by Haffelner (1984; Haffelner, in litt.).

One other point needed to be verified before determining which lectotypification should be retained. The lectotypification by Clements and Shear (1931) could have been interpreted as a mechanical method of selection since I. chrysophana was the first name listed in the protologue of Ionaspis, in which case the choice could have been superseded by a more recent lectotypification as stipulated in Article 8.1 (c). Clements and Shear (1931), however, were critical in their selection of generic types, and followed the methods recommended by the International Code in effect at that time. In their introduction, Clements and Shear clearly indicate that they did not make any mechanical selections. The fact that the name designated (I. chrysophana) was the first listed by Th. Fries (1871) is only pure coincidence. Since, the lectotypification of Ionaspis by Clements and Shear (1931) is regarded here as valid, the selection of I. epulotica as the lectotype of the genus by Haffelner (1984) is therefore superseded by I. chrysophana.

Ionaspis chrysophana (Körb.) Th. Fr. in B. Stein was regarded as a synonym of I. suaveolens (Fr.) Th. Fr. in B. Stein by Magnusson (1933) and Santesson (1984). The former author did study the identity of both species and wrote:

> The name chrysophana has caused me like many other lichenologists much trouble. The first sample of Koerber exs 8. that I brought home (from Pavia) was an Aspicilia-species; it is not in the museums at Stockholm or Uppsala and a specimen from Oslo agreed well with I. odora. The specimen in hb. Koerber (Leiden), too, seems to be I. odora as well as a small specimen from "Kleine Schneegrube", the locality of

the authentic specimen. In neither of these the colour of the hymenium answers the description "schön lauch-grün" of Körber. The real and rather good authentic specimen examined by me agrees well with Körber's description and also perfectly with I. suaveolens Schaer. with its negative NO_3 reaction. Evidently Körber himself did not know his own species well, or he neglected to examine the specimens microscopically, and certainly this has been the cause of the following constant confusion. The disc of I. odora may be rather dark but forms another kind of colouring matter taking a violet stain in KOH.

Both I. chrysophana and I. suaveolens were listed in the protologue of the genus Ionaspis by Th. Fries (1871). Ionaspis chrysophana was first described by Körber in 1855 under the name Aspicilia chrysophana. The epihymenial negative NO_3 reaction recorded on type material of I. chrysophana by Magnusson (1933) clearly indicates that Aspicilia chrysophana Körber is the same species as what is usually called I. suaveolens.

However, in typifying suaveolens, we must follow the protologue of Fries's (1825) publication of Gyalecta suaveolens which mentions among other things: "*Apotheciis immersis hyalino-incarnatis, demum margine proprio prominulo.*" Although no specimens are cited, reference is made to "Urceol. *Ach. Mscr.*" The single specimen in H-Ach labelled Urceolaria suaveolens (no. 1063; 66!) is pale fruited and clearly corresponds to what is called I. odora, the epihymenial pigment having a KOH + violet reaction.

The confusion occurred when Schaerer published Urceolaria suaveolens a year later, also citing "Urceolaria suaveolens. *Ach! in litt.* ", but referring to Lich. exs. no. 124. In his discussion, Schaerer (1826: 70)

distinguished his suaveolens from Acharius's Gyalecta odora (published by Schaerer as a new species in the same paper), mentioning that the former has "discus ater". In the description of Gyalecta odora (Schaerer, 1826: 80), he mentions the color of the disk being *"disco carneo-rubescente"*. Thus, Schaerer's "type" of U. suaveolens (Lich. exs. no. 124, with dark apothecia, not the part of the exsiccata with pale apothecia) is not the same as the true type in the Acharian herbarium that Fries (1825) used as the basis for his Gyalecta suaveolens, and as Magnusson (1933) pointed out, was pale fruited. If Gyalecta suaveolens and G. odora are synonymous, the name suaveolens, unfortunately, has priority and now represents the pale fruited species, with the dark fruited species requiring a name. Fortunately, the name Aspicilia chrysophana Körber is available and should be taken up for this species as I. chrysophana (Körber) Fries, which also happens to be the type species of the genus Ionaspis.

Concerning I. suaveolens and I. odora, Magnusson (1933), states:

> The specimen in hb. Ach. (Hfs.) is I. odora (hymenium K+ violet, apothecia punctiform, ± pale to dark) like Schaer. exs. 124 (in my herb.) which has the same qualities. There has been great uncertainty among the lichenologists of all times concerning these names, suaveolens and odora. They were confused from the very first, also in the exsiccata, and nobody has examined the authentic specimens in detail. As it is probable that Acharius never saw real suaveolens, I prefer to place Schaerer as the author although even he has partly confused the two species.

Unaware of Fries' earlier publication of Urceolaria suaveolens Magnusson (1933) suggested, with good reasons, that Schaerer (1826) should be regarded as the author of the epithet suaveolens and Schaerer's exsiccatus used as the type. This is unfortunately not possible.

5.2. PRELIMINARY TREATMENT OF THE NORTH AMERICAN SPECIES

5.2.1. Key to the North American species of Hymenelia

1. Apothecia black, dark pigment HNO_3 + violaceous pink.....2
- Apothecia pale yellowish if old herbarium specimen, pinkish if recently collected, pigment when present HNO_3 -.....3

2. Margin (0-)51 - 99(-168) µm thick; ascospores (7.5-)9 - 16(-17.5) X (5-)6.5 - 11(-12.5) µm; hymenium (50-)75 - 140(-175) µm high; thallus epilithic or endolithic, silicolous or calcicolous.....H. haematina
- Margin (12-)22 - 38(-72) µm thick; ascospores (11-)14 - 19(-25) X (8-)9.5 - 12(-14) µm; hymenium (100-)115 - 160(-185) µm high; thallus endolithic, calcicolous.....H. melanocarpa

3. Margin gelatinous (translucent and flexible when wet); lateral excipulum propium (largest part near the surface of the apothecia) (0-)50 - 60(-110) µm thick.....Hymenelia sp.#2
- Margin opaque and rigid when wet; lateral excipulum propium (largest part near the surface of the apothecia) (0-)56 - 94(-225) µm thick.....4

4. Hymenium (65-)80 - 130(-150) µm high; ascospores (5.4-)7.1 - 9.3(-11.2) µm wide; apothecial disk diameter (70-)120 - 245(-360) µm; margin (24-)63 - 105(-145) µm thick; thallus cortex absent or present.....5
- Hymenium (85-)130 - 165(-210) µm high; ascospores (7.6-)9.4 - 11.7(-13.2) µm wide; apothecial disk diameter (80-)195 - 495(-720) µm; margin (0-)71 - 146(-241) µm thick; thallus cortex present.....6

5. Mostly collected in temperate zone, Great lake region, also found in the arctic; thallus coarse granular-leprose, cortex absent; calcicolous; hymenium (70-)80 - 110 µm high.....H. epulotica ssp. meridionalis
- Mainly collected in arctic-alpine (south to the southern Rocky Mountains), also boreal; thallus rugose to subgranulose or smooth, cortex present or absent; silicolous; hymenium (65-)80 - 135(-150) µmthick.....H. epulotica ssp. silicicola

6. Conidia (3.9-)5.3(-6.4) µm long; subhymenium (29-)40(-50) µm high; ascospores (11.2-)12.6 - 17.3(-20.0) µm long; apothecial density (2-)4(-7) /6.25 mm^2.....Hymenelia sp. #1
- Conidia (5.9-)7.4 - 8.7(-9.8) µm long; subhymenium (45-)58(-70)µm high; ascospores (12.5-)14.9 -19.1(-20.8) µm long; apothecial density 5 - 12 (-14) /6.25 mm^2 ....H. epulotica ssp. epulotica

5.2.2. Description of the species of Hymenelia

"Hymenelia haematina (Körber) Lutzoni"

Aspicilia haematina Körber, Parerga (1860) p. 100. Type: Germany "Auf gneussartigem Gestein (näherer Standort unbekannt)." L (not seen). - *Ionaspis haematina* (Kbr.) Th. Fr., Lich. Scand. I (1871) p. 273.

Aspicilia cyanocarpa Anzi, Manipulus (1862) p. 145. Type: Italy "Sulle rupi di Mica-schisto alquanto umide, al termine superiore della regione del mugo, sopra i casolari di Cerèna in val del Forno (prov. di Sóndrio), Anzi L. rar. Lang. exs. no. 79" (not seen). - *Ionaspis cyanocarpa* (Anzi) Th. Fr., Lich. Scand. I (1871) p. 273. - *Lecanora cyanocarpa* (Anzi) Nyl., apud Stzbg. in Bericht über die Thätigk. St. Gallisch. Naturw. Gesellsch. 1880. p. 384. - *Ionaspis cyanocarpa* (Anzi) Th. Fr. f. *calcicola* H. Magn., Medd. från Göteborgs Bot. Trädg. VIII (1933) p. 33. - *Ionaspis cyanocarpa* (Anzi) Th. Fr. f. *depauperata* H. Magn., Medd. från Göteborgs Bot. Trädg. VIII (1933) p. 33.

Aspicilia cinereorufescens γ *heteromorpha* Krmph., Lich. fl. Bayerns (1861) p. 175. Type: Germany "Auf dem Karwendel an der Rosslähne bei circa 4000' an Kalkfelsen und ebenso auf der Röthensteinalpe bei Fegernsee bei 5100'. K. (2.)" M (not seen). - *Aspicilia heteromorpha* (Krmph.) Rehm, Beitr. Flecht. fl. Allgäu (1863) p. 105. - *Ionaspis heteromorpha* (Krmph.) Th.

Fr., "implicitly" Lich. Scand. I (1871) p. 273. - *Ionaspis heteromorpha* (Krmph.) Th. Fr. var. *regelii* Räs., Hedwigia, LXXXI (1944a) p. 233.

Lecanora ochraceella Nyl., Flora (1868) p. 162. Type: Holland "Ad saxa calcarea, J. E. Zetterstett" H, UPS (both not seen) - *Aspicilia ochraceella* (Nyl.) Arn., Flora (1870) p. 470. - *Ionaspis ochraceella* (Nyl.) H. Magn., Medd. från Göteborgs Bot. Trädg. VIII (1933) p. 33.

Lecanora acharii β *rhodopis* b. *melanopis* Sommerf., Suppl. (1826) p. 89 (sec. spec. U.) Type: O (not seen) - ?*L. rhodopis* v. *melanopis* (Sommerf.) Th. Fr., Lich. spits. (1869) p. 24. -*Ionaspis melanopis* (Sommerf.) Blombg. et Forss., Enumer. Plant Scandin. (1880) p. 101.

Lecanora schismatopis Nyl., Flora (1884) p. 213. Type: "Super saxa calcarea cum Lecanora calva, Dicks." H (not seen). -*Ionaspis schismatopis* (Nyl.) Hue, Lich. morph. et anat. (1912) p. 119. -*Ionaspis schismatopis* (Nyl.) Hue var. *Lyngei* H. Magn., Medd. från Göteborgs Bot. Trädg. VIII (1933) p. 39.

Ionaspis annularis H. Magn., Medd. från Göteborgs Bot. Trädg. VIII (1933) p. 35. Type: Sweden, Torne lappmark "on the banks of a torrent, Vrang" holotype: UPS (not seen). -*Ionaspis annularis* H. Magn. var. *macrospora* Räs., Ann. Bot. Soc. Zool.-Bot. Fenn. Vanamo XX no. 3 (1944b) p. 28.

Ionaspis reducta H. Magn., Medd. från Göteborgs Bot. Trädg. VIII (1933) p. 34. Type: USSR "Novaya Zemlya. Matotchkin Shar, under Mt Wilezek, 1921, Lynge, 3 specimens (called arctica)" O (not seen).

Ionaspis arctica Lynge, Lich. Nov. Zemlya (1928) p. 43. Type: USSR, Novaya Zemlya "II. Matotchkin Shar: Mt. Wilczek. Serebryanka Fjord. IV. Mashigin Fjord: South side of Blaafjell Basin, Strömsnes Bay and Sol Bay. V. Admiralty Peninsula. VI. Pankratyeff Peninsula. Lynge" O (not seen).

Ionaspis spitsbergensis H. Magn. ("ad int."), Medd. från Göteborgs Bot. Trädg. VIII (1933) p. 34 (nom. inval., provisor.). Type: Norway "Spitsbergen. Bellsund, near the Calypso shore, 1926, Lynge" O (not seen).

Ionaspis aigneri A. Zahlbr., Ann. Mycol. (1936) p. 165. Type: Southern Austria "Niederösterreich: an losen Kalksteinen der "Großen Schütt" über dem Mittelsee bei Lunz, ca. 800 m. (J. Aigner) und zwischen dem vorderen un biateren Rotmoor am Obersee, ca. 1100 m (K. Redinger)." W (not seen).

Characterization: Apothecial density 5.0 -10.5- 16.0 / 6.25 mm2, disk 175 -255- 335 µm in diameter, margins 51 -75- 99 µm thick; lateral excipulum propium 20 -51- 87 µm thick; hymenium 75 -105- 140 µm high; subhymenium 24 -36- 47 µm high; hypothecium thickness very variable, 0 -29- 50 µm high; dark parts of the apothecia HNO_3 + violaceous pink; ascospores 9.0 -12.2- 16.0 X 6.5 -8.7- 11.0 µm.

Description: Thallus (old herbarium specimens) orange yellow (69,70, 73), or light grayish yellowish brown (79), or pale yellow to yellowish white (89, 92), or medium gray (265); when recently collected and dry, pale yellowish pink to brownish pink(29-33), or light to grayish reddish brown (45, 46), or brownish orange (54), or light brown (57), or pale to dark orange yellow (72,73), or light grayish to light yellowish brown (76, 79); mostly epilithic but

can be endolithic when growing on calcareous rocks in very dry sites, in the latter case, taking an H. melanocarpa appearance; continuous, rimose and/or rimose-areolate. Photobiont Trentepohlia.

Apothecia becoming confluent to fusing, circular to irregular, (3.3-)5.0 -10.5- 16.0(-27.0) /6.25 mm^2. Disk black (267), very concave or concave to flat when young, becoming almost flat to convex in maturity, in some cases remaining concave or very concave, (72-)175 -256- 336(-674) µm diameter. Margins not prominent to slightly prominent or lower than the substrate when young, becoming slightly prominent to prominent or rarely very prominent and constricted at the base or very rarely remaining not prominent in maturity, (0-)51 -75- 99(-168) µm thick.

Apothecial anatomical characters: Epihymenium bluish green (161, 165, 166), or olive green to brownish black, olive black, or blackish green (65, 96, 114, 126, 128, 146, 147, 151, 152); HNO_3 + violaceous pink, KOH negative. Epihymenium color diffusing into the hymenium; color thickness (30.0)44.3 -46.5- 48.7(-76.5) µm. Hymenium (50.0-)75.2 -106.1- 138.0(-175.0) µm high; rarely IKI + blue; HNO_3 + violaceous pink, KOH negative. Subhymenium hyaline; (17.5-)24.2 -36.4- 46.6(-71.4) µm high; IKI + blue or negative; HNO_3 and KOH negative. Hypothecium hyaline; 0.0 -28.7- 50.0(-87.5) µm high; HNO_3 and KOH negative; mostly textura angularis. Lateral excipulum propium hyaline to reddish black (24), dark olive brown (96) dark grayish olive (111), blackish green (152), or very dark bluish green (166); (0.0-)20.0 - 51.2- 86.7(-142.5) µm thick; HNO_3 + violaceous pink, KOH negative; textura prismatica, oblita, or porrecta. Basal excipulum propium hyaline to grayish yellowish brown (80), dark grayish olive (111), very dark green (147), also

hyaline or olive black (114), or very dark bluish green (166); 0.0 -13.0- 23.3(-30.6) µm thick; HNO_3 + violaceous pink, KOH negative; textura very variable. Excipular dark color continuous or discontinuous. Epipsamma absent, color of the disk given by pigments in the epihymenium.

Paraphyses undulated; dichotomously ramified at the apex, usually with, but sometimes without, ramification below the apex; anastomosed; mostly slightly constricted but occasionally absent, rarely moniliform; the same thickness from top to bottom or larger at the apex. Ascus tholus IKI negative. Ascospores (7.5-)9.0 -12.2- 16.0(-17.5) X (4.9-)6.5 -8.7- 11.0(-12.5) µm; not halonate but a thin and dense epispore, reminiscent of the mucilaginous sheath containing the aggregated ascospores as they are expelled from the ascus, can be seen; uniseriate or aseriate.

Pycnidia: (50-)70 -80- 100.0(-145) µm diameter, sections KOH -, wall continuously black or restricted to the region surrounding the ostiole; conidia bacilliform, (3.9-)5.0 -5.4- 5.9(-8.0) X 1.0(-1.7) µm.

Habitat: Submerged in small creeks or rivers or growing in the sprayed zone of falls. Also growing in intermittent creeks or on cliffs intermittently wet bordering rivers or even in extremely dry habitats such as the summit of small hills blown by strong wind. Colonizing siliceous or calcareous rocks.

Distribution: Arctic-alpine (Fig. 18).

Examined specimens: Canada. NORTHWEST TERRITORIES: Bathurst Island, *Innes-Taylor* 46 (CANL), *Brodo* 19433, 19282A & B, 19284A (CANL); Great Slave Lake, *Thomson* 12003 (CANL, MIN), 12023 (CANL, WIS, MIN), *Oldenburg* 46-1258 (WIS); Arctic Red River, *Bird & Thomson* 19873 (CANL);

Southern Baffin Island, *Weber* S 23959, S 23965, S 23966 (COLO), *Lutzoni & Proulx* 15, 86, 124, 181, 183 (CANL); Northern Baffin Island, *Hale* 786 (WIS); Holman, *Lutzoni & Proulx* 367, 503, 513, 514 (CANL); Cambridge Bay, *Lutzoni & Proulx* 336, 339, 351, 340 (CANL); Southern Cornwallis Island, *Lutzoni & Proulx* 194, 208, 247,250, 265, 269, 277, 294 300 (CANL); Southampton Island, *Weber* S 23670 (COLO); Devon Island, *Schulten* 16 (WIS). BRITISH COLUMBIA: Fairy Lake, *Brodo* 21357 (CANL); Wokkpash Lake, *Brodo* 21357 (CANL). YUKON: Goz Lake, *Scotter* 19622 (CANL).QUÉBEC: mont Albert, *Lutzoni* 870926-1c (1/3) (CANL).

United States: ALASKA: Okpilak Lake, *Thomson & Shushan* 10148, 10180 (WIS)

Eurasia. SWEDEN: Värmland Prov., *Muhr* 7650 (CANL); Öland, Zetterstedt 1867 (holotype of Ionaspis ochraceella Nyl.) (H:Nyl 25030); Torne Lappmark, *Häyrén* 24-07-1916 (H), *Magnusson* 8601 (M), *Weber* S 15286 (WIS). WEST GERMANY: Bayern, I. Heteromorpha (Kbr.) Arn., *Krempelhuber*, Syntype 3418 (M). ITALY: Prov. sondrio, Bormio, Val del Forno, Anzi 79 (isotype of Ionaspis cyanocarpa Anzi) (M). AUSTRIA: Tirol, *Arnold* 219 (M). USSR: Siberia, Behring's Strait, Konyambay, Exped. Vega, Almquist 25230 (holotype of Ionaspis schismatopis Nyl.) (H).

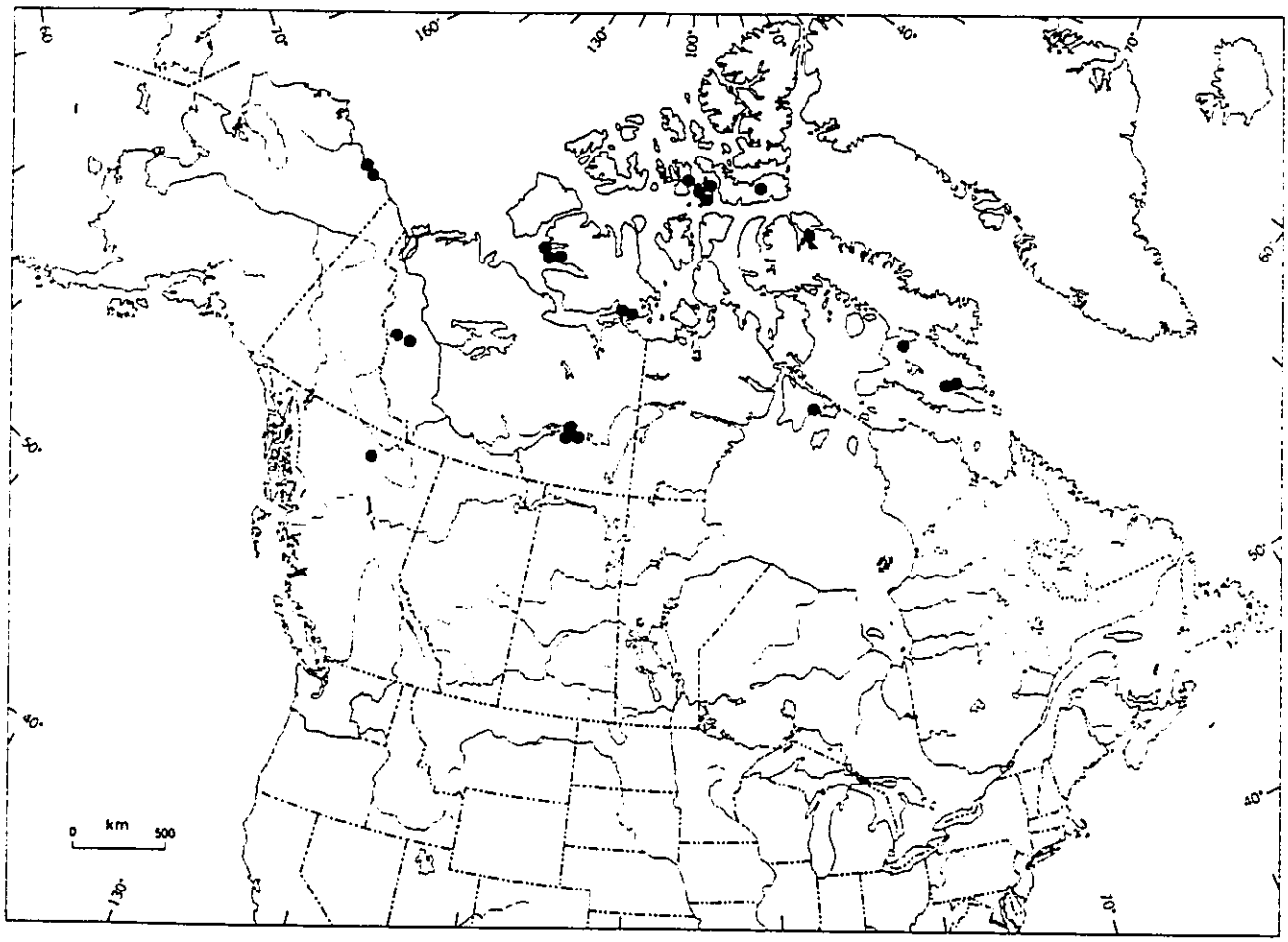


Figure 18. Preliminary North American distribution of "Hymenelia haematina (Körber) Lutzoni"

Taxonomical notes: As defined here, H. haematina includes all Magnusson's (1933) 13 taxa, excluding H. melanocarpa, having an HNO_3 + violet reaction of the coloured part of their apothecia. The reduction of 15 taxa to only one may appear radical but should be seen within the following context. It correlates quite well with the systematic studies of the genus Acarospora, where Magnusson (1923) recognized 199 species, 64 of which were new species each based on a single specimen or, at best, very few examples. Subsequently Magnusson (1929) published 93 new species most of which represent variants of a few common species (Weber, 1962). Weber estimated that the realignment of the A. smaragdula complex would involve reduction to synonymy of roughly 90 of Magnusson's species. In his revision of the genus Acarospora sugenus Xanthothallia, Weber (1968) reduced over 80 taxa to only two. In this sense, the results of the present study are in line with those of Weber (1962). It also confirms that some crustose lichens are very plastic and that many recognized taxa represent mere environmental modifications (Weber 1962; Poelt 1973b). Weber (1962) also concluded that crustose lichens of areas with rigorous climates like that of the Arctic are especially subjected to environmental modifications. Furthermore, H. haematina, being mostly found in aquatic habitats, can be substantially modified by the abrasion of sediments transported by rapidly flowing water.

There were a lot of difficulties in trying to recognize the different taxa retained by Magnusson (1933). This is responsible for the wide range of opinions expressed by lichenologists on the labels of packets containing specimens belonging to this group. There are three main reasons for this confusion: 1) several new taxa (I. spitbergensis, I. cyanocarpa f. depauperata,

I. cyanocarpa f. calcicola, I. annularis, and I. reducta), described by Magnusson (1933) were based on one or at the most 3 specimens, 2) the part of Magnusson's key dealing with these taxa is based on the assumption that populations found on different rock types (calcicolous versus non-calcicolous) are different taxa, and 3) many diagnostic characters used by Magnuson (1933) to describe new taxa are known to be highly "plastic" (Table 10). Magnusson (1933) himself was aware of the lack of reliability of some characters he used to describe new species of Ionaspis when he states: " But as many species are very similar in structure one is forced to rely mainly upon external characters."

No character was found to explain the clusters produced by the flexible sorting analysis within the haematina group. The differences between the groups were so small that it became clear that the haematina group is a continuum. Indeed, a more detailed analysis of the characters used by Magnusson (1933; Table 10), and Räsänen (1944a,b) to differentiate the taxa here lumped under H. haematina, shows that these characters are related to environmental variation.

The first character used in Magnusson's key within his section Caerulescentes was the nature of the rock, that is, calcicolous versus non-calcicolous. This character is crucial since the recognition of many species in this group is based on the assumption that lichens growing on different rock types are different taxa. In Magnusson's key (1933) Ionaspis spitsbergensis H. Magn., I. cyanocarpa (Anzi) Th. Fr., and I. haematina (Krmph.) Th. Fr. were considered as non-calcicolous species, whereas I. annularis H. Magn., I.

Table 10. List of taxa described by Magnusson (1933) with their associated diagnostic characters included in H. haematina.

Taxa	Diagnostic characters
I. spitbergensis	- minute areoles - thick apices of the paraphyses
I. cyanocarpa f. depauperata	- deeply concave apothecia - slender paraphyses ("due to severe climatic conditions"; Magnusson 1933)
I. cyanocarpa f. calcicola	- color of the thallus - smooth to slightly cracky surface of the thallus - apothecia more sunken in the thallus
I. annularis	- pale ochraceous thallus color - ± radiating structure - prominent apothecia with smooth circular margin - thin branched paraphyses
I. reducta	- reduced thallus - thallus pale dirty yellow - margin of apothecia blackish and prominent
I. schismatopis var. lyngei	- thallus thinner - rimose areolate - apothecia smaller - disk concave

reducta H. Magn., I. heteromorpha (Krmph.) Arn., I. ochraceella (Nyl.) H. Magn., and I. schismatopis (Nyl.) Hue were considered as calcicolous species. However, the organization of his key is in contradiction with his discussion on the substrate, where he specifies (Magnusson 1933: 8) that "there is no sharp limit between calcicolous and non-calcicolous species in this genus." He further says that I. haematina is strictly graniticolous, that I. cyanocarpa seems to grow generally on granitic or slightly calciferous rock, and that most species are exclusively calcicolous. It is quite likely that this character was set *a priori* by Magnuson (1933), since the latter mentions that it was difficult to distinguish I. heteromorpha from I. cyanocarpa when the latter was growing on calcareous rock, a situation which he considered rare. I agree with Weber's (1962) point of view when he says, concerning the genus Acarospora, that: "Perhaps Magnusson's faith in the validity of the habitus led him to search for anatomical characters to justify the "habitus"-taxa, and this resulted in unworkable character-separations. The height of the hymenium, thickness of cortex, width of paraphyses, and thickness of algal layer show differences within certain rather coarse limits, but these cannot be relied upon when the hiatus is only five or ten microns." In fact, when not taking into account the nature of the substrate, the limits between several taxa of Ionaspis become very vague. This is the case of I. spitbergensis versus I. reducta and I. heteromorpha, as well as I. cyanocarpa and I. haematina versus I. ochraceella and I. schismatopis.

The question is: are populations growing on different rock types (calcareous versus non-calcareous) necessarily different taxa? For lichenized fungi it seems that this is usually the case. Some taxa have been reported in

the literature as having a wide ecological range, but rarely are species mentioned that grow on both calcareous and acid rocks. In the case of H. haematina, perhaps the calcicolous populations are from a different taxon than the non-calcicolous ones. If this were the case this would imply 1) that the paucity of characters in this group makes it impossible to perceive differences, or 2) that the speciation process is a relatively recent event with differences that are strictly physiological. Even if the latter hypothesis were revealed to be true, the question still remains whether they should be considered as different taxa, and what hierarchical rank they should be given. Nevertheless, this would mean, at the most, that there are 2 taxa, not 15.

This character was never significant in the numerical analysis that would explain any potential clusters suggested by the flexible sorting method. Although the matrix was split into two groups, the calcicolous versus the non-calcicolous individuals, these groups were not significant at all, having a probability greater than mahalanobis distance = 0.55.

Finally there is a correlation in H. haematina between the nature of the rock and the growth form adopted by the lichen. The typical endolithic thalli were found in very xeric habitats, such as the top of a convex hill where polygonous soil is found and subjected to strong winds. The epilithic ones are found in running water or in related habitats. All intermediaries between these thallus types can be found in intermittent creeks for instance. Finally, epilithic specimens growing on acid rock were never found in xeric habitats. This strongly suggests that it is only one species and that it can grow in xeric habitats when calcareous rocks are present that permit endolithic growth.

The shape of the paraphyses, that is, slender versus wider at the apex, was used as an important character in Magnusson's key. Any character dealing with the apical region of the paraphyses is difficult to observe on hymenelioid lichens since they are embedded in an hymenial gel. Moreover, it appears to be a variable character within the same apothecia. Even though in the present study only radial sections (not tangential) obtained both by hand section and freezing microtome were used, the variation within the same section was so wide that it was always difficult to decide how to describe the paraphyses. It was soon realised that it was impossible to make reliable measurements on them. At the most, a general description (wider versus slender apex for example) of what appears to be the mature paraphyses was made. Even so, never was this character shown to be part of the explanation by PCA for the groups suggested by the cluster analysis.

The following characteristics of the thallus, that is, the texture, color, structure, thickness, as well as the height of the apothecial margin, are known to be very variable, and dependent on external factors such as the texture, structure, type of rock, luminosity, and degree of humidity. In some instances - the color of the margin of the apothecia being one example - the whole range of variation could be seen on the same thallus.

Finally, the diameter of the apothecial disk and the hymenium height were the only quantitative data used by Magnusson in his key dealing with this subgroup of the section Caerulescentes. In the present study the best split possible was for two groups (Fig. 19). The disk diameter found by Magnusson (1933), as well as the ascospore dimensions, hypothecium height,

density of apothecia, apothecial margin thickness, and subhymenium height were shown by the PCA or the CVA to be the most significant characters, for explaining these two groups. However, when looking at the variation of these characters, the difference between these two groups was so narrow that they were not really distinguishable (Fig. 19).

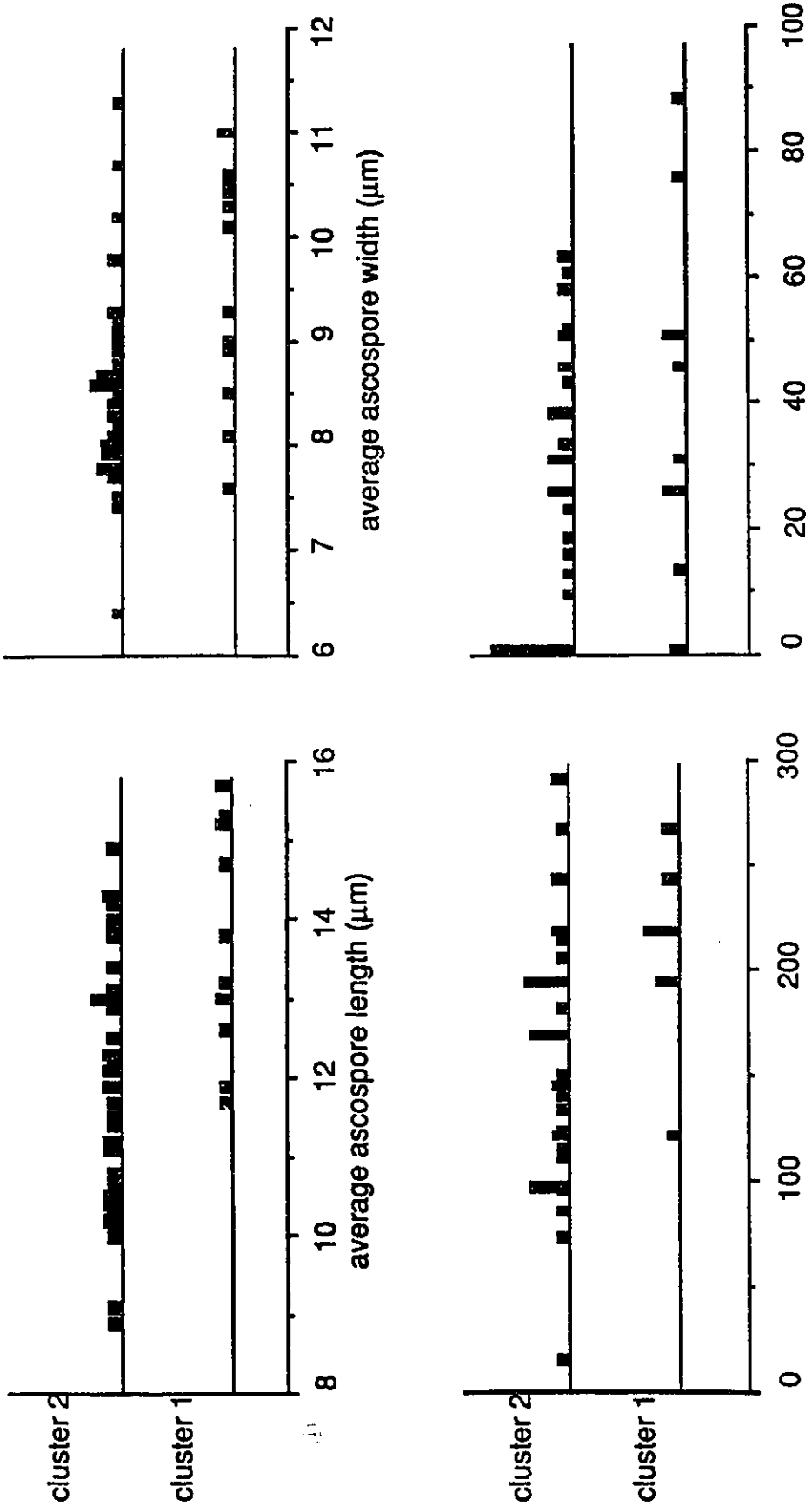


Fig. 19. Frequency of measurements for the most significant characters, as suggested by PCA and CVA, for the most significant clusters within the haematina group.

Hymenelia melanocarpa (Krmph.) Arn.

Flora (1869) p. 255. -*Hymenelia prevostii* ß *melanocarpa* Krmph., Flora (1852) p. 25. tab. I fig. 2. Type: M (not seen). -*Lecanora prevostii* f. *melanocarpa* (Krmph.) Stzbgr., Bericht. über die Thätigk. St. Gallisch. naturw. Gesellsch. (1880) p. 383. -*Ionaspis melanocarpa* (Krmph.) Arn., Lich. Ausfl. XXIII (1887) p. 134. -*Ionaspis melanocarpa* var. *crustosa* H. Magn., Medd. från. Göteborgs Bot. Trädg. VIII (1933) p. 41.

Ionaspis cyrtaspis auct., fide Santesson (1984).

Hymenelia prevostii var. *melanocarpa* f. *lecanorina* Krmph., Flora vol. XXXV (1852) p. 25. Type: M (not seen). -*Ionaspis cyrtaspis* f. *lecanorina* (Krmph.) Zahlbr., Cat. Lich. Univ. vol. 2 (1924) p. 688.

Ionaspis melanocarpa f. *minutella* Arn., Lich. ausfl. XXIII (1887) p. 134. Type: "an Steinen und Blöcken im Felsengerölle au der Nordseite, Arn. exs. 1115" (not seen). -*Ionaspis cyrtaspis* f. *minutella* (Arn.) Zahlbr., Cat. Lich. Univ. vol. 2 (1924) p. 688.

Lichen punctatus Engl., Bot. vol. VII (1798) tab. 450 (non Dicks.). Type: unknown. -*Lecanora subfusca* var. *punctata* Link, Grundriss der Kräuterkunde vol. III (1833) p. 194. -*Parmelia subfusca* var. *dicolor* f. *punctata* Torss., Enum. Lich. et Bussac. Scandin. (1843) p. 18. -*Hymenelia prevostii* ß *melanocarpa* Krmph. a *punctata* Krmph., Flora (1852) p. 25. -*Aspicilia epulotica* var. *punctata* Mudd, Manual Brit. Lich. (1861) p. 54. -*Lecanora lacustris* f. *punctata* Leight., Lich.-Flora Great Brit. edit. 3. (1879) p. 196.

Characterization: Apothecial density **4.0 -7.7- 10.9** / 6.25 mm2, disk **150 -240- 330** µm in diameter, margins **22 -30- 38** µm thick; lateral excipulum propium **34 -40- 45** µm thick; hymenium **115 -140- 165** µm high; subhymenium **29 -41- 53** µm high; hypothecium absent, exceptionally present to a maximum height of 25 µm; dark parts of the apothecia HNO_3 + violaceous pink; ascospores **14.1 -16.3- 19.0 X 9.4 -10.7- 12.1** µm.

Thallus endolithic. Photobiont Trentepohlia.

Apothecial fusion present or absent, subangular to irregular, (4.0-) **7.7- 10.9**(-14.0) /6.25 mm^2. Disk black (267), almost flat to flat when young, remaining this way or rarely becoming concave in maturity, (95-)**150 -240- 330**(-480) µm diameter. Margins slightly prominent (when compared to the disk in this case) in maturity, (12.0-)**22.1 -30.2- 38.3**(-72.3) µm thick.

Apothecial anatomical characters: Epihymenium mostly deep bluish green (161), but also very dark green (147); HNO_3 + violaceous pink, KOH negative. Epihymenium color diffusing into the hymenium; color thickness (30.0)**41.2 -44.2- 47.2**(-60.0) µm. Hymenium (100.0-)**116.4 -139.9- 163.4**(-187.5) µm high; rarely IKI + blue; HNO_3 + violaceous pink, KOH negative. Subhymenium hyaline; (20.0-)**28.6 -40.7- 52.8**(-62.5) µm high; rarely IKI + blue; HNO_3 and KOH negative. Hypothecium hyaline; absent (-25.0) µm high; HNO_3 and KOH negative. Lateral excipulum propium blackish green (152), very dark bluish green (166), or bluish black (193); (10.0-)**34.4 -39.6- 44.8**(-75.0) µm thick; HNO_3 + violaceous pink, KOH negative; textura prismatica or globulosa. Basal excipulum propium hyaline to brownish black (62, 65), very dark green (147), or black (267); **17.5 -19.7- 23.8** µm thick; HNO_3 +

violaceous pink, KOH negative; textura mainly globulosa but also intricata or epidermoidea. Excipular dark color continuous. Epipsamma absent, color of the disk given by pigments in the epihymenium.

Paraphyses dichotomously ramified at the apex, usually with, but sometimes without ramification below the apex, or usually without ramification at the apex when moniliform; usually more anastomosed when not moniliform; mostly moniliform but also submoniliform or slightly constricted; generally larger toward the apex. Ascus tholus IKI -. Ascospores (11.2-)**14.1** -16.3- **19.0**(-25.0) X (8.0-)**9.4** -10.7- **12.1**(-13.8) µm; not halonated but a thin and dense epispore, reminiscent of the mucilaginous sheath containing the aggregated ascospores as they are expelled from the ascus, can be seen; aseriate, sometimes uniseriate.

Pycnidia: (50-)**65** -85- **95**(-120) µm diameter, wall continuously black; conidia bacilliform, longely rectangular or elliptic, (4.0-)**4.6** -5.0- **5.5**(-5.9) X **1.0**(-2.0) µm.

Habitat: Mostly found on boulders in rivers, colonizing the part just above the summer water level. Also found on dry cliffs along rivers or vertical face of boulders on alpine ridges. Colonizing calcareous rocks.

Distribution: Arctic-alpine (Fig. 20).

Examined specimens: Canada. NORTHWEST TERRITORIES: Eastern Victoria Island, *Lee & Kittle* 09-1975 (CANL); Bathurst Island, *Brodo* 19352 (CANL); Holman, *Lutzoni & Proulx* 366 (CANL); Southern Cornwallis Island, *Lutzoni & Proulx* 207, 208, 246, 253 (CANL); Southampton Island, *Weber* S

23650-2x (COLO); Devon Island, *Schulten* 17 (WIS). BRITISH COLUMBIA: Wokkpash Lake, *Brodo* 21524 (CANL).

United States: ALASKA: North Slope Borough, *Nash* 14846 (COLO); Okpilak Lake, *Thomson & Shushan* 10140-2x (WIS)

Taxonomic notes: At first glance it might be difficult to distinguish Hymenelia melanocarpa from endolithic H. haematina, but most of the time they can be easily recognised by their morphology, anatomy, and habitat (table 11). These results confirm the deduction made for H. haematina, i. e. the presence of a continuum of epilithic to endolithic form as we go from aquatic to xeric habitat. It is important to note that H. melanocarpa is related to aquatic habitat contrarily to the endolithic form of H. haematina. However, in one case, both apothecial types could be seen on the thallus (Southern Cornwallis Island, Lutzoni & Proulx, 269, CANL). This might be the result of hybridization. Hymenelia melanocarpa is the most uniform species within the genus Hymenelia in North America; it does not show such a wide range of variation as in H. haematina and H. epulotica.

It was not possible to split H. melanocarpa further using numerical techniques. Paraphyses constriction (moniliform versus not constricted) was examined as a potential diagnostic character to separate this taxon into two taxa. No correlation of this character could be made with any other character. A close observation of paraphyses shows that both types were often seen on the same individual. Once again, this suggests that the shape of paraphyses is not useful within the genus Hymenelia.

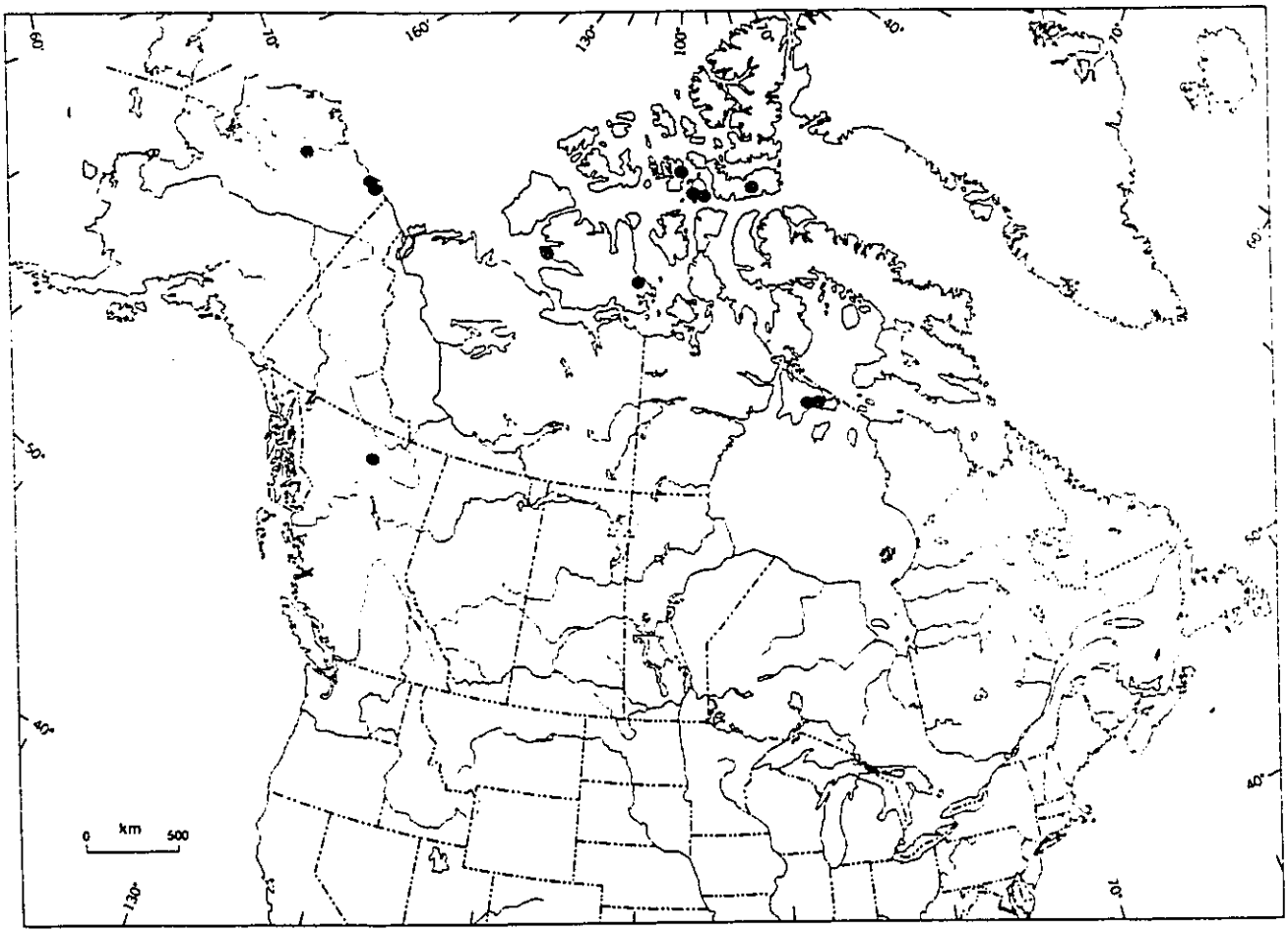


Figure 20. Preliminary North American distribution of Hymenelia melanocarpa (Krmph.) Arn.

Table 11. Differences between the endolithic form of Hymenelia haematina and Hymenelia melanocarpa.

Diagnostic characters	H. haematina (endolithic)	H. melanocarpa
Hymenium thickness (µm)	75.0 -98.3- 118.5	116.4 -139.9- 187.5
Apothecia margin thickness (µm)	39.2 -76.3- 113.4	20.6 -38.3- 56.0
Excipulum propium	continuous or not	continuous
Paraphyses apices	dichotomously ramified	dichotomously ramified or not
Paraphyses constriction	rarely moniliform	often moniliform
Ascospores length (µm)	(9.2-)10.9 -12.4- 13.9 (-15.0)	(11.2-)14.4 -16.3- 19.0 (-25.0)
Pycnidia diameter (surface view, µm)	(50-)55 -60- 70 (-85)	(50-)65 -85- 95 (-120)
Habitat	generally in extremely dry sites, e.g., fellfield on summit of hills.	on boulders in rivers, just above water level, or other habitats related to aquatic environment.

Hymenelia epulotica (Ach.) Blomb. & Forss. ssp. epulotica

Enumerantur Plantæ Scandinaviæ (1880), p. 101. -*Gyalecta epulotica* Ach., Lich. Univ. (1810) p. 151 tab. 1 fig. 7. Type: "Anglia, Harriman 15" lectotype here designated: H-Ach 57!; isolectotypes: BM (not seen), UPS!

Hymenelia prevostii v. *patellula* Arn., Lichenol. Fragm. VII Flora (1874) p. 381. Type: unknown. -*Ionaspis epulotica* v. *patellula* (Arn.) H. Magn., Medd. från. Göteborgs Bot. Trädg. VIII (1933) p. 13.

Characterization: Apothecial density **5.0 -8.6- 11.5** / 6.25 mm2; subhymenium (45.0-)57.8(-70.0) µm thick; ascospore **14.9 -17.0- 19.1** µm long; conidia 7.4 -8.1- 8.7 µm long.

Description: Thallus pinkish white to grayish yellowish pink, or light to light grayish yellowish brown or yellowish white (9, 32, 76, 79, 92), epilithic or endolithic, continuous, rimose to rimose-areolate. Photobiont Trentepohlia.

Apothecial fusion present, circular, subangular, or irregular, (5.0-)8.6-11.5(-14.0) /6.25 mm^2. Disk light to grayish pink, or pale yellowish pink, or yellowish white (4, 7, 8, 31, 92), very concave or concave, rarely flat when young, remaining concave or very concave or becoming very concave, concave or almost flat in maturity, (80-)**190 -300- 420**(-600) µm diameter. Margins not prominent or slightly prominent when young, becoming slightly prominent to prominent in maturity, (24.1-)**66.3 -101.9- 137.4**(-241.0) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 and KOH negative. Hymenium hyaline; (112.5-)**132.2 -164.5- 196.8**(-212.5) µm high; IKI

negative; HNO_3 and KOH negative. Subhymenium hyaline; (45.0-)57.8(-70.0) µm high; HNO_3 and KOH negative. Hypothecium hyaline; absent(-75.0) µm high; HNO_3 and KOH negative. Lateral excipulum propium hyaline; (37.5-)53.2 -76.3- 99.4(-107.5) µm thick; HNO_3 and KOH negative. Basal excipulum propium hyaline; HNO_3 and KOH negative.

Epipsamma absent. Paraphyses ramified below the apex, dichotomously ramified or not at the apex; slightly constricted rarely submoniliform; anastomosed; larger or not at the apex. Ascus tholus IKI -. Ascospores (12.5-)14.9 -17.0- 19.1(-20.8) X (8.2-)9.8 -11.1- 12.2(-13.0) µm; not halonate, mostly uniseriate rarely only aseriate.

Pycnidia: (25-)50 -65- 80(-120) µm diameter, completely hyaline; conidia bacilliform, (5.9-)7.4 -8.1- 8.7(-9.8) X 1.0 µm.

Habitat: found on boulders in brooklets, in intermittent brooklets, on wet cliffs, or in the spray zone of falls. Always on calcareous rocks.

Distribution: Arctic (Fig. 24).

Examined specimens: Canada. NORTHWEST TERRITORIES. Victoria Island, Cambridge Bay, Greiner Lake, *Lutzoni & Proulx* 343, 344, 347, 348 (CANL). Southern Cornwallis Island, *Lutzoni & Proulx* 249 (CANL); Trafalgar Lake, *Lutzoni & Proulx* 310 (CANL); Mc Master river, *Lutzoni & Proulx* 221 (CANL); Allen river, *Lutzoni & Proulx* 259, 261 (CANL); Mecham river, *Lutzoni & Proulx* 192 (CANL).

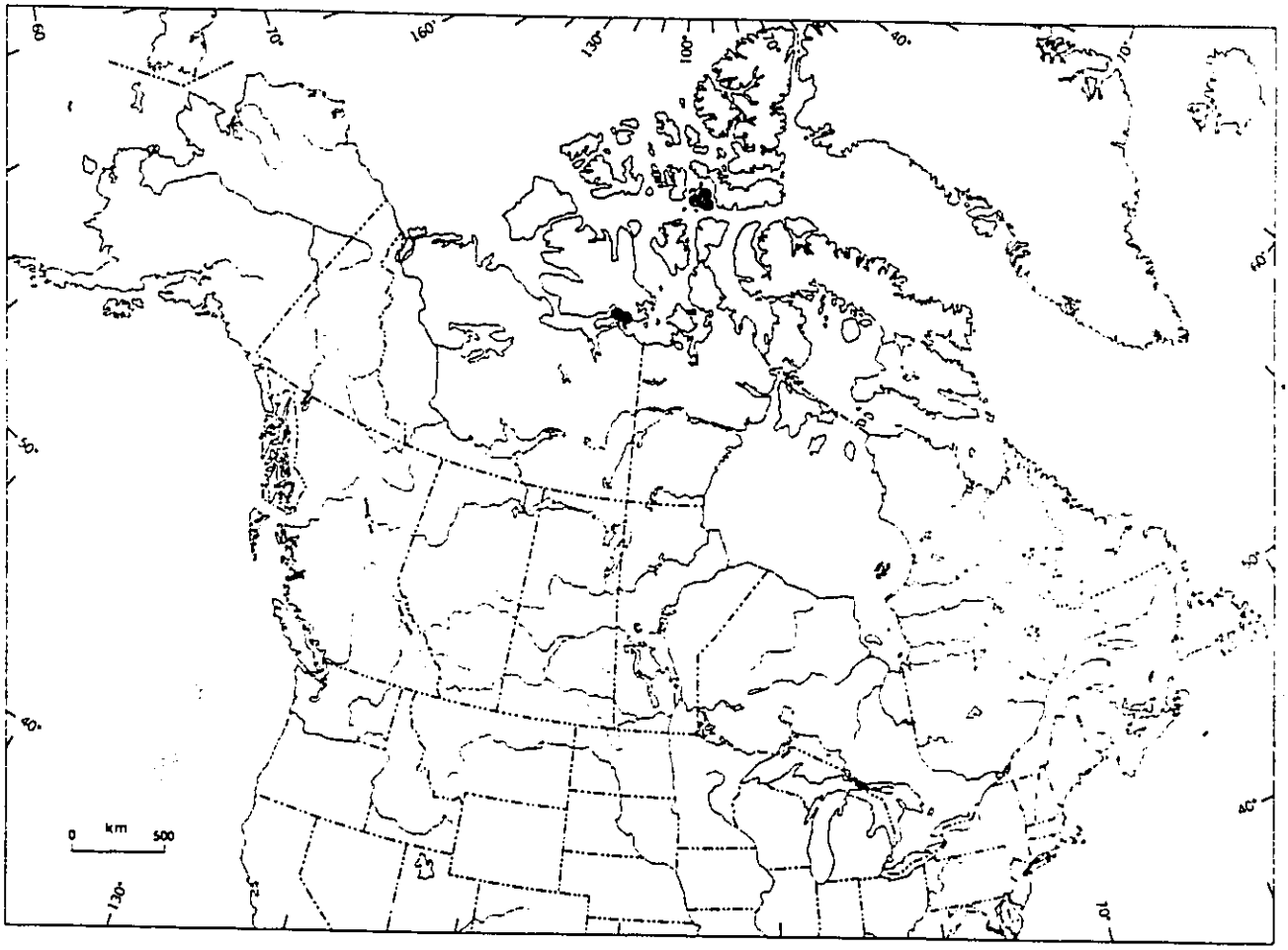


Figure 21. Preliminary North American distribution of Hymenelia epulotica (Ach.) Blomb. & Forss. ssp. epulotica.

"Hymenelia epulotica (Ach.) Blomb. & Forss. ssp. meridionalis Lutzoni"

Characterization: Thallus without any cortex, coarse granular-leprose; apothecial density 3.0 -6.4- 9.3 / 6.25 mm2, disk 120 -200- 280 µm in diameter, margins 59 -82- 105 µm thick, sections HNO_3 and KOH negative; lateral excipulum propium 48 -67- 84 µm thick; hymenium 80 -95- 110 µm high; subhymenium (22.5-)33.6(-45.0) µm high; hypothecium 24.7 -35.1- 45.5 µm high; ascospores 12.4 -14.7- 16.9 X 6.9 -8.0- 9.3 µm; ascus tholus IKI -; mostly in the Great lake region, but also in the Arctic; on calcareous rock.

Description: Thallus yellowish gray, epilithic, continuous or pored, usually very thin, granulose, rimose when thicker. Photobiont Trentepohlia.

Apothecial fusion present, circular to subangular, (3.0-)6.4- 9.3(-11.2) /6.25 mm^2. Disk light to moderate pink (4, 5, 7), or light yellowish pink (28), rarely yellowish white (92), very concave to concave when young, becoming concave to almost flat in maturity, (70-)120 -200- 280(-360) µm diameter. Margins slightly prominent when young, becoming prominent to very prominent and constricted at the base in maturity, (36.2-)59.0 -81.8- 104.6(-120.5) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 and KOH negative. Hymenium hyaline; (70.0-)80.7 -94.5(-112.5) µm high; rarely IKI + blue; HNO_3 and KOH negative. Subhymenium hyaline; (22.5-)33.6(-45.0) µm high; IKI negative; HNO_3 and KOH negative. Hypothecium hyaline; (17.5-)24.7 -35.1- 45.5(-50.0) µm high; HNO_3 and KOH negative; textura epidermoidea. Lateral excipulum propium hyaline; (25.0-)48.2 -66.0- 83.7(-

137.5) µm thick; HNO_3 and KOH negative; textura prismatica. Basal excipulum propium hyaline; HNO_3 and KOH negative; textura angularis.

Epipsamma absent. Paraphyses dichotomously ramified at the apex, usually with ramifications below the apex; mostly slightly constricted or submoniliform, rarely moniliform; anastomosed; larger at the apex. Ascus tholus IKI -. Ascospores (10.0-)**12.4 -14.7- 16.9**(-20.0) X (5.4-)**6.9 -8.0- 9.3**(-10.2) µm; rarely halonated (1/10); aseriate.

Pycnidia: rare, (50-)**80- 115**(-145) µm diameter, completely hyaline; conidia bacilliform, (3.7-)**3.9**(-4.2) X 1.0 µm.

Habitat: On calcareous rocky lakeshores, but also in intermittent creeks and on humid cliffs.

Distribution: Mostly temperate, Great Lakes region; also found in the Arctic (Fig. 21).

Examined specimens: Canada. ONTARIO: Bruce County, Gillies Lake, *Wong* 2120- (CANL, MICH, MIN, COLO). NORTHWEST TERRITORIES: Victoria Island, Holman *Lutzoni & Proulx* 512 (CANL); Devon Island, *Barrett* 1071 (WIS).

United States. MICHIGAN: Delta County, Charboneau Point. Vězda EXS 1955 (DUKE); Mackinac County, Island Point Campground, *Wetmore* 29753 (MIN), *Buck* 74.10.5 (NY), *Brodo* 22436 (CANL).

Taxonomical notes: See taxonomical notes under H. epulotica ssp. silicicola.

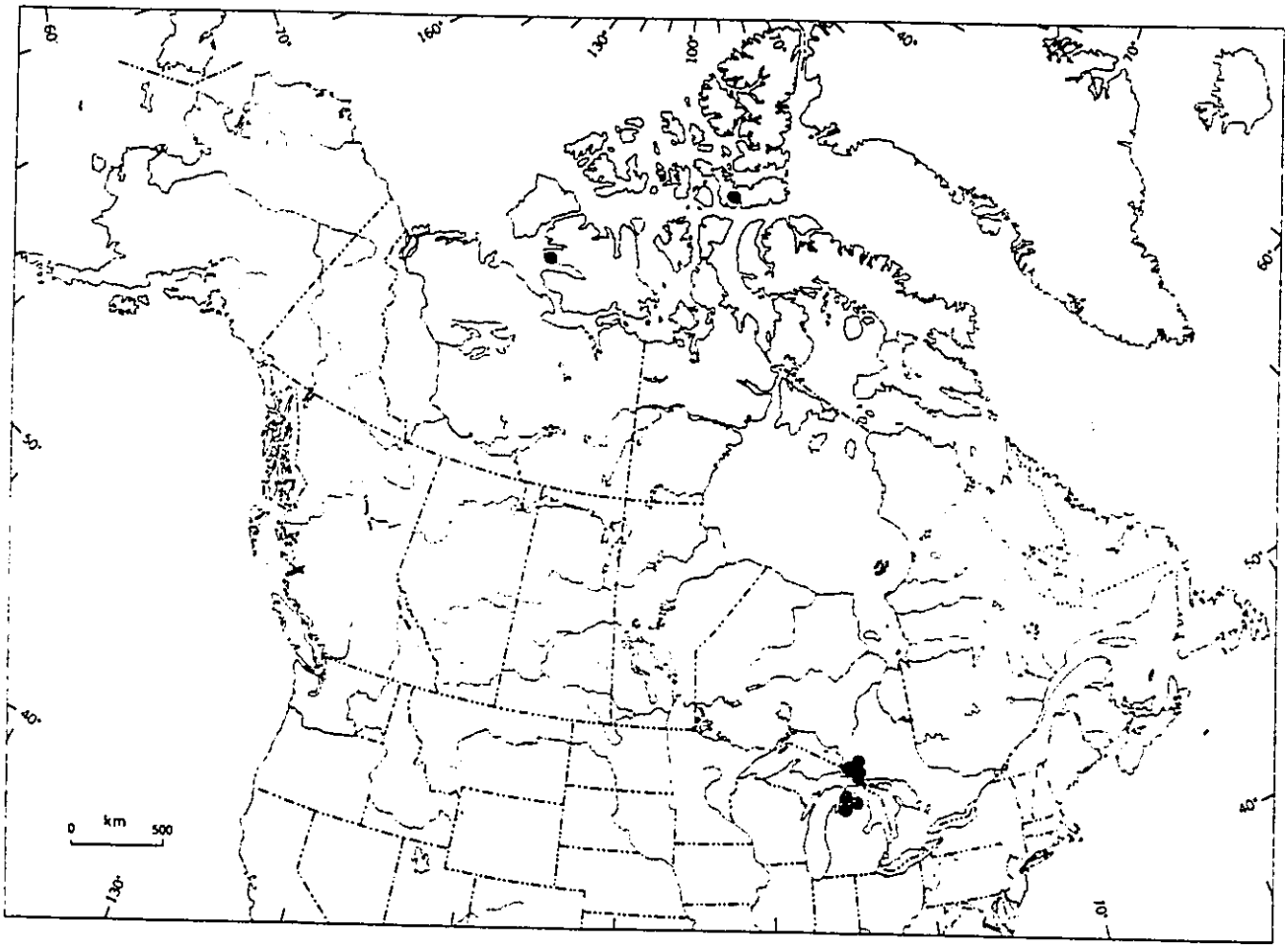


Figure 22. Preliminary North American distribution of "Hymenelia epulotica (Ach.) Blomb. &Forss. ssp. meridionalis Lutzoni".

"Hymenelia epulotica (Ach.) Blomb. & Forss. ssp. silicicola Lutzoni"

Characterization: Thallus thinly corticated or cortex absent, surface rugose to subgranulose or smooth; apothecial density **4.3 -6.9- 10.7** / 6.25 mm2, disk **120 -170- 210** µm in diameter, margins **66 -86- 105** µm thick, sections HNO_3 and KOH negative; lateral excipulum propium **60 -68- 75** µm thick; hymenium **80 -110- 135** µm high; subhymenium **20.0 -35.4- 46.2** µm high; hypothecium **0.0 -26.1- 52.6**; ascospores **12.7 -14.0- 15.4 X 7.3 -7.7- 9.3** µm; ascus tholus IKI -; mainly Arctic-alpine (south to the southern Rocky Mountains), but also boreal; on acid rock.

Description: Thallus light yellowish brown or grayish yellowish brown, epilithic, continuous or pored, rimose to rimose-areolate, surface rugose to subgranulose. Photobiont Trentepohlia.

Apothecial fusion present or absent, circular to subangular, (4.3-)6.9(-10.7) /6.25 mm^2. Disk pinkish gray to grayish to pale yellowish pink, or light orange yellow, or yellowish white (8, 9, 31, 70, 73), very concave to concave when young, becoming concave to almost flat in maturity, (70-)120 -170- 210(-290) µm diameter. Margins slightly prominent when young, becoming prominent to very prominent and constricted at the base in maturity, (24.1-)66.4 -85.6- 104.9(-144.6) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 and KOH negative. Hymenium hyaline; (65.0-)82.5 -108.2- 133.9(-150.0) µm high; rarely IKI + blue; HNO_3 and KOH negative. Subhymenium hyaline; (20.0-)35.4-46.2(-55.0) µm high; rarely IKI + blue; HNO_3 and KOH negative. Hypothecium hyaline; (0.0-)26.1- 52.6(-85.0) µm high; textura angularis.

Lateral excipulum propium hyaline; (25.0-)59.6 -67.2- 74.7(-137.5) µm thick; HNO_3 and KOH negative; textura prismatica. Basal excipulum propium hyaline; (10.0-)16.2(-22.1) µm thick; HNO_3 and KOH negative; textura prismatica or oblita to porrecta.

Epipsamma absent. Paraphyses dichotomously ramified at the apex with ramifications below the apex; slightly constricted or submoniliform, rarely moniliform; anastomosed; larger at the apex. Ascus tholus IKI -. Ascospores (8.5-)12.7 -14.0- 15.4(-18.7) X (5.5-)7.3 -7.7- 9.3(-11.2) µm; rarely halonate; aseriate rarely uniseriate.

Pycnidia: (75-)90 -95- 100.0(-110) µm diameter, completely hyaline; conidia bacilliform, (3.4-)4.4(-5.9) X 1.1 µm.

Habitat: Mostly found on boulders in brooklets, but also on rocky lakeshores or on humid cliffs. Always on acid rocks.

Distribution: Mainly Arctic-alpine (south to the southern Rocky Mountains), but also boreal (Fig. 22).

Examined specimens: Canada. NORTHWEST TERRITORIES. Southern Baffin Island: Apex, *Weber* 23950,23966 (COLO), *Lutzoni & Proulx* 15, 123, 85 (CANL); Iqaluit, *Lutzoni & Proulx* 11 (CANL); Nettilling Lake, *Lutzoni & Proulx* 180 (CANL); Victoria Island: Holman, *Lutzoni & Proulx* 432 (CANL). BRITISH COLUMBIA. Queen Charlotte Islands, *Brodo* 26813 (CANL). NEWFOUNDLAND. Crabbs, *Arnold* 97.9.7 (MIN).

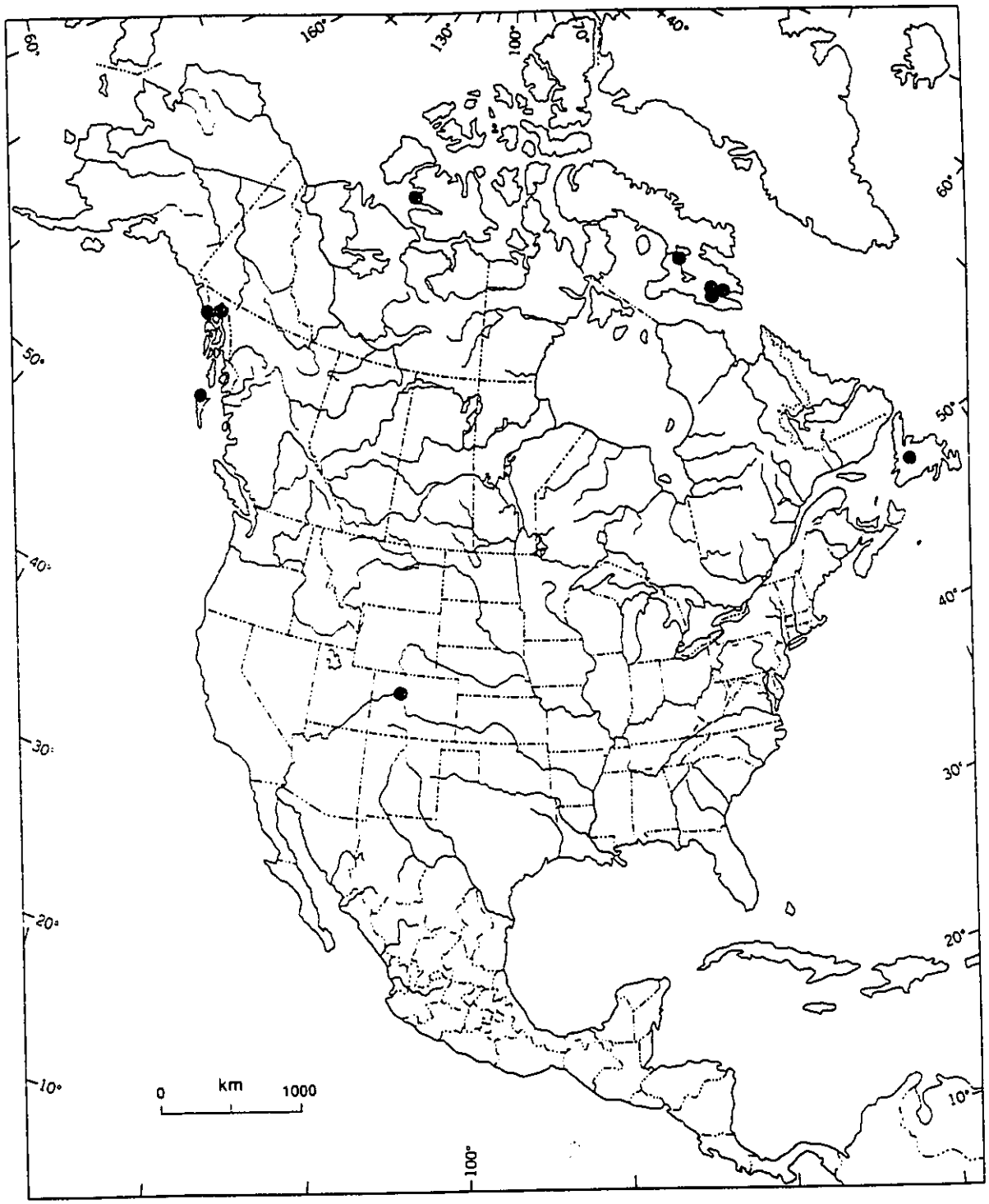


Figure 23. Preliminary North American distribution of "Hymenelia epulotica (Ach.) Blomb. & Forss. ssp. silicicola Lutzoni".

United States. ALASKA. Mosquito Flats, *Thomson & Ahti* 21937-2X (CANL); COLORADO. Summit Co., Monte Cristo Creek, *Shushan* s1-6641 (WIS).

Taxonomical notes: Hymenelia epulotica ssp. meridionalis could not be shown to be significantly different from H. epulotica ssp. silicicola using the canonical discriminant analysis. Most of their main differences are qualitative characters that cannot be used in such an analysis. However, the very peculiar granular thallus of H. epulotica ssp. meridionalis, its restriction to calcareous rock (versus acid rock for H. epulotica ssp. silicicola) and the allopatric distribution of the two taxa distinguish them. Hymenelia epulotica ssp. meridionalis is the southernmost species of the genus Hymenelia in North America with a population found in the Great Lakes region. This type of distribution is very unusual within Hymenelia. The population of H. epulotica ssp. silicicola in contact with the arctic population of H. epulotica ssp. meridionalis have some individuals with granular-leprose thallus characteristic of the meridionalis subspecies. The situation described here for these two taxa fits the description of a subspecies better than it does a variety.

The reasons for using the subspecies rank rather than the variety rank is related to the definiton of these two ranks as described in Hawksworth (1974): "the 'subspecies' rank is used where two or more populations separated either geographically, ecologically or both throughout most of their range and distinguished by characters which might be used as criteria at the rank of species have intermediates where their distibrutions overlap...so that it is not possible to place some individuals satisfactorily in

one subspecies or another." Again, according to Hawksworth (1974), "Varieties are based on characters which are not regarded as meriting separation at the rank of species or subspecies and which are distinct from all other varieties within the species (i.e. intermediates should not occur)."

"Hymenelia sp. # 1"

Characterization: Similar to H. epulotica ssp. epulotica, but apothecial density lower (**1.7 -4.2- 7.0** / 6.25 mm2); subhymenium narrower (28.9-)39.9(-50.0) µm high; ascospores slightly shorter, **12.6 -15.0- 17.3** µm long; and the conidia much shorter, (3.9-)5.3(-6.4) µm long.

Description: Thallus pale yellowish pink, pale orange yellow, or yellowish white (31, 73, 92), epilithic, continuous, rimose to rimose-areolate. Photobiont Trentepohlia.

Apothecial fusion present, circular, subangular, or irregular, (1.7-)4.2(-7.0) /6.25 mm^2. Disk pinkish white to pale pink (4, 7, 9), or pale yellowish pink (31), very concave or concave when young, becoming concave or almost flat to flat in maturity, (140-)**200 -390- 570**(-720) µm diameter. Margins not prominent or slightly prominent when young, becoming prominent to very prominent and constricted at the base in maturity, (0.0-)**76.6 -115.8- 155.1**(-216.9) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 and KOH negative. Hymenium hyaline; (85.0-)**124.8 -130.1- 135.4**(-162.5) µm high;

rarely IKI + blue; HNO_3 and KOH negative. Subhymenium hyaline; (28.9-)39.9(-50.0) µm high; IKI rarely + blue; HNO_3 and KOH negative. Hypothecium hyaline; (0.0-)75.2- 159.9(-225.0) µm high; HNO_3 and KOH negative; textura globulosa or angularis. Lateral excipulum propium hyaline; (0.0-)61.9 -89.4- 116.8(-225.0) µm thick; HNO_3 and KOH negative; textura angularis or prismatica. Basal excipulum propium hyaline; (17.5-)22.2(-28.5) µm thick; HNO_3 and KOH negative; textura angularis or prismatica.

Epipsamma absent. Paraphyses ramified below the apex rarely not dichotomously ramified at the apex; slightly constricted rarely moniliform; anastomosed; larger at the apex or without a widening at the apex. Ascus tholus IKI -. Ascospores (11.2-)12.6 -15.0- 17.3(-20.0) X (7.6-)9.0 -10.1- 11.2(-13.2) µm; halonate or not, when they are so, the halo is very dense and is reminiscent of the gelatinous envelope embeding the discharged ascospores, rarely diffusely halonate (1/6); aseriate rarely uniseriate.

Pycnidia: (75-)100 -125- 170(-215) µm diameter, completely hyaline; conidia bacilliform, (3.9-)5.3(-6.4) X 1.2 µm.

Habitat: Found on calcareous boulders in brooklets. Always on acid rocks.

Distribution: Arctic-alpine (Fig. 23).

Examined specimens: Canada. NORTHWEST TERRITORIES. Southampton Island: Coral Harbor, *Weber* 23643 (COLO); Victoria Island: Holman, *Lutzoni & Proulx* 493, 375 (CANL). BRITISH COLUMBIA. Northern Rocky mountains, Fairy Lake, *Brodo* 21674 (CANL), Wokkpash Lake, *Brodo* 21509 (CANL). QUÉBEC. Mont Albert, *Lutzoni* 870926-1a(1/3) (CANL).

Taxonomical notes: This taxon is not easily distinguished from H. epulotica ssp. epulotica; more material has to be seen before any taxonomic decision can be taken. An exhaustive study of all the type specimens of the hymenelioid lichens is also required before this taxon can be named.

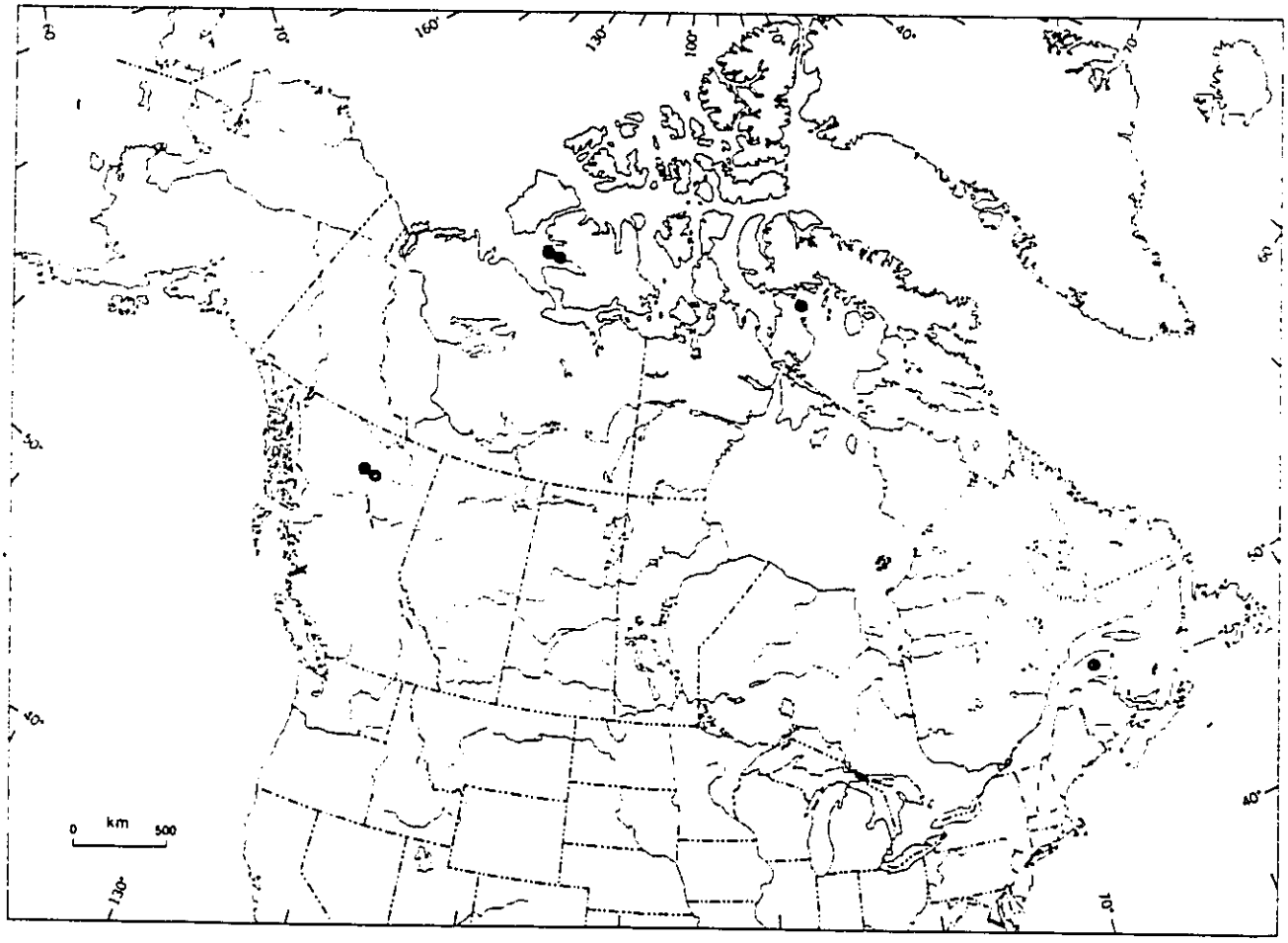


Figure 24. Preliminary North American distribution of Hymenclia sp. # 1.

Hymenelia sp. # 2

Characterization: A pale-fruited species with moderately dense apothecia (4.8 -8.1- 11.4 / 6.25 mm2), with thick prominent gelatinous margins, constricted at the base. The subhymenium is (12.5-)33.5- 52.8 µm thick, and ascospores [illegible] -13.4- 14.9 µm long. The conidia are short (3.2-3.9 µm long) and bacilliform.

Description: Thallus moderate orange, light to light grayish yellowish brown, or dark grayish yellow (53, 76, 79, 91), epilithic, continuous or porous, rimose to rimose-areolate, or smooth, subgranulose and non corticated. Photobiont Trentepohlia.

Apothecial fusion present, circular, subangular, or elongate, (3.5-)4.8 - 8.1- 11.4(-14.0) /6.25 mm^2. Disk pinkish white to grayish pink, pale orange yellow, yellowish white, or light gray (4, 7, 8, 9, 28, 73, 92, 264), very concave to concave when young, remaining this way in maturity, (70-)120 -200- 280(-390) µm diameter. Margins gelatinous (translucent and flexible when wet) not prominent or slightly prominent when young, becoming prominent to very prominent and constricted at the base in maturity, (60.2-)84.3 -117.2- 150.2(-289.2) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 and KOH negative. Hymenium hyaline; (72.5-)99.0 -131.4- 163.8(-187.5) µm high; rarely IKI + blue; HNO_3 and KOH negative. Subhymenium hyaline; (12.5-)33.5- 52.8(-75.0) µm high; HNO_3 and KOH negative. Hypothecium hyaline; (0.0-)13.1 -31.6- 49.1(-60.0) µm high. Lateral excipulum propium hyaline; (0.0-)48.6

-54.6- 60.5(-112.5) µm thick; HNO_3 and KOH negative. Basal excipulum propium hyaline; HNO_3 and KOH negative.

Epipsamma absent. Paraphyses dichotomously ramified at the apex, sometimes also ramified below the apex; slightly constricted, sometimes submoniliform or moniliform; anastomosed; larger or not at the apex. Ascus tholus IKI -. Ascospores (8.2-)12.3 -13.4- 14.9(-21.8) X (5.5-)7.4 -8.4- 9.4(-11.2) µm; rarely halonate, when so, the halo is very dense and is reminiscent of the gelatinous envelope embedding the discharged ascospores, rarely diffusely halonate (1/15), aseriate or uniseriate.

Pycnidia: 60 -70- 75 µm diameter, completely hyaline, prominent, rare; conidia bacilliform, (3.2-) -3.6- (-3.9) X 1.0 µm.

Habitat: Mostly found in dry habitats such as fellfields, scree slopes and abandoned channels, occasionally in brooklets. Generally on calcareous rocks.

Distribution: Arctic (Fig. 25).

Examined specimens: Canada. NORTHWEST TERRITORIES. Victoria Island, Cambridge Bay, *Thomson* 13463-2X (WIS), *Weber* 23739 (COLO); base of Mont Pelley, *Lutzoni & Proulx* 350 (CANL); Holman *Lutzoni & Proulx* 388,392 (CANL). Southern Cornwallis Island, *Lutzoni & Proulx* 219, 331 (CANL), *Weber* 23861 (COLO); Trafalgar Lake, *Lutzoni & Proulx* 293, 316 (CANL), Mecham river, *Lutzoni & Proulx* 193 (CANL).

United States. NORTHERN ALASKA. Franklin Bluffs, Sagavanirktok River, *Thomson et. al.* 10798-2X (US); Okpilak River at Okpilak Lake, *Thomson & Shushan* 10231 (WIS).

Taxonomical notes: This easily recognized taxon, with its thick, gelatinous apothecial margins, might already have an existing name. An exhaustive study of all the type specimens of the hymenelioid lichens is required before this taxon can be considered a new species.

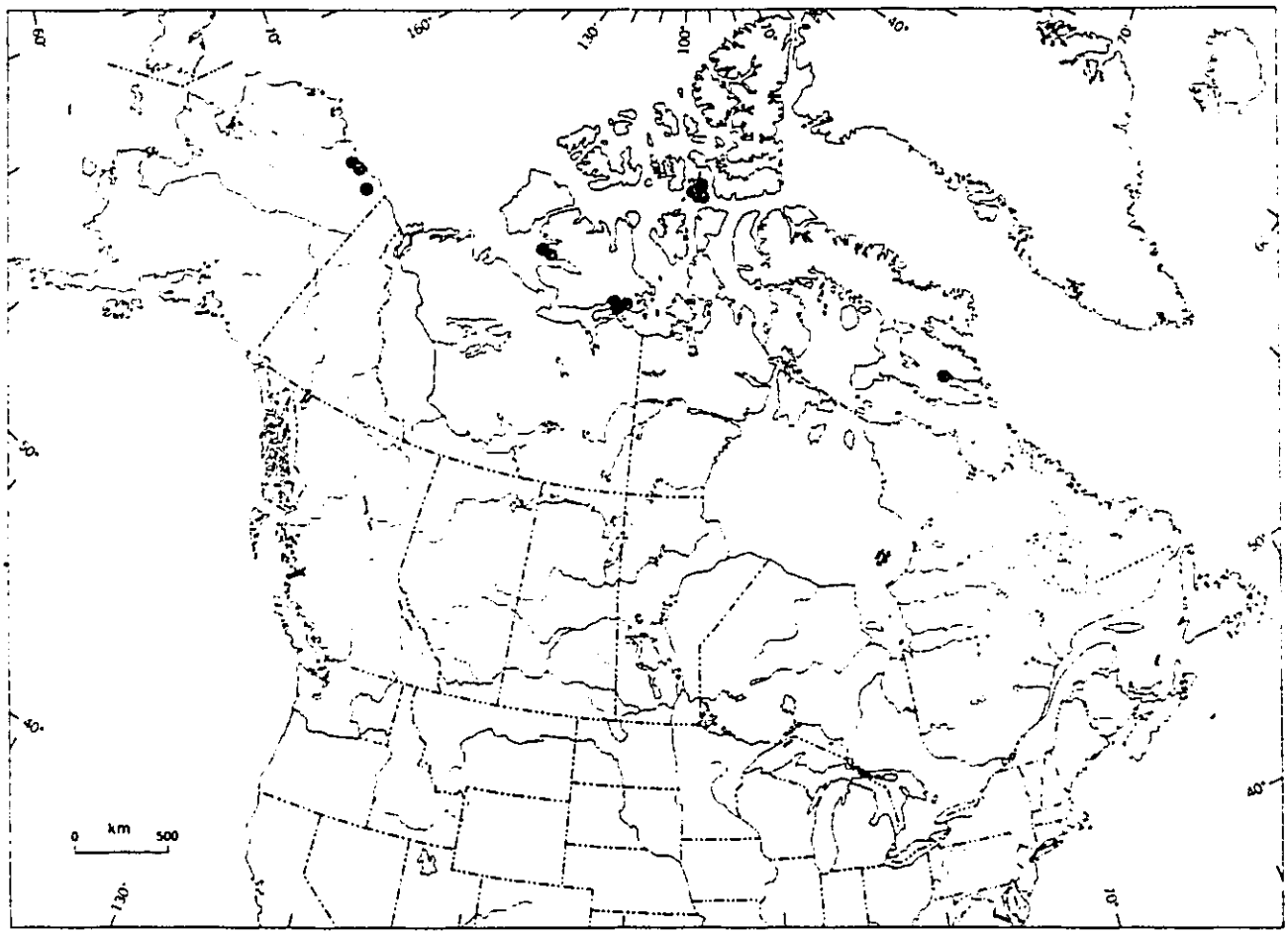


Figure 25. Preliminary North American distribution of Hymenelia sp. # 2.

5.2.3. Key to the North American species of "Hymenelicila"

1. Apothecial disk color variable, mostly yellowish to reddish brown; heliophilous, in brooklets or steams, but also found in openings of deciduous forests, on wet cliffs or rocky lakeshores; thallus color variable with a tinge of yellow, brown, or orange; ascospores (8.0-)12.5 - 18(-21.5) X (4.5-)6.5 - 8.5(-11) µm; apothecial disk 110 - 290 µm diameter; hypothecium 13 - 70 µm high.....H. lacustris
- Apothecial disk mostly whitish, sometimes brownish on the edge; sciaphilous; on dry boulders on deciduous forest floors, sometimes at the edge of forests; thallus light olive gray, or yellowish to brownish gray; ascospores (9.5-)11 - 14(-16.5) X (3-)5 - 6.5(-8) µm; apothecial disk 100 - 220 µm diameter; hypothecium 8 -44 µm high.....H. alba"

5.2.4. Description of the species of "Hymeneliella"

"Hymeneliella lacustris (With.) Lutzoni" (description includes specimens of Hymenelia ceracea (Arn. in Krempelh.) Poelt & Vězda collected in Fundy National Park)

Lichen lacustris With., A Botan. Arrang. Brit. Plants, edit. 3, vol. IV, p. 21 tb. XXXI (1796). Type: "on the shore Llyn Aled lake, growing on stones of granite which are covered with water in the winter, I. Wynne Griffith" (quoted from Withering, W. 1830. A Botan. Arrang. Brit. Plants, edit. 7, vol. IV, p. 18) BM (not seen). - *Hymenelia lacustris* (With.) Poelt & Vězda, Bibl. Lichenol. 16 (1981).

For detailed synonymy see Zahlbruckner, A. 1928. Catalogus lichenum universalis. Vol. 5.

Characterization: Thallus color variable, light to dark yellowish brown, orange-yellow, or yellowish grey, with yellowish to reddish brown disks, 1.1-2.9 mm in diameter; in sunny habitats, in or near water, or sometimes on boulders in openings of deciduous forests.

Description: Thallus color variable, light to strong brown, or light to moderate orange yellow, or light to strong yellowish brown, or grayish yellow, or yellowish white to yellowish gray (55, 57, 70, 71, 73, 74, 75, 76, 77, 79, 90, 92, 93); epilithic; continuous or agglomerated; rimose to rimose-areolate. Photobiont Trebouxia but sometime Trentepholia or both together.

Apothecial fusion present, circular, subangular, or irregular, (2.8-)**7.7 -16.5- 25.3**(-42.0) /6.25 mm^2. Disk color variable, pale yellowish to brownish pink, or grayish reddish orange, or moderate to strong reddish brown, or light to brownish orange, or light to dark grayish brown, or light brownish gray, or pale to deep orange yellow, or light to dark grayish yellowish brown, or yellowish white to light gray (31, 33, 39, 40, 41, 43, 50-54, 55-63, 69, 72, 73, 75, 76, 79, 81, 92, 93, 264), very concave to flat when young, remaining this way, or becoming concave or almost flat in maturity, (30-)**110 -200- 290**(-730) µm diameter. Margins not prominent or slightly prominent when young, remaining this way or becoming slightly prominent to prominent in maturity, (0.0-)**40.9 -67.0- 93.2**(-265.1) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 and KOH negative. Hymenium hyaline; (45.0-)**78.6** -**96.2**- **113.8**(-135.0) µm high; mostly IKI + blue; HNO_3 and KOH negative. Subhymenium hyaline; (10.0-)**18.3** - **25.8**- **33.3**(-50.0) µm high; mostly IKI + blue; HNO_3 and KOH negative. Hypothecium hyaline; (0.0-)**12.7** -**41.6**- **70.5**(-122.5) µm high. Lateral excipulum propium hyaline; (0.0-)**21.9** -**50.2**- **80.5**(-125.0) µm thick; HNO_3 and KOH negative; mostly prismatica. Basal excipulum propium hyaline; (0.0-) **13.6**- **25.9**(-37.5) µm thick; HNO_3 and KOH negative; mostly prismatica but also oblita.

Epipsamma is present and responsible for the color of the disk. Paraphyses simple, ramified at the apex only, or ramified below and at the apex; slightly constricted, sometimes not constricted, submoniliform, or moniliform; anastomosed; generally larger at the apex. Ascus tholus IKI -. Ascospores (8.0-)**12.5** -**14.2**- **17.9**(-21.6) X (4.5-)**6.6** -**7.5**- **8.4**(-11.2) µm; agglomerated when ejected from ascus, when separated from each other they can loose the gelatinous matrix, if not, the ascospore will be halonated; halo thin and dense; mostly aseriate.

Pycnidia: (40-)**50** -**60**(-70) µm diameter, completely hyaline or external wall reddish to yellowish brown ; conidia bacilliform, (2.9-)**3.7**(-4.4) X **1.0** µm.

Habitat: Generally found on boulders in brooklets or streams, but also found on boulders in openings or at the edges of deciduous forests, on wet cliffs, or rocky lakeshores. Always on acid rocks.

Distribution: Appalachian-Great Lakes region, west coast (as in Lecanora cinereofusca H. Magn. (Brodo, 1984), and a few arctic localities (Fig. 26).

Examined specimens: Canada. BRITISH COLUMBIA. Queen Charlotte Islands: Graham Island, Brodo 10400-2X (WIS), 10494, 12987 (CANL); Moresby Island, Brodo 10996, 14089, 26727 (CANL). NEW BRUNSWICK. Fundy National Park, Gowan 1982, 2031, 2351, 2911, 3218, 3223, 3233, 3344, 5023 (CANL). NORTHWEST TERRITORIES. Southern Baffin Island: Iqaluit, Lutzoni & Proulx 14, 182 (CANL); Northern Baffin Island: Clyde Fiord, Hale 762 (CANL); Barnes Ice Cap, Hale 559 (CANL). ONTARIO. Muskoka district, Henssen & Cain 14113 p (CANL); Lake Superior Provincial Park, Brodo 7133-2X (CANL, MIN); Thunder Bay District, Brodo 6613 (CANL). QUÉBEC. Schefferville, Dolly Ridge, Weber s 23888 (COLO); Parc de la Vérendrie, Brodo 14820 (CANL); Parc de la Gaspésie, mont Albert, Sirois & Lutzoni 10617-L13b (QEF); Parc des Laurentides, Chute de la Rivière Noire, Roy C-28-79 (QFA, CANL); Forêt Montmorency, Brodo 20609 (CANL); Gatineau County, Luskville Falls, Brodo 5573-2X (CANL, WIS); Great Whale River, Marr M550-2X (MIN, WIS).

United States. ALASKA. North Slope Borough, Anaktuvuk Pass, Nash 14831 (ASU); Franklin Bluffs, Sagavanirktok River, Thomson et al. 10798 (WIS). GEORGIA. Towns County, Blue Hole Falls, Harris 11255 (NY). MASSACHUSETTS. New Bedford, Lowland Spring, Willey (US); Fair Haven, Willey (1877) (US); New Bedford, Willey (1881) (US). MICHIGAN. Isle Royale, Mt. Franklin, Thomson 17283 (WIS). MINNESOTA. Lake County, Wetmore 21862 (MIN); Harding, Fink 2.08. 1901-3X (NY, US), Fink 1518 (MIN); Voyageurs National Park, Wetmore 38351 (MIN). NEW

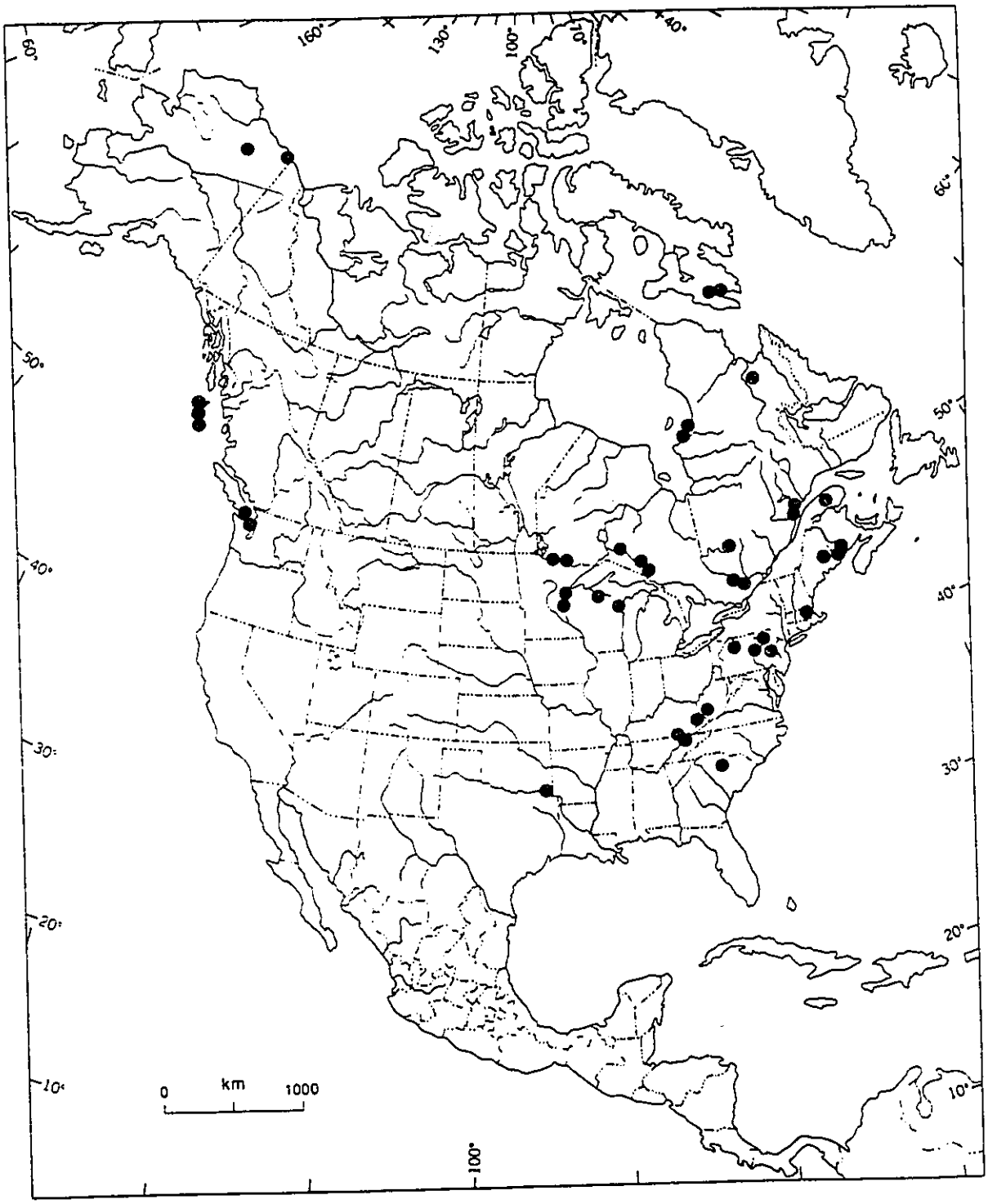


Figure 26. Preliminary North American distribution of "Hymeneliella lacustris (With.) Lutzoni".

HAMPSHIRE. Livermore Falls, Willey (US). NEW JERSEY. Darlington, Nearing (1944) (NY); Haskell, Nearing (1944) (NY). NEW YORK. Tuxedo, Nearing 1944 (NY); Catskills Anderson 5.1935 (NY); Ulster County, High Falls Creek, Harris 13215 (NY). NORTH CAROLINA. Transylvania County, White Water Gorge, Culberson & Nebel 10117 (DUKE). OKLAHOMA. Thomson 8666 (WIS). PENNSYLVANIA. Clarion County, Cook Forest State Park, Brodo 5561 (CANL). SOUTH CAROLINA. Green (1883) (PH); Carlisle, Green 238 EXS (DUKE). TENNESSEE. Great Smoky Mountains, Degelius (1939) (US); Carter County, Cherokee National Forest, Buck 1091 (NY). VIRGINIA. Giles County, Mountain Lake, W. L. Culberson 11472 (WIS, DUKE). WASHINGTON. Olympic National Park, Brodo 15417 (CANL); Quinault Valley, Thomson 15361 (WIS).

Taxonomical notes: The only North American records of Hymenelia ceracea were based on collections from Fundy National Park (Gowan & Brodo, 1988). These specimens appeared to be indistinguishable from H. lacustris. The type of H. ceracea should be checked to see if those specimens of Fundy National Park truly represent H. ceracea. If so, the inclusion of H. ceracea within H. lacustris should be investigated.

"**Hymeneliella alba** Lutzoni"

Characterization: A sciaphilous species of deciduous forest boulders, with a greenish grey thallus and whitish to slightly brownish apothecial disks. The spores are smaller (esp. narrower) than those of H. lacustris and the hypothecium is narrower.

Description: Thallus light olive gray (112), or yellowish to brownish gray (64, 93), epilithic, continuous, rimose or rimose-areolate, **1.3-4.6-8.5** cm diameter; photobiont trebouxioid.

Apothecial fusion present, round to subangular rarely irregular, **5.0 - 13.3- 19.7**(-32.5) /6.25 mm^2; disks light gray to yellowish white (92, 264), or light to deep orange (51-53), or light to light grayish yellowish brown (76, 79), shape stable from young to mature stages, staying concave, almost flat or flat, at the most becoming almost flat in maturity, (48.2-)**97.3 -157.7- 218.1**(-337.4) µm diameter; margins not prominent at most slightly prominent when young, remaining this way or becoming slightly prominent to rarely prominent in maturity, (0.0-)**23.3 -48.4- 73.4**(-120.5) µm thick.

Apothecial anatomical characters: Epihymenium hyaline; HNO_3 and KOH negative. Hymenium hyaline; (57.5-)**70.8 -87.5- 104.3**(-127.5) µm high; IKI negative; HNO_3 and KOH negative. Subhymenium hyaline; (12.5-)**20.5-** 27.5(-42.5) µm high; IKI + blue or negative; HNO_3 and KOH negative. Hypothecium hyaline; (0.0-)**8.4 -26.4- 44.4**(-87.5) µm high. Lateral excipulum propium hyaline; (8.0-)**36.6 -40.4- 44.2**(-100.0) µm thick; HNO_3 and KOH negative; textura very variable. Basal excipulum proprium hyaline; (0.0-)**5.5**(-12.5) µm thick; HNO_3 and KOH negative; textura prismatica or oblita.

Paraphyses mostly isolated, straight, without ramification except at the apex, sometimes ramified below the apex, poorly anastomosed, slightly constricted to moniliform, larger at the apex; ascus tholus IKI-; ascospores (9.5-)**11.1 -12.4- 13.8**(-16.5) X (3.0-)**5.2 -5.8- 6.4**(-8.0) µm, mostly halonate with

halo dense (as for H. lacustris) to very diffuse, mostly aseriate rarely uniseriate.

Pycnidia: (25-)40(-70) µm diameter, hyaline to tan, imbedded to prominent; conidia bacilliform, (2.5-)3.3(-3.9) X 1.0 µm.

Habitat: On dry siliceous boulders on deciduous forest floors. Sometimes in forests openings.

Distribution: Appalachian-Great Lakes region (Fig. 27).

Examined specimens: Canada. NEW BRUNSWICK: Fundy National Park, *Gowan* 2241 (CANL). ONTARIO: Algoma District, *Brodo* 6948 (CANL, WIS); Clarendon, *Wong* 2895 (CANL); Slate Islands, Patterson Island, *Wetmore* 25144 A (MIN). QUÉBEC: Saint-Aubert, *Jean et al.* 9794-L3 (CANL), 9785-L6, 9785-L4, 9788-L2, 9788-L1 (QEF); Ste-Louise, *Jean* 9772-L3 (QEF); St-Damase, *Jean et al.* 9790-L4 (1/2) (QEF); St-Marcel, *Jean & Lutzoni* 9841-L1 (QEF); Calumet, *Brodo* 25021 (CANL); Mont Orford, *Nuyt* 9373 1/4, 10.177 L1 (QEF).

United States. ILLINOIS: Randolph County, Piney Creek Ravine, *Skorepa* 2605 (WIS). MASSACHUSETTS: Cape Cod, Morris Island, *Brodo* 4399b (CANL). MICHIGAN: Mecosta County, *Harris* 12768-A-2X (NY, MICH). MINNESOTA: Chengwatana State Forest, *Schuster* 399, 692a-2X (MIN, CANL). NEW JERSEY: Oakland, *Nearing* (MICH). NEW YORK: Tuxedo, Kakiat Trail, *Nearing* (US); Warrren County, Pack Demonstration forest, *Harris* 16381 (NY). NORTH CAROLINA: Whiteside Mtn., *Harris* 13767 (NY). OHIO: Cuyahoga Valley Nat. Rec. Area, *Wetmore* 54062 (MIN).

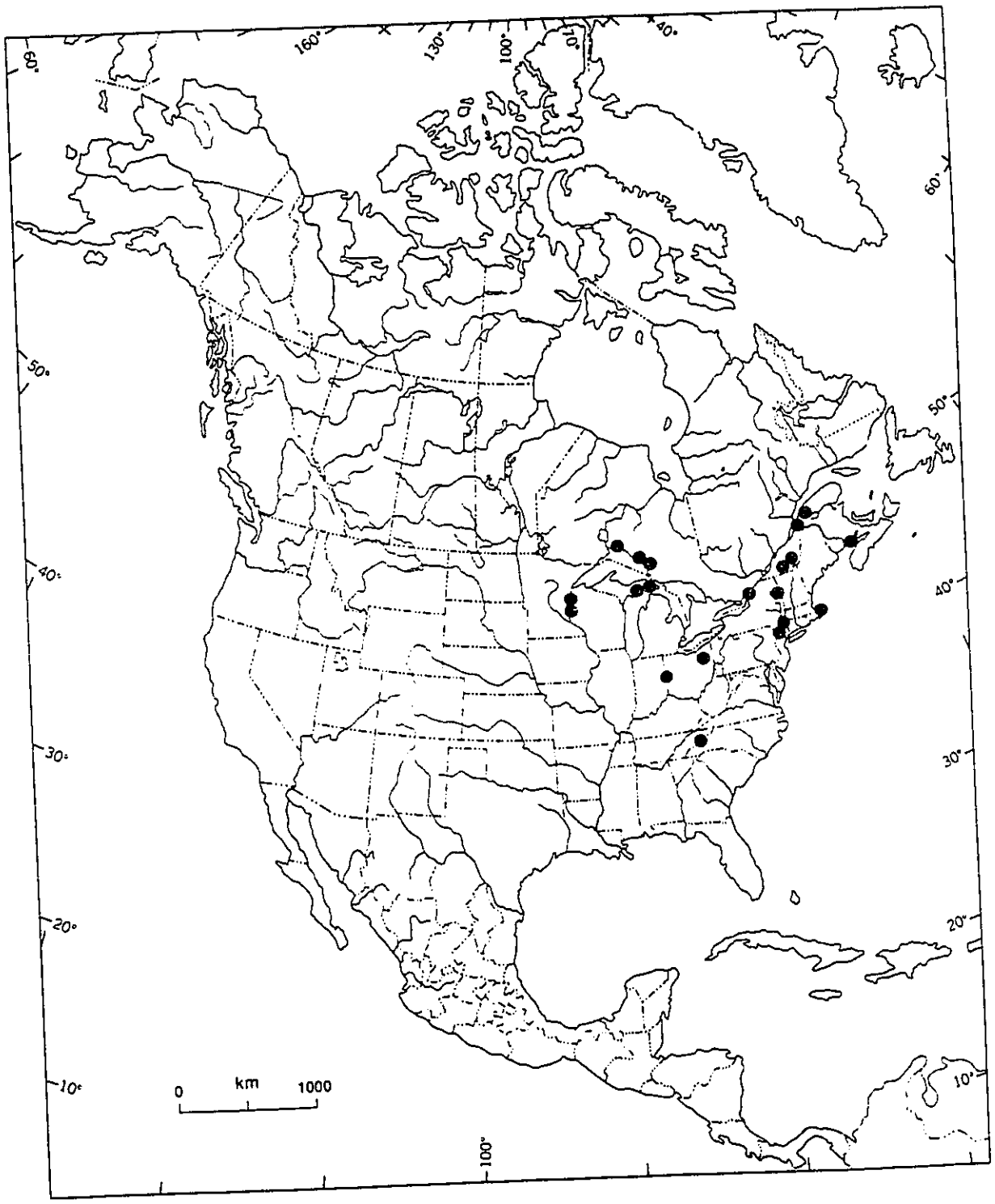


Figure 27. Preliminary North American distribution of "Hymeneliella alba Lutzoni".

Taxonomical notes: Hymeneliella alba had previously been identified as Ionaspis odora in North America (Brodo 1968). Hymeneliella alba is easily distinguished from I. odora by the absence of an epihymenial pigment and the presence of Trebouxia instead of Trentepohlia. Hymeneliella alba is found on small boulders in temperate deciduous forests, whereas I. odora is found in boreal alpine areas in the marginal zone of rivers and lakes, or at some distance from the water (Magnusson, 1933; and Jørgensen, 1989).

5.2.5. Key to the North American species of Ionaspis

1. Apothecia 17 - 36 /6.25 mm^2; disk light grayish reddish brown to grayish brown, 180 - 480 µm diameter; margin 14 - 58 µm thick. Subhymenium 26 - 70 µm thick; IKI negative. Northwestern cordillera.....**I. lavata**

11. Apothecia 10 - 15 /6.25 mm^2; disk same color as I. lavata but often darker, (72.3-) 165.3 (-265.1) µm diameter; margin 37 - 164 µm thick. Subhymenium 20 - 49 µm thick; IKI positive. Arctic.....**Ionaspis sp. #1**

5.2.6. Description of the species of Ionaspis

Ionaspis lavata H. Magn.

Medd. Göteb. Bot. Trädg. 8. p. 26 (1933). Type: United States, Washington, Mt. Rainier, near Paradise Glacier at 8000 ft., S. Foster (holotype: FH, but absent from packet fide Brodo[1968]; isotype: UPS!).

Characterization: Apothecial density **16.8 -25.6- 36.0** / 6.25 mm2; disk light grayish reddish brown to grayish brown, **185 -330- 475** µm in diameter; margins **14 -36- 58** µm thick; subhymenium **26.0 -47.9- 69.8** µm high, IKI negative; Northwestern cordillera.

Description: Thallus pinkish white (9) or pale yellowish pink (31) or yellowish white (92), epilithic, continuous, rimose or rimose-areolate; photobiont trentepohlioid.

Apothecial fusion present, subangular or irregular, **16.8 -25.6- 36.0** /6.25 mm^2; disks light to dark grayish reddish brown (45-47) or light to dark

Apothecial fusion present, subangular or irregular, **16.8 -25.6- 36.0** /6.25 mm^2; disks light to dark grayish reddish brown (45-47) or light to dark brown (57, 59) or light to grayish brown (60, 61), very concave to concave when young, remaining concave or becoming concave to almost flat or convex in maturity, (96.4-)**184.4 -330.3- 476.2**(-674.8) µm diameter; margins not prominent when young, remaining not prominent or occasionally becoming slightly prominent, rarely becoming prominent in maturity, (0.0-)**14.1 -36.2-** 58.2(-120.5) µm thick.

Apothecial anatomical characters: Epihymenium dark orange yellow (72) strong to light yellowish brown (74, 76, 79); HNO_3 + orange, KOH + dark violet. Hymenium hyaline or strong to light yellowish brown (74, 76), color thickness 0.0 - 42.5 µm; (62.9-) **92.2- 122.4**(-162.5) µm high; IKI negative; HNO_3 + orange, KOH + dark violet. Subhymenium hyaline; (17.5-)**26.0 -47.9- 69.8**(-82.5) µm high; IKI negative. Hypothecium hyaline or strong yellowish brown (74); (0.0-)**15.1 -38.5- 61.9**(-75.0) µm high; textura prismatica and/or angularis. Lateral excipulum propium light yellowish brown (76); (0.0-)**25.6 - 37.0-** 48.3(-150.0) µm thick; textura prismatica. Basal excipulum propium light yellowish brown (76); 0.0 - 20.0 µm thick; textura prismatica.

Paraphyses not isolated, undulated, usually with ramifications at the apex and below the apex, anastomosed or not, slightly constricted or without any constriction, larger at the apex; ascus tholus IKI-; ascospores (8.5-)**10.2 - 11.4-** 14.6(-16.2) X (4.8-)**5.8 -6.7- 7.7**(-9.5) µm, not halonate, aseriate.

Pycnidia: same color as disk, (30-)**55- 90**(-95) µm diam.; conidia filiform or bacilliform, very variable in length, (3.9-) 6.5 (9.3) X 0.8 µm.

Habitat: On acid rocks only, in brooks.

Distribution: Northwestern cordillera (Fig. 28).

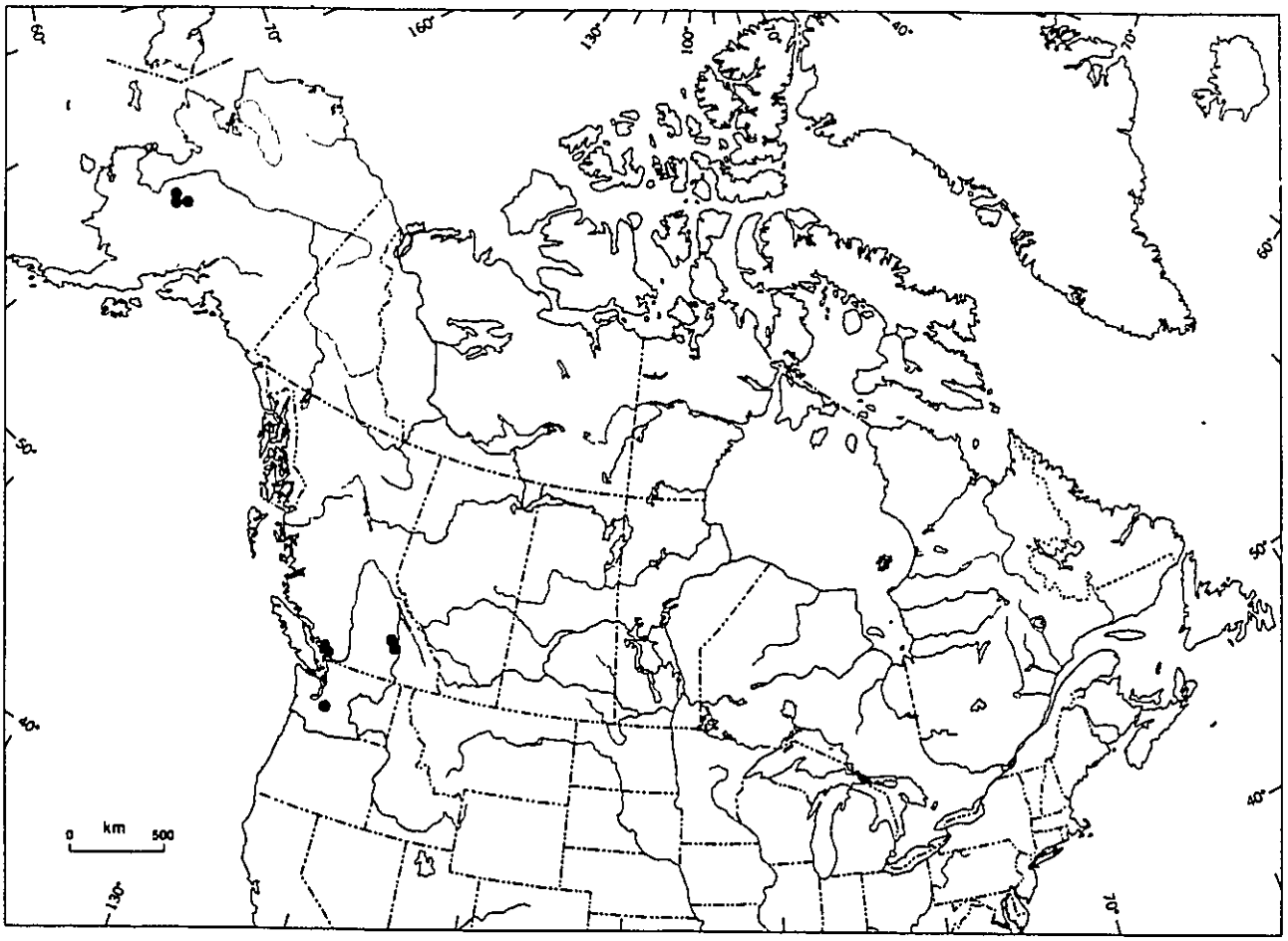


Figure 28. Preliminary North American distribution of Ionaspis lavata H. Magn.

Examined specimens: Canada. BRITISH COLUMBIA: Revelstoke National Park, Otto 3376,3095 (CANL), Garibaldi Park, Otto 8059, 8060, L-38611, L-38612 (COLO).

United States. ALASKA: Mt. McKinley National Park, Weber & Viereck s-7052-2X, S 7019 (COLO, US).

Taxonomic notes: This taxon may contain more than one species. The variation of thallus color is not due to the environment. The variation of conidial size also suggests that several taxa may be involved.

Ionaspis sp. #1

Characterization: Apothecial density **10.2-11.5-15.0** / 6.25 mm2; disk same color as I. lavata but often darker, **72.3 -165.3 - 265.1** µm in diameter; margins **37 -87- 164** µm thick; subhymenium **19.6 -34.3- 49.0** µm high, IKI positive; Arctic.

Description: Thallus dark grayish yellow (91), epilithic, continuous, rimose-areolate; photobiont trentepohlioid.

Apothecial fusion present, round to subangular or irregular, **10.2 - 11.5- 15.0** /6.25 mm^2; disks dark grayish reddish brown (47) to light grayish brown (60) to grayish yellowish brown (80), or brownish gray (63, 64) to dark gray (266), concave when young, remaining concave or becoming almost flat in maturity, (72.3-) **165.3** (-265.1) µm diameter; margins slightly prominent when young, remaining this way or becoming prominent in maturity, (24.1-)**36.9 -87.4- 163.5**(-216.9) µm thick.

Apothecial anatomical characters: Epihymenium hyaline or light orange (70), or grayish to dark yellow (88, 90), or dark grayish olive (111); HNO_3 + orange, KOH + dark violet. Hymenium hyaline; (50.0-)**61.7 -101.4- 141.1**(-150.0) µm high; IKI negative. Subhymenium hyaline; (12.5-)**19.6 -34.3- 49.0**(-55.0) µm high; IKI positive. Hypothecium hyaline or grayish yellowish brown (80); (0.0-)**17.3 -45.4- 73.5**(-90.0) µm high; textura prismatica. Lateral excipulum propium hyaline; (30.0-) **65.4** (-112.5) µm thick; textura prismatica. Basal excipulum propium grayish yellowish brown (80); **10.0** µm thick; textura prismatica.

Paraphyses, with ramifications at the apex or simple, constricted or submoniliform, larger at the apex; ascus tholus IKI-; ascospores (10.0-) **11.8** (-15.0) X (5.0-) **7.2** (-8.8) µm, not halonate, aseriate.

Pycnidia: not prominent, same color as disk, (25-) **45**- 65(-70) µm diam. Conidia bacilliform, (3.9-)**4.5 -5.4- 6.5**(-7.8) X 1.0 µm.

Habitat: On acid rocks only; in rivers, rarely on wet cliffs.

Distribution: Arctic (Fig. 29).

Examined specimens: Canada. NORTHWEST TERRITORIES: Northern Baffin Island, Head of Clyde Fiord, *Hale* 763-3X (CANL,US,WIS); Southern Baffin Island, Iqaluit, *Lutzoni & Proulx* 12, 154-2X (CANL); Coppermine, *Lutzoni & Proulx* 365.

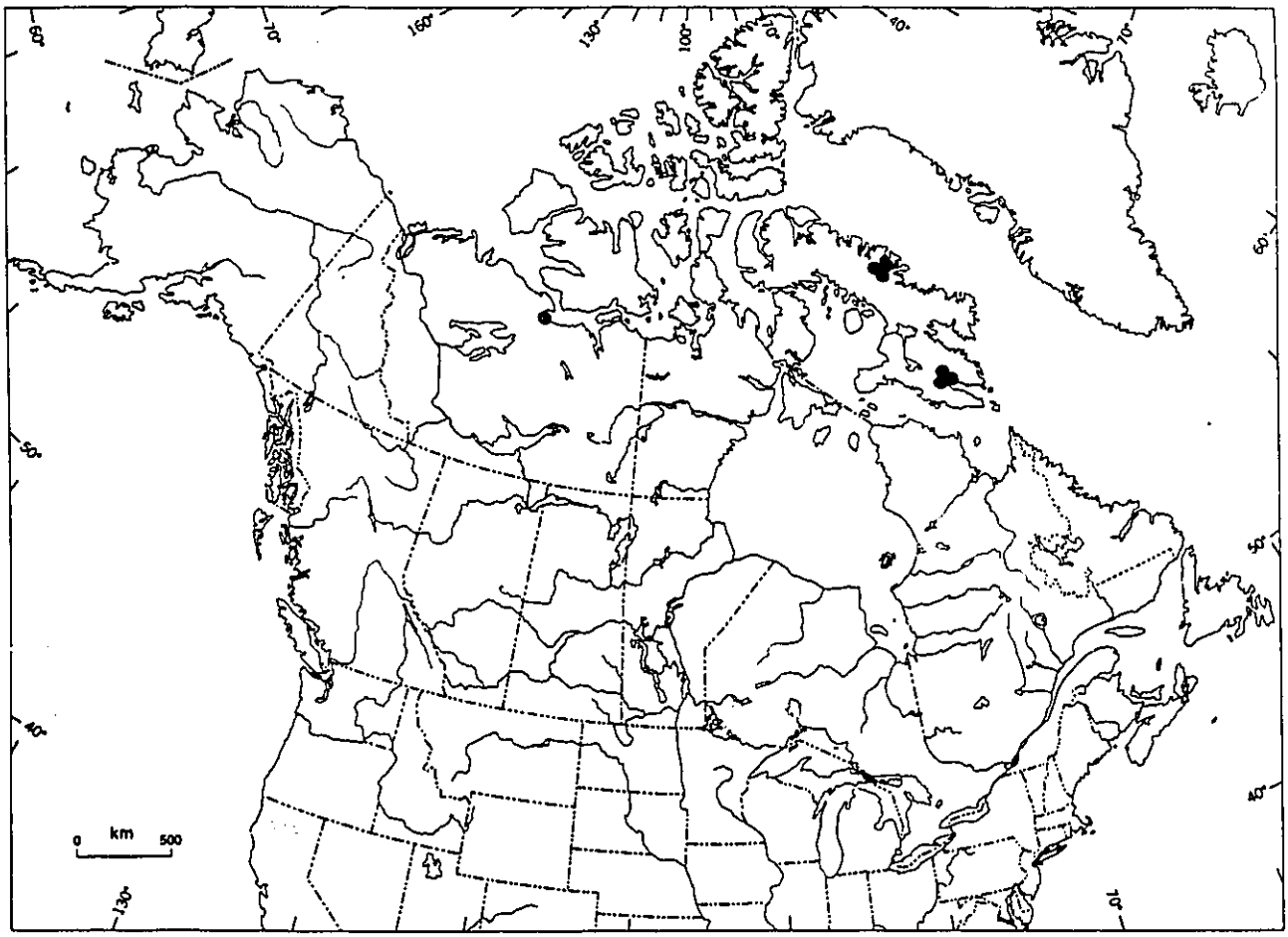


Figure 29. Preliminary North American distribution of Ionaspis sp. # 1.

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APPENDIX

Appendix A: Results and general information for each sample subjected to electrophoresis. The sample type indicates if the sample comes from a mixture of thalli or a unique thallus. The remarks gives the habitat - the nature of the rock - and the location. The abbreviations for each category found in that column are: bro=submerged or just above water in a brook; cal=calcareous rock; Cam=Cambridge Bay; dbo=dry bolder; fel=fell-field; Hol=Holman; ibr=intermittant brook, dry at the moment of collection; Iqa=Iqaluit region; Lak=bordering a lake; mAl=mont Albert, Gaspé peninsula; Net=Nettilling lake, Southern Baffin Island; Ott=Ottawa region; Res=Resolute region; riv=submerged or just above water level in river; sil=siliceous rock; SJP=Saint-Jean-Port-Joli region, Québec; slo=dry slope; Tra=Trafalgar lake region, Cornwallis island; wcl=wet cliff.

taxa	remarks	sel. no.	elec. no.	sample type	PGI 1	PGI 2	PGI 3	PGI 4	PGI 5	PGI 6	PGI 7	PGI 8	PGI 9	PGI 10	PGI 11	PGI 12	PGI 13	PGI 14	PGI 15	6-PGD 1	6-PGD 2	6-PGD 3	6-PGD 4	6-PGD 5	6-PGD 6	6-PGD 7	6-PGD 8	6-PGD 9	6-PGD 10	6-PGD 11	6-PGD 12	6-PGD 13	6-PGD 14	IDH 1	IDH 2
"alba" group	dbo-sil-SJP	870923	39	mixture			1																											
			39	unique			1																							1			1	
			39	unique			1																											
			39	unique	1	1																												
			39	unique			1																											
			39	mixture			1																											
Aspicilia cinerea	dbo-sil-Ott	600	44	mixture										1														1						
			37	mixture										1														1						
Eiglera flavida	riv-cal-Res	195	62-1	mixture							1		1																					
		220	59	mixture				1			1																							
			59-8	mixture							1																	1					1	
	riv-sil-Iqa	156	74-2	mixture						1	1														1	1								
epulotica group	bro-cal-Hol	493	20	mixture				1	1																									
			20	mixture					1																									
	bro-cal-Tra	310	47	mixture							1												1		1									1
			47	mixture							1														1									1
			47	mixture							1																							
	bro-sil-Hol	497	18	mixture				1	1																									
	bro-sil-Iqa	11	70-1	mixture				1			1																							
		123	66-1	mixture							1												1		1									1
			66-2	mixture							1																							
		85	72-1	mixture				1	1														1		1									1
	dbo-cal-Hol	392	27	mixture				1	1																									
			27	mixture				1																										
			27	mixture															1															
			27	mixture																			1		1									
	fel-cal-Cam	338	45	mixture				1	1																									
	fel-sil-Hol	475	21	mixture				1	1														1		1									1
	ibr-cal-Cam	347	36	mixture				1	1																									
			36	mixture																			1		1									
	ibr-cal-Res	278	51	mixture					1		1										1			1										1
	lak-sil-Net	180	64-2	mixture				1																										
	riv-cal-Cam	343	43	mixture				1	1																1									
	riv-cal-Res	259	55	mixture							1																							
			55	mixture							1													1										
		261	54	mixture							1																							
			54	mixture							1																							
			54	mixture							1													1										
	riv-sil-mAl	870926	75-1	unique				1	1																1									
	wcl-cal-Res	193	60-3	unique				1			1												1		1									
			60-4	mixture				1		1															1									1
			60-5	mixture				1	1		1							1				1		1										
		221	58-3	unique					1															1										
			58-1	unique							1											1												
			58-2	unique					1		1																							
			58-5	unique							1											1		1										1
	wcl-sil-Hol	429	24	mixture																			1		1									1
			24	mixture															1															
			24	mixture																	1			1										
		506	14	mixture					1		1																							
haematina group	bro-sil-Cam	351	35	mixture							1				1						1	1	1											1
	bro-sil-Hol	367	33	mixture							1										1													1
		498	17	mixture				1	1			1									1													1
			17	mixture				1	1			1																						
			17	mixture				1	1			1									1													
	bro-sil-Iqa	124	73-1	mixture							1	1																						1
	dbo-cal-Hol	398	26	mixture												1					1											1		
			26	mixture				1	1								i				1			1										
	dcl-cal-Res	250	56-2	unique					1			1										1												
			56-4	unique					1			1																					1		
			56-5	unique							1										1													1
	ibr-cal-Res	277	52	mixture				1			1			1							1													
			52	mixture							1			1							1	1												1
			52	mixture							1			1																				
	lak-sil-Net	181	68-1	mixture							1																							
	riv-cal-Cam	345	41	mixture						1													1											1
			41	mixture							1																							
			41	mixture							1												1											
	riv-cal-Hol	371	32	mixture							1			1							1	1	1											1

taxa	remarks	col. no.	elec. no.	sample	type	PGI 1	PGI 2	PGI 3	PGI 4	PGI 5	PGI 6	PGI 7	PGI 8	PGI 9	PGI 10	PGI 11	PGI 12	PGI 13	PGI 14	PGI 15	6-PGD 1	6-PGD 2	6-PGD 3	6-PGD 4	6-PGD 5	6-PGD 6	6-PGD 7	6-PGD 8	6-PGD 9	6-PGD 10	6-PGD 11	6-PGD 12	6-PGD 13	6-PGD 14	IDH 1	IDH 2
haematina group	riv-cal-Hol	371	32	mixture								1			1																				
			32	mixture					1	1		1			1							1													
		380	31	mixture							1												1											1	
		389	28	mixture					1	1		1	1		1							1													1
			28	mixture								1			1																				1
			28	mixture					1	1		1			1							1													
	riv-sil-mAl	870926	76-2	mixture					1				1									1													
			76-1	mixture								1										1													1
	slo-cal-Tra	300	49	mixture								1																							
	wcl-cal-Res	194	61-2	mixture								1			1							1	1	1											1
	wcl-sil-Hol	431	23	mixture									1																						
			23	mixture					1			1			1																				
		503	16	mixture								1			1																				
		507	15	mixture					1	1		1	1		1							1													1
			15	mixture						1			1																						
			15	mixture					1	1			1									1													
lacustris group	bro-sil-Iqa	182	63-1	mixture				1																						1					
			63-7	unique														1												1					1
	bro-sil-Ott	601	38	mixture		1	1	1		1																				1					
			38	mixture		1	1	1										1																	
	cre-sil-Iqa	182	63-6	unique				1																						1				1	
melanocarpa group	dcl-cal-Res	246	57-1	unique						1		1																							
			57-4	unique											1																				
			57-5	unique								1																							
			57-6	unique								1																							
			57-7	unique								1																							
			57-9	unique								1																							
odora group	riv-sil-Iqa	154	65-1	mixture		1	1	1	1					1							1														
			65-2	mixture		1		1																								1	1		1	
			65-4	mixture		1	1														1													1	